EXPLORING METABOLOMIC AND TRANSCRIPTOMIC INSIGHTS INTO LIGNAN BIOSYNTHESIS PATHWAYS IN *POLYGONATUM SIBIRICUM* AND *POLYGONATUM KINGIANUM* VAR. *GRANDIFOLIUM*

SHI, G. – LAN, D. – XIAO, Q. – HUANG, C. – HONG, J.*

Hubei Key Laboratory of Biological Resources Protection and Utilization, Hubei Minzu University, Enshi 445000, China
(phone: +86-0718-843-7326; fax: +86-0718-843-7326)

Corresponding author
e-mail: 442052525@qq.com

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Abstract. The yield and disease resistance of *Polygonatum sibiricum* and *Polygonatum kingianum* var. *grandifolium*, two *Polygonatum* species grown in Enshi Prefecture, differed significantly across regions. A data review revealed that lignans in the plants were linked to plant resistance. In order to investigate the phenomena and mechanisms that underpin such differences, we conducted a systematic analysis of the two plants' metabolites in this study. At the same time, we interpreted the transcriptome data to identify genes linked to lignan biosynthesis and to investigate the roles of these genes in the biosynthesis pathways and regulatory networks. Both *sibiritum* and *Polygonatum kingianum* var. *grandifolium* were found to contain particular lignans, but their metabolome distributions were differed markedly. The expression of pinoresinol in *Polygonatum kingianum* var. *grandifolium* was significantly down-regulated, possibly due to a reorientation of the phenylalanine metabolic pathway. This phenomenon may have made *Polygonatum kingianum* var. *grandifolium* more resilient than *sibiritum*. A number of lignan biosynthesis-related genes were also identified by transcriptome analysis, indicating their importance in the lignan biosynthesis regulatory network. This work reveals lignan biosynthesis pathways in these species, offering new insights into their therapeutic potential and resistance mechanisms, as well as possible targets for future genetic improvement and drug development.
Keywords: *lignan biosynthesis, metabolic redirection, phenylalanine metabolism, plant disease resistance, pinoresinol*

Introduction

Polygonatum is widely used in traditional Chinese medicine and is known for its various health benefits, including its ability to prevent cancer, treat cardiovascular disease, and alleviate exercise-induced fatigue (Li et al., 2022; Xian et al., 2023; Lin et al., 2024). Owing to the diverse benefits of *Polygonatum* plants, the Enshi region in Hubei Province, with its unique mountainous terrain, has become a key cultivation base for traditional Chinese medicinal materials. Local residents are primarily engaged in the cultivation of medicinal herbs, with *Polygonatum* species occupying a significant position. In particular, *Polygonatum kingianum* var. *grandifolium* and *Polygonatum sibiricum* Red are widely cultivated for their medicinal value. However, when *Polygonatum kingianum* var. *grandifolium* and *sibiritum* were cultivated in different regions, we observed significant differences in their resistance. *Polygonatum* plants are known to contain the following types of bioactive components: flavonoids, polysaccharides, alkaloids, saponins, and lignans (Lu et al., 2023; Yang et al., 2024). Lignans play a significant role in plant resistance, and studies have shown that the presence of lignans is associated with increased resistance to pests such as longhorn beetles (Luo et al., 2024). Additionally,

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lignans have been shown to increase the defensive ability of plants against herbivores and microbial attacks (Fang et al., 2018). Recent studies suggest that lignans also possess the ability to resist diseases (Qie et al., 2022). In addition to their role in plant defense mechanisms, lignans have also gained attention for their extensive medicinal value. Research indicates that lignans possess antitumor activity and are capable of inhibiting the growth and spread of cancer cells (Liao et al., 2024). Additionally, the anti-inflammatory properties of lignans suggest their potential application prospects in the treatment of inflammation-related diseases (Xiong et al., 2025). Lignans are also used in the adjunctive treatment of tuberculosis, potentially by enhancing the body's immune response or directly inhibiting the growth of *Mycobacterium tuberculosis* (Jubilee et al., 2024). Considering the significant role of lignans in plant resistance, to explore the possible reasons for the differences in resistance capabilities between *sibiritum* and *Polygonatum kingianum* var. *grandifolium*, we employed metabolomics and transcriptomics approaches to compare the content of lignans and their biosynthetic pathways in these two species. We meticulously mapped the metabolic network of lignans and identified key biosynthetic genes and metabolites. Our study aims not only to reveal the differences in lignan synthesis between the two *Polygonatum* species but also to apply these findings to practical production. This guidance can inform the cultivation and improvement of *Polygonatum* plants, thereby enhancing their resistance and medicinal value.

The following important questions are the focus of this study: Initially, the lignans of two varieties of *Polygonatum* will be compared, and their types, contents, and structures will be examined. Second, to investigate the factors that result in the more rapid growth of *Polygonatum kingianum* var. *grandifolium*. We will determine the physiological and genetic elements influencing its growth benefits through field research and biological analysis. This will give local farmers in Enshi Prefecture direction on which planting varieties to use. Third, to elucidate the possible lignan production mechanism. We hope to identify the important genes that are involved in the process and suggest gene targets for more studies on *Polygonatum* growth and development and secondary metabolite synthesis by employing contemporary molecular biology approaches.

Materials and methods

Sample collection

In this study, the *Polygonatum kingianum* var. *grandifolium* used was sourced from a local variety in Laifeng County, Enshi Prefecture, Hubei Province, whereas *sibiritum* was obtained from a local variety in Hanzhong city, Shaanxi Province. Both species were introduced and propagated by the Key Laboratory of Bioresource Protection and Utilization in Hubei Province. All of the test plants were three years old, and the culture substrate was subsoil made by combining peat and vermiculite soil in an 8:1 ratio. The samples were authenticated by Dr. Liao Chaolin from the Hubei Academy of Agricultural Sciences, Institute of Medicinal Materials. Following the sampling guidelines provided by Wuhan Mitwell Biotechnology Co., Ltd. In June 2022, we collected three root samples each of *sibiritum* and *Polygonatum kingianum* var. *grandifolium*. Each sample has a weight of 1 gram. Among them, *sibiricum* is designated DHHJ, and *Polygonatum kingianum* var. *grandifolium* is designated DYHJ.

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Metabolomic analysis

Metabolomic profiling was performed using ultra-performance liquid chromatography-tandem mass spectrometry (UPLC-MS/MS) (SHIMADZU Nexera X2 UPLC coupled to an Applied Biosystems 4500 QTRAP MS/MS) by Metware Biotech Co., Ltd. (Wuhan, China). Chromatographic separation employed an Agilent SB-C18 column (1.8 μm, 2.1 × 100 mm) maintained at 40°C. The mobile phase consisted of (A) ultrapure water with 0.1% formic acid and (B) acetonitrile with 0.1% formic acid, delivered at 0.35 mL/min with 4 μL injection volume. The gradient program was: 5% B (0.00 min), linear increase to 95% B (9.00 min), 95% B (9–10 min), decrease to 5% B (10–11.10 min), and re-equilibration at 5% B (11.10–25.00 min).

MS detection utilized both positive and negative electrospray ionization (ESI+/-) modes with ion spray voltages of +5500 V and –4500 V, respectively. Source parameters included: 550°C ion source temperature, 50 psi (GSI), 60 psi (GSII), and 25 psi (CUR) gas pressures, with collision-induced dissociation in high sensitivity mode. Acquired data underwent multivariate analysis (PCA, PLS-DA, OPLS-DA), differential metabolite screening (fold change > 2 or < 0.5, VIP > 1), and KEGG pathway enrichment analysis.

Transcriptomic analysis

Total RNA was extracted from Polygonatum rhizomes using the Plant RNA Kit R6827-02 (OMEGA, USA), followed by comprehensive quality assessment: RNA integrity and contamination were evaluated via 1.0% agarose gel electrophoresis, purity determined with a Qsep400 High-Throughput Nucleic Acid Analyzer (BiOptic Inc., Taiwan), concentration measured using a Qubit 4.0 Fluorometer (Thermo Fisher Scientific, USA), and integrity verified with an Agilent 2100 Bioanalyzer (Agilent Technologies, USA). Qualified RNA samples (RIN ≥ 8.0) were processed into cDNA libraries on an MGISP-960 automated workstation (MGI Tech, China), with library construction completed at Maiwei Biotechnology Co., Ltd. (Wuhan, China). Libraries underwent sequential QC: preliminary quantification (Qubit 2.0 Fluorometer), fragment size distribution analysis (Agilent 2100 Bioanalyzer), and effective concentration quantification via qPCR (Illumina-compatible standards) prior to paired-end sequencing on Illumina NovaSeq 6000 (150 bp).

Raw sequencing data were processed through Fastp (v0.23.2) for adapter trimming and quality filtering (phred score ≥20). De novo transcriptome assembly was performed with Trinity (v2.15.1, min_kmer_cov=2), followed by clustering/deduplication via Corset (v1.09) and coding sequence prediction using TransDecoder (v5.7.0). Filtered transcripts were functionally annotated against seven databases: KEGG (Release 107.0), Nr (e-value ≤1e-5), Swiss-Prot, GO, COG, and TrEMBL (Diamond v2.1.8) along with Pfam (HMMER v3.3.2, E-value ≤0.01).

Data analysis

Data analysis and graphical generation were performed via the data processing cloud platform provided by MetWare Metabolism, which can be accessed via the following link: https://cloud.metware.cn/. For queries related to KEGG pathways and enzyme information, we referred to the official website of the KEGG database, available at https://www.kegg.jp/kegg/kegg1.html. Additionally, data on chemical structures were sourced from ChemSRC, accessible through the following link: https://www.chemsrc.com/.

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Results

Differences in lignan compounds between two species of polygonatum

After conducting an in-depth analysis of the metabolomic data, we detected a total of 17 lignans (*Fig. 1D, Table 1*). Among these lignans, Eleutheroside E was specific to *Polygonatum kingianum* var. *grandifolium*, whereas Cycloolivil was specific to *sibiritum*. To more intuitively display the distribution of lignans in these two species of *Polygonatum*, we constructed a Venn diagram, which clearly revealed the shared and unique lignan species between the two *Polygonatum* species (*Figure 2C*). Furthermore, to further investigate the differences in the metabolomic data of these lignans, we performed principal component analysis (PCA), the results of which indicated that the distribution of these lignans in the metabolome clearly differed (*Fig. 1A*). Finally, to quantitatively assess the significance of the differences in metabolites between different groups, we implemented orthogonal partial least squares discriminant analysis (OPLS-DA) (*Fig. 1B, Fig. 1C*).

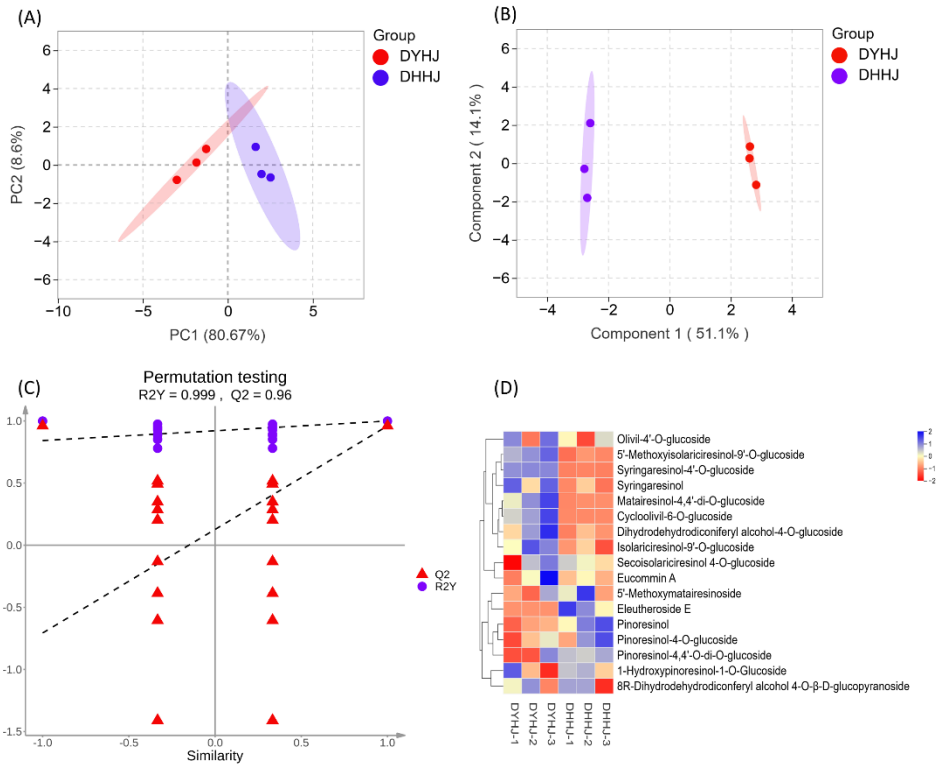

Figure 1. *(A) PCA of lignans in the samples. (B) OPLS-DA of lignans in the samples. (C) Validation plot of OPLS-DA for lignans in the samples. (D) Cluster analysis of lignans in the samples*

We employed volcano plot analysis to conduct an in-depth comparative study of the metabolomic data. Volcano plot analysis allowed us to intuitively identify significant differences in the expression of metabolites between the two species of *Polygonatum.* Five metabolites were found to be up-regulated for expression, while one metabolite was found to be down-regulated (*Fig. 2A*). Specifically, we found that one lignan was downregulated and that five lignans were upregulated in *Polygonatum kingianum* var.

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grandifolium (DYHJ) compared with *sibiricum* (DHHJ). Furthermore, we conducted a KEGG enrichment analysis on these differentially expressed lignan metabolites to explore their roles in metabolic pathways. The analysis revealed that these lignan compounds are enriched in the phenylpropanoid metabolic pathway.

Table 1. *17 lignans and their associated signaling pathways*

Compounds	CAS	cpd_ID	kegg_map
5'-Methoxymatairesinoside	1691201-82-7	-	-
Pinoresinol	487-36-5	C05366	ko00998,ko01100,ko01110
Pinoresinol-4,4'-O-di-O-glucoside	63902-38-5	-	-
Syringaresinol	21453-71-4	C10889	-
Matairesinol-4,4'-di-O-glucoside	-	-	-
5'-Methoxyisolariciresinol-9'-O-glucoside	-	-	-
Pinoresinol-4-O-glucoside	41607-20-9	C17529	-
Syringaresinol-4'-O-glucoside	7374-79-0	C10890	-
Cycloolivil-6-O-glucoside	-	-	-
8R-Dihydrodehydrodiconferyl alcohol 4-O-β-D-glucopyranoside	-	-	-
Isolariciresinol-9'-O-glucoside	63358-12-3	-	-
Secoisolariciresinol 4-O-glucoside	-	-	-
Eleutheroside E	39432-56-9	C20786	-
1-Hydroxypinoresinol-1-O-Glucoside	81495-71-8	-	-
Olivil-4'-O-glucoside	76880-93-8	-	-
Dihydrodehydrodiconiferyl alcohol-4-O-glucoside	-	-	-
Eucommin A	99633-12-2	C10560	-

Note: CAS: ACS-assigned global identifier for a chemical substance. cpd_ID: internal compound accession code. kegg_map: KEGG pathway code(s) where the compound is implicated

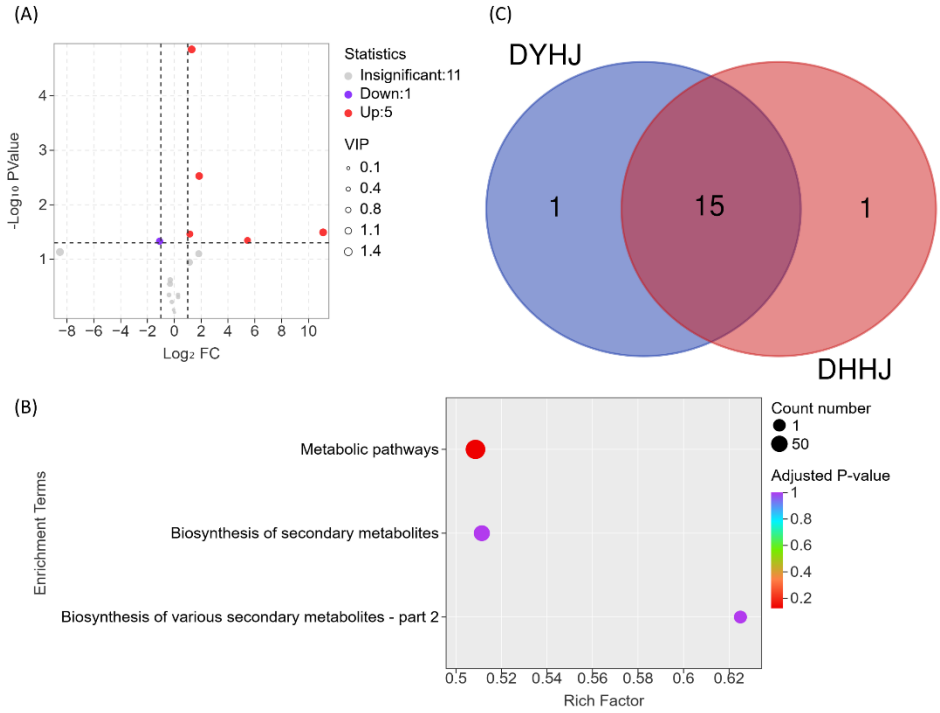

Figure 2. *(A) Volcano plot analysis of lignans in the samples. (B) KEGG enrichment analysis of lignan metabolites. (C) Venn diagram of lignan species between Polygonatum kingianum var. grandifolium (DYHJ) and sibiricum (DHHJ)*

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Transcriptomic analysis of the lignan biosynthesis pathway

We employed Gene Ontology (GO) enrichment analysis to explore genes associated with the biosynthesis of lignans (*Fig. 3A*). The GO analysis revealed a series of genes that may be involved in the lignan biosynthesis pathway and categorized their functions. Cellular constituents, molecular operations, and bioenergetic processes are illustrated by GO circular diagrams. Understanding the mechanism of lignan production and its possible applications in plant and human health can be improved by using GO circle diagrams, which show the enrichment of lignan-related genes in various functional classes (*Fig. 3B*). This analysis not only provided insights into the roles of these genes in biological processes and molecular functions but also highlighted their distribution within cellular components. Through this functional classification, we were able to more precisely understand the mechanisms by which these genes are involved in lignan synthesis and their positions within regulatory networks.

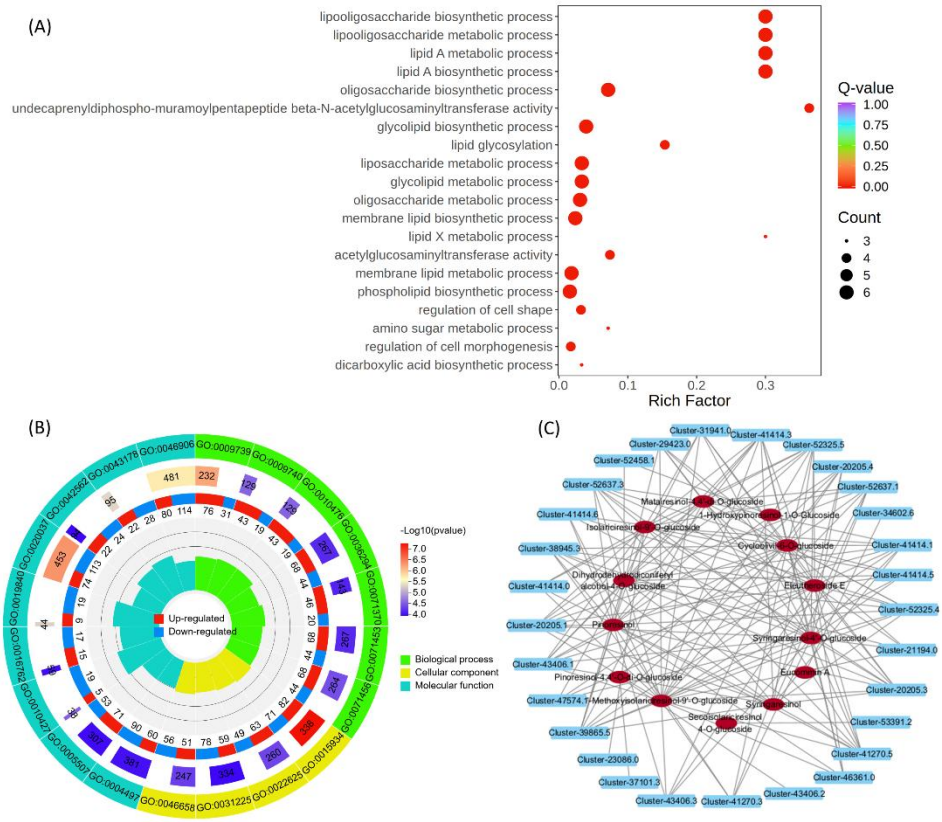

Figure 3. *(A) GO enrichment analysis. (B) GO functional classification. (C). Correlation network analysis of lignans and genes, with red representing different lignans and blue representing genes*

Integrated transcriptomic and metabolomic analysis

Through integrated analysis of transcriptomic and metabolomic data, we identified Cluster-20205.1 as a key hub node that may be closely associated with the biosynthesis of lignans (*Fig. 3C*). This gene set likely plays a central role in regulating the lignan synthesis pathway. Furthermore, clustering heatmap analysis of the differentially expressed genes and metabolites revealed that Cluster-52458.1 and Cluster-21194.0

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presented similar expression patterns across multiple lignan synthesis-related metabolites (*Fig. 4A*). The consistency of this pattern suggests that these two gene sets may have a synergistic effect within the lignan synthesis regulatory network. Additionally, the correlation map between genes and lignan metabolites further revealed the strength of their associations. For example, genes related to 5'-methoxyisolariciresinol-9'-O-glucoside may play crucial roles in the activity or regulation of this metabolite (*Fig. 4B*).

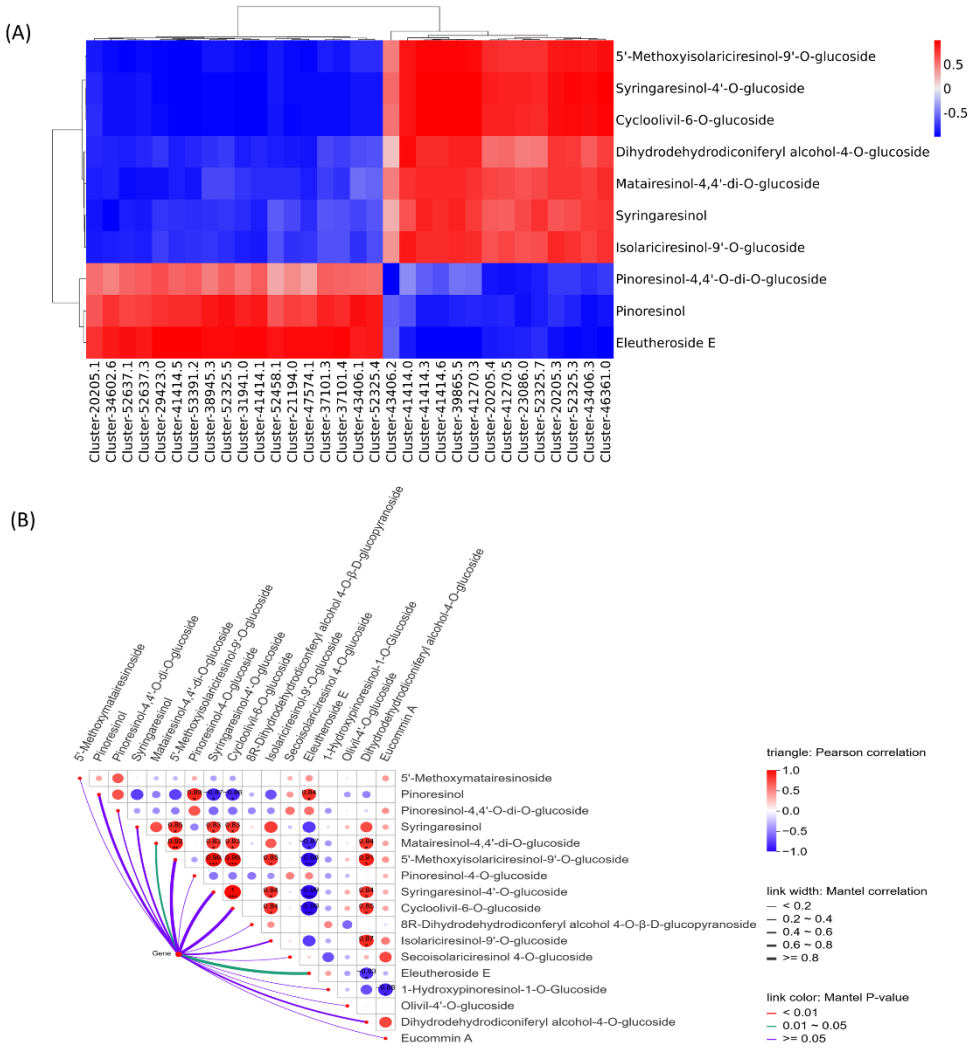

Figure 4. *(A) Cluster analysis of differentially expressed lignans and genes, with red indicating high expression and green indicating low expression. (B) Correlation map between lignans and genes*

In *Polygonatum* species, lignan biosynthesis begins with phenylalanine. Through a series of enzymatic reactions and metabolic processes involving PAL (phenylalanine ammonia-lyase), 4CL (4-coumarate: CoA ligase), and CAD (cinnamyl alcohol dehydrogenase), phenylalanine is converted into pinoresinol, a key intermediate in the lignan synthesis pathway. Pinoresinol subsequently undergoes further modification and transformation to ultimately form a diverse array of lignan compounds (*Fig. 5*).

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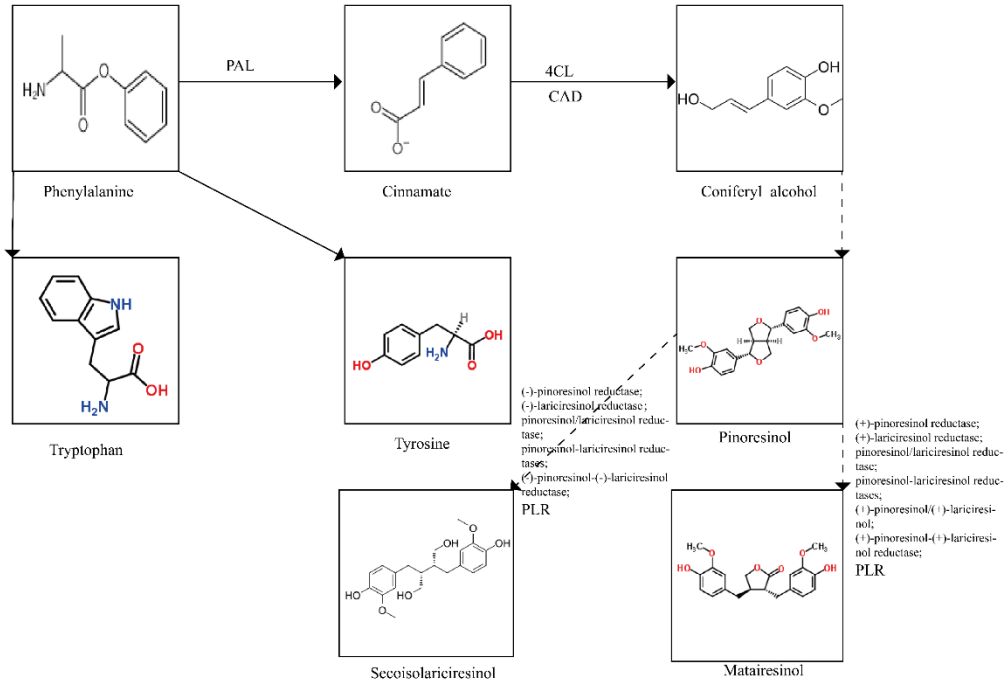

Figure 5. *Partial synthesis diagram of lignans*

Phenylalanine is the precursor for the synthesis of cinnamonate and is also transformed into tryptophan (Tryptophan) in the lignan biosynthesis pathway. Tryptophan levels in *Polygonatum kingianum* var. *grandifolium* were considerably higher than those in the control (*sibiricum*), according to metabolite tests. Nonetheless, this variation showed a down-regulation of pinoresinol levels. Accordingly, it is possible that some regulatory mechanisms in the metabolic pathway that prevent the synthesis of pinoresinol or redirect a portion of the metabolic flow to other pathways, which alters the final pinoresinol content, are responsible for the up-regulation of tryptophan rather than a direct increase in pinoresinol.

Discussion

The yield characteristics, chemical composition, lignan content, and antioxidant potential of the six varieties of flax (*Linum usitatissimum* L.) varied greatly, according to studies, and these variances were largely controlled by the variety and growth environment (Jarošová et al., 2024). The study specifically noted that while crude protein and oil content exhibited a negative association, seed production and the concentration of important lignans, isolarectin diglucoside, were significantly impacted by changes in precipitation. These results emphasize how crucial environmental control and variety screening are to maximizing the nutritional value of plants and the buildup of bioactive lignans. A thorough understanding of the molecular basis underlying these variations, particularly the primary regulatory mechanisms of particular lignans synthesis pathways, is still lacking, despite the fact that such studies have shown phenotypic differences in lignans content and their environmental dependencies in flax. By systematically profiling lignan metabolites and dissecting their biosynthetic regulatory networks in *sibiricum* and *Polygonatum kingianum* var. *grandifolium*, this study directly addresses this pivotal

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scientific question. The 17 lignans found in this investigation might show accumulation patterns resembling those found in flax seeds, indicating a reliance on environmental conditions. According to this theory, the quantity and make-up of particular lignans in Polygonatum species may affect the plant's ability to withstand biotic (like pathogen infection and insect pests) and abiotic (like drought and salinity) stresses by controlling their roles as secondary metabolites linked to defense. Future research should focus on clarifying the distinct roles played by various lignan components in the development of Polygonatum's stress resistance, including biotic and abiotic resistance, as well as their mechanisms of environmental response. In specifically, Cycloolivil in *sibiritum* has the ability to generate a specific glycosidic structure called Cycloolivil-6-O-glucoside by binding with a sugar chain. The glycosidic form of cycloolivil, a lignan with anti-inflammatory activities, may have a substantial effect on its pharmacological characteristics and bioavailability (Yoon et al., 2024). Eleutheroside E, which is specific to *Polygonatum kingianum* var. *grandifolium*, has antioxidant, antifatigue, anti-inflammatory, antibacterial, and immunomodulatory effects (Jia et al., 2023). Metabolomic studies revealed that, compared with that in *sibiritum*, the expression level of pinoresinol in *Polygonatum kingianum* var. *grandifolium* was significantly lower. Pinoresinol is a key intermediate in the biosynthetic pathways of various lignans. Within plants, it is converted into other lignan derivatives through specific enzymatic reactions, with the enzyme podophyllotoxin 6-hydroxylase (PLR) playing an essential role in this transformation process. As a key enzyme for the synthesis of other lignans, the activity of PLR directly affects the efficiency of the conversion of pinoresinol into downstream lignans (Xiao et al., 2021). In *Polygonatum* plants, the biosynthesis of lignans begins with phenylalanine. Initially, phenylalanine is converted into cinnamate, which is then further transformed into coniferyl alcohol. Ultimately, through a series of complex biochemical reactions, coniferyl alcohol is converted into proresinol. However, the mechanism of lignan synthesis in *Polygonatum* differs from the traditional pathway. It does not follow the path of other plants that first synthesize coumaric acid (Zhang et al., 2024). Instead, it synthesizes coniferyl alcohol directly after the formation of cinnamic acid. This direct pathway to coniferyl alcohol may be unique to the *Polygonatum* genus.

Through an integrated analysis of metabolic pathways, we found that the downregulation of pinoresinol expression in *Polygonatum* may be associated with the redirection of the phenylalanine metabolic pathway. Phenylalanine may be preferentially used for the synthesis of tryptophan and tyrosine, and the expression levels of these two amino acids in the metabolites are upregulated. Researchers have also analyzed the impact of the oriental fruit moth on the degradation of chestnut rose juice via metabolomics. Multiple metabolites in the phenylalanine and tryptophan metabolic pathways were upregulated, indicating that phenylalanine may be preferentially used for the synthesis of these amino acids (Ren et al., 2023). This metabolic redirection may affect the biosynthesis of pinoresinol, which in turn influences the overall synthesis of lignans.

The differential content of lignans in *sibiritum* and *Polygonatum kingianum* var. *grandifolium* is a key factor in determining their distinct functional properties. Considering the content of lignans, it may be more appropriate to choose the cultivation of *Polygonatum kingianum* var. *grandifolium* in areas prone to pests and diseases. This is because lignans have been proven within plants to possess the ability to resist pathogenic fungi and pests, thereby enhancing the plant's natural defense mechanisms (Choi et al., 2009; Vogt et al., 2013).

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In the integrated analysis combining metabolomics and transcriptomics, we found that 5'-methoxyisolariciresinol-9'-O-glucoside was strongly correlated with the expression of multiple genes. Furthermore, the correlation between this compound and Proresinol-4,4'-O-glucopyranoside is also significant, which may suggest that they play interconnected roles in the biosynthetic pathway of lignans. This close association could be crucial for understanding the regulatory mechanisms of lignan synthesis in *Polygonatum* species. Furthermore, the potential antisepticemic effects of 5'-methoxyisolariciresinol-9' warrant further investigation, as it may hold significant therapeutic value in clinical applications (Zheng et al., 2011). These findings still require validation through further experimental research. Before the potential benefits of these compounds can be translated into clinical applications, rigorous scientific validation must be conducted to ensure the accuracy and reliability of the results.

In the lignan biosynthetic pathway, Cluster-20205.1 has been identified as a key node, whereas Cluster-52458.1 and Cluster-21194.0 are two genes associated with multiple steps in lignan synthesis. Although the potential key roles of these genes have not yet been definitively validated, once their functions are confirmed in *Polygonatum* species, they could have significant implications for molecular breeding strategies, particularly in enhancing plant disease resistance (Liu et al., 2024). Further research will help clarify the specific mechanisms by which these genes function in lignan synthesis, providing a scientific basis for the genetic improvement of *Polygonatum* species.

Conclusions

This study comprehensively applied metabolomic and transcriptomic techniques to analyze the key differences in lignan synthesis pathways between *sibiritum* and *Polygonatum kingianum* var. *grandifolium*. We identified 17 lignans, including Eleutheroside E, which is specific to *Polygonatum kingianum* var. *grandifolium,* and Cycloolivil, which is specific to *sibiritum*, and clarified their distribution differences in the two species through PCA and OPLS-DA. Metabolomic results revealed the downregulation of pinoresinol in *Polygonatum*, which may be related to the redirection of the phenylalanine metabolic pathway, affecting the overall synthesis of lignans. Transcriptomic analysis revealed that genes such as Cluster-20205.1, Cluster-52458.1, and Cluster-21194.0 are closely related to lignan biosynthesis and may play a core role in regulatory networks. Selected genes will be subjected to qRT-PCR verification in order to assess reproducibility and validate transcriptome findings. Future functional research will examine their functions in the manufacture of medicinal compounds and Polygonatum resistance mechanisms, offering molecular targets for pharmaceutical development and breeding enhancement.

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