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RECEIVED 30 September 2025

ACCEPTED 27 October 2025

PUBLISHED 06 November 2025

CITATION

Wu S, Jie H, Xing H and Jie Y (2025) Mining
key genes for ramie (*Boehmeria nivea* L.)
adaptation to poor soil condition using
transcriptome analysis.
Front. Sustain. Food Syst. 9:1716412.
doi: 10.3389/fsufs.2025.1716412

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Mining key genes for ramie (*Boehmeria nivea* L.) adaptation to poor soil condition using transcriptome analysis

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Introduction: Agricultural land degradation threatens food security and agricultural ecosystem sustainability, necessitating phytoremediation to address this problem. Ramie (*Boehmeria nivea* L.), a cash crop known for its resilience in marginal environments and multiple ecological benefits, represents a promising candidate for this purpose. However, lack of varieties tolerant to poor soil limits this potential, necessitating genetic improvement.

Methods: This study was therefore designed to identify key genes involved in ramie's adaptation to poor soil conditions and to further explore the underlying molecular mechanisms. Leaf RNA from two ramie varieties, the tolerant Xiangzhu XB (XZ-XB) and the sensitive Xiangzhu 3 (XZ-3), was analyzed using high-throughput sequencing.

Results: After processing high-quality clean data, comparative transcriptome analysis revealed 1,908 differentially expressed genes (DEGs) between XZ-XB and XZ-3, among which 1,116 were up-regulated and 792 were down-regulated in XZ-XB relative to XZ-3. Notably, four up-regulated DEGs displayed fold changes greater than 9,500, while four down-regulated DEGs showed fold changes exceeding 1,000. Functional annotation linked the DEGs to critical processes as transporter activity, proteases regulation, purple acid phosphatase activity, etc. The findings also revealed that tolerant genotype likely enhance survival under poor soil condition by down-regulating senescence-promoting genes and up-regulating stress-signaling pathways.

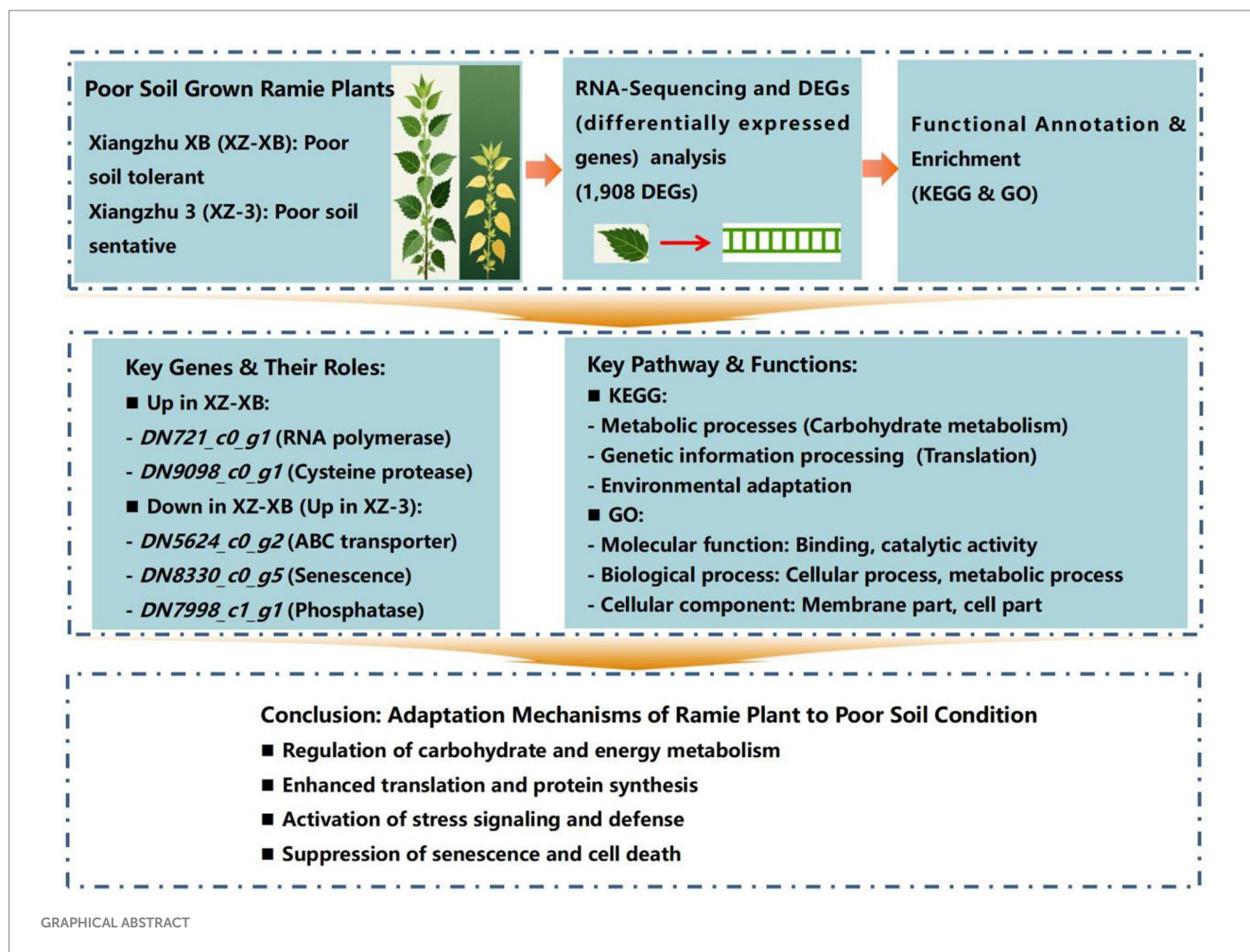
Discussion: Results of this study provide valuable genetic resources and candidate targets for molecular breeding of ramie varieties with enhanced resilience to nutrient-poor soils. By the help of molecular breeding, the process will be speed up to develop nutrients-deficiency resilient ramie varieties as a sustainable, plant-based strategy for restoring degraded agricultural ecosystems and enhancing land productivity.

KEYWORDS

fiber crop, marginal land, infertile soil, molecular breeding, gene screening

1 Introduction

Agricultural land degradation poses a significant threat to global food security and ecosystem sustainability. More than 60% of the world's agricultural land is already degraded (Pravalie et al., 2021), a situation exacerbated by intensive farming, climate change, and industrial pollution (Talukder et al., 2021; Chaudhuri et al., 2023). Degraded soils are typically characterized by nutrient depletion, heavy metal contamination, structural deterioration (e.g., soil compaction),



and loss of organic matter (Hossain et al., 2020). These characteristics, acting as environmental stress factors, ultimately undermine both crop productivity and environmental health. As the contradiction between population growth and reduced grain yield caused by soil degradation intensifies, along with the growing conflict between people's pursuit of high-quality food and the decline in food quality due to soil degradation, the restoration and fertility improvement of degraded soils have become increasingly urgent (Mosier et al., 2021).

Currently, a comprehensive set of techniques has been developed to manage degraded cropland, targeting various degradation situations. For instance, application of some amendments has been confirmed effective in treating saline-alkali degraded land (Xu et al., 2023; Li et al., 2025). Similarly, the application of soil conditioners and lime to adjust pH has proven beneficial in addressing degradation in red soil cropland (Li et al., 2024; He et al., 2025). Furthermore, for commonly encountered degraded croplands, degradation can be halted through strategies such as rational crop rotation and intercropping, the cultivation of green manure and cover crops, and the promotion of conservation tillage (Hussain et al., 2021; Perveen et al., 2025). These techniques have proven effective in ameliorating lightly to moderately degraded soils. However, their efficacy is limited in severely degraded soils. In such settings, phytoremediation has emerged as a preferred strategy due to its cost-effectiveness, ease of implementation, and multifunctional ecological benefits (Phang et al., 2024). However, the widespread adoption of phytoremediation is constrained by the lack of plant species that combine strong

adaptability, high remediation efficiency, and particularly the ability to generate economic returns (Lee et al., 2025).

Ramie (*Boehmeria nivea* L.), a perennial fiber crop known for its resilience in marginal environments and multiple ecological benefits, is a promising candidate for the phytoremediation and sustainable utilization of degraded lands (Wu et al., 2022; Chen et al., 2023). The well-developed underground system (deep root, extensive rhizomes/radish roots) allows it to improve soil structure after planting, and decomposition of these biomass can contribute to an increase of soil organic carbon content (Zhu et al., 2021; Liu, 2022). Furthermore, the soil stabilization provided by these extensive underground systems, coupled with the rainwater interception by the high-coverage leaves, gives ramie cultivation excellent potential for preventing soil erosion (Wang et al., 2021). Additionally, ramie exhibits remarkable tolerance to multiple heavy metals as Cd, Mn, and Cr (Wu et al., 2022; An et al., 2023). Coupled with its well-established processing technologies for non-food applications (such as in textiles), this makes it a key plant species for the utilization and remediation of heavy metal-contaminated soils. Despite these advantages, most existing ramie varieties have been bred for multiple annual harvests, generally exhibiting high soil nutrient requirements. When applied to the remediation of degraded soils, these varieties tend to accelerate the decline of soil fertility. Moreover, these high nutrient-demand varieties limit the remediation potential of ramie in poor, degraded soil scenarios. Therefore, breeding nutrient-efficient ramie varieties is essential to fully realize the crop's potential in marginal environments.

Molecular breeding offers a powerful approach to accelerate the development of such improved varieties. Although preliminary studies (Tan, 2015; Zheng, 2014; Hou, 2018) have identified genes (such as *BnNRT1.1* and the *BnGS* gene family) involved in ramie's tolerance to nitrogen, phosphorus, and potassium deficiencies, these findings remain fragmented. A systematic understanding of the molecular mechanisms underlying ramie's adaptation to poor soil is still lacking, hindering the development of targeted breeding strategies.

As a highly heterozygous species with an unannotated genome, ramie presents challenges for genomic studies. For such species, transcriptome sequencing technology is an efficient and cost-effective means for functional gene discovery, and it has been widely used, particularly for screening key genes involved in stress responses. Therefore, this study employed a comparative transcriptomic analysis of two ramie varieties with contrasting adaptability to poor soil. Our objectives were to identify critical genes and regulatory pathways associated with nutrient stress tolerance, (1) uncover the molecular basis of ramie's adaptation to poor soil, and (2) provide genetic resources and candidate genes for molecular breeding aimed at enhancing ramie's resilience in degraded environments.

2 Materials and methods

2.1 Experimental materials and sampling methods

Based on long-term screening results for poor soil tolerance germplasm, Xiangzhu XB (XZ-XB) and Xiangzhu 3 (XZ-3) were identified as tolerant and sensitive materials, respectively, under nutrient-deficient soil conditions (Wu et al., 2021a; Wu et al., 2021b). XZ-XB's tolerance stems from its strong root system, efficient nutrient retranslocation to roots, conservative aboveground nutrient use, and supportive rhizosphere microbiome. In contrast, XZ-3's sensitivity is due to its weaker root system, inefficient nutrient cycling, higher nutrient loss during harvest, and less favorable microbial community. These traits collectively explain their contrasting adaptability to nutrient-deficient soils. Utilizing these two genotypes, we conducted a comprehensive transcriptomic analysis to compare their gene expression profiles, with the aim of identifying key regulatory genes associated with ramie's tolerance to poor soil. Sampling was carried out in early December 2020 from the long-term impoverished soil experimental base of the Ramie Research Institute of Hunan Agricultural University in Huarong (29°32'46"N, 112°39'57"E, 73 m a.s.l.). This experiment was established at 2010 on a poor sandy red soil, which is characterized to have a total nitrogen of 0.69 g kg⁻¹, available phosphorus of 9.62 mg kg⁻¹ and exchangeable potassium of 56.53 mg kg⁻¹. From each of the three biological replicate plots per variety, three normal and disease-free plants per replicate were selected and pooled to form one biological replicate. Young leaves were collected, washed, surface-sterilized with 75% ethanol, and approximately 100 g of tissue was immediately frozen in liquid nitrogen for subsequent RNA extraction.

2.2 High-throughput sequencing workflow

Total RNA was extracted from the collected samples using the TRIzol Plant RNA Extraction Kit, followed by concentration, purity, and integrity detection. After passing quality checks, the mRNA was

enriched using Oligo dT, fragmented, reverse-transcribed into cDNA, and adaptors were ligated. Finally, sequencing was performed on the Illumina Novaseq 6,000 platform provided by Majorbio Bio-pharm Technology Co., Ltd.

2.3 Analysis of the sequencing data

The raw sequencing reads were subjected to quality control inspection and filtering to generate clean data. Subsequent analyses were then performed using the Majorbio Cloud Platform.¹ On this platform, the clean data from each sample were assembled using the Trinity software. Differential expression analysis was conducted with the DESeq2 software, with screening thresholds set at $|\log_2FC| \geq 1$ and $p\text{-adj} < 0.05$, where FC represents the fold change. Functional annotation of the differentially expressed genes was conducted by aligning the assembled transcript sequences against six major databases: NR (Non-Redundant Protein Database), Swiss-Prot (Annotated Protein Sequence Database), Pfam (Protein Family Database), COG (Clusters of Orthologous Groups), GO (Gene Ontology), and KEGG (Kyoto Encyclopedia of Genes and Genomes). Annotation results from each database were compiled and statistically summarized.

2.4 Real-time fluorescence quantitative PCR (qRT-PCR) detection

To verify the reliability of the transcriptome sequencing results, four genes with significantly differential expression levels were selected for qRT-PCR detection to analyze their expression patterns. The same batch of RNA used for transcriptome sequencing was employed for qRT-PCR. The ramie actin gene (Actin) was used as the internal reference gene, and the Applied Biosystems™ PowerUp™ SYBR™ Green Master Mix (Thermo Fisher, Shanghai, China) was used to prepare the reaction system according to the manufacturer's instructions. The reaction system was processed using an ABI 7300 Real-Time PCR System (Applied Biosystems, USA). Primers for each target gene were designed using Primer 3 software (as shown in Table 1), while the internal reference gene primers were referenced from the sequence provided in Ma's study (Ma et al., 2017). The PCR amplification program was as follows: pre-denaturation at 95 °C for 5 min, followed by 40 cycles of denaturation at 95 °C for 30s, annealing at 55 °C for 30s, and extension at 72 °C for 30s. After completion, the relative expression levels of the target genes were calculated using the 2^{-ΔΔC_t} method.

3 Results

3.1 Transcriptome sequencing quality analysis and unigene functional annotation

This study obtained a total of 38.08 Gb clean data from the six samples of XZ-XB and XZ-3, with each sample yielding over 6.18 Gb of clean data. All samples exhibited Q20 values of >97% and Q30

¹ www.majorbio.com

TABLE 1 Primers for qRT-PCR of the tested gene and reference gene.

Unigene	Primer name	Primer sequence	Products size (bp)
TRINITY_DN9098_c0_g1	9,098-F	5'-GTCCTTCACCCTGGTCCGT-3'	244
	9,098-R	5'-CGCCTTTTCAATCTTTGC-3'	
TRINITY_DN41995_c0_g1	41,995-F	5'-CATACACACAACACAAGT-3'	268
	41,995-R	5'-CGTCAAGAAGATCACCTC-3'	
TRINITY_DN721_c0_g1	721-F	5'-CCCAATCGGTGTGTAGTG-3'	240
	721-R	5'-AAGGTGGTCATAGGAGGC-3'	
TRINITY_DN11078_c0_g1	11,078-F	5'-ACCGCCGCTATCACGTTA-3'	148
	11,078-R	5'-CCGCTCGCCAGGCTATTT-3'	
Actin	Actin-qPCR-F	5'-GCTCCGTTGAACCCTAAG-3'	1782
	Actin-qPCR-R	5'-GCTCCGATTGTGATGATT-3'	

TABLE 2 Results of the unigene annotated in the annotation database.

Annotation database	Number of the annotated unigene	Percentage of the annotated unigene to the total Unigene
NR database	27,640	53.71%
Swiss-prot Database	22,094	42.94%
Pfam Database	22,610	43.94%
COG Database	23,896	46.46%
GO Database	23,041	44.78%
KEGG Database	14,035	27.28%
Annotated in all the above database	9,846	19.13%

values of >93%, indicating that the data quality met the requirements for subsequent analyses. After assembly and quality evaluation of all high-quality reads using Trinity, 88,861 transcripts and 52,759 unigenes were obtained, with N50 values of 1,827 and 1,824, respectively. The length of the unigenes ranged from 201 bp to 13,439 bp, with an average length of 934.23 bp.

The assembled unigenes were aligned against six major databases (NR, Swiss-Prot, Pfam, COG, GO, and KEGG) using BLAST software to retrieve functional annotations. As shown in Table 2, among these databases, the NR database had the highest annotation rate, with 27,640 unigenes annotated, accounting for 53.71% of the total. In contrast, the KEGG database had the lowest annotation rate of 27.28%, with only 14,035 unigenes annotated. The annotation rates in the other four databases were relatively consistent (approximately 45%), which correspond to about 23,000 annotated unigenes each.

Integrative analysis of the annotation results from all six databases revealed that 9,846 unigenes were co-annotated across all databases, representing 19.13% of the total unigenes. These results indicate that the functional annotation rate of ramie unigenes remains relatively low.

3.2 Analysis of differential gene expression patterns

Differential gene expression between XZ-XB and XZ-3 under poor soil conditions was analyzed using DESeq2 (results shown in Figure 1). Using the criteria of $FC \geq 2$ and FDR (False Discovery

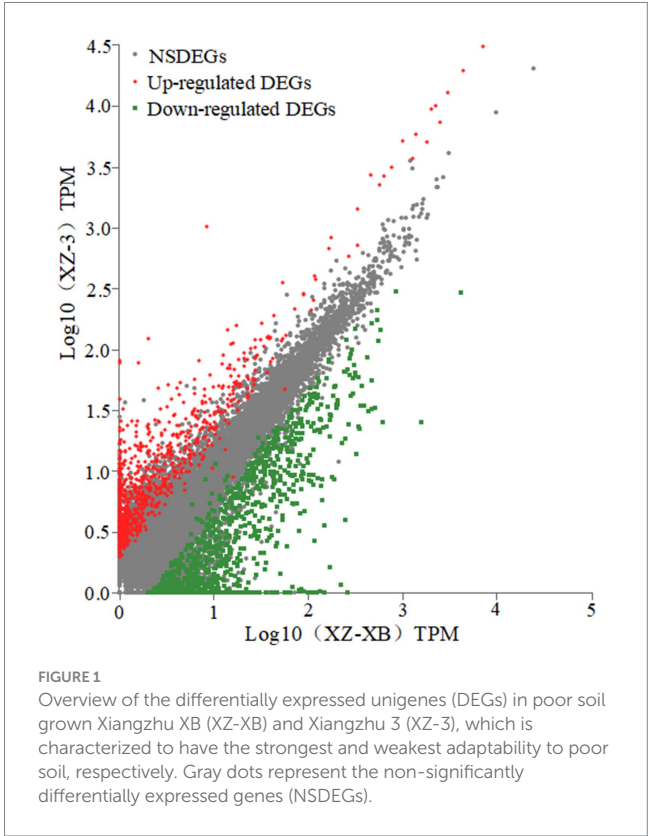


TABLE 3 The first and last top four different expressed genes between Xiangzhu XB (XZ-XB) and Xiangzhu 3 (XZ-3) under poor field soil condition.

Gene ID	Fold change (XZ-XB /XZ-3)	Gene expression model (XZ-XB/ XZ-3)	Gene function			
			GO database	COG database	Swiss-Prot database	Pfam database
DN721_c0_g1	17,508	Up-regulated	FnM	FnM	RNA1 polyprotein	Viral RNA-dependent RNA polymerase
DN9098_c0_g1	12,396	Up-regulated	Membrane component, Cysteine-type peptidase activity	Protein containing DUF246 domain	Viral cathepsin	Papain-family cysteine protease, Peptidase C1 family
DN7103_c0_g1	11,266	Up-regulated	FnM	FnM	FnM	Plant transposase
DN11078_c0_g1	9,735	Up-regulated	FnM	FnM	FnM	FnM
DN41995_c0_g1	1/2793	Down-regulated	FnM	FnM	FnM	FnM
DN5624_c0_g2	1/1630	Down-regulated	Transmembrane transport Integral component of plasma membrane ATP binding ATPase activity	Defense mechanism	ABC transporter	ABC transporter plant PDR protein
DN8330_c0_g5	1/1218	Down-regulated	Proteolysis involved in cellular protein catabolic process, Extracellular space, Cysteine-type endopeptidase activity	Pentatricopeptide repeat-containing protein	Senescence-specific cysteine protease	Papain-family cysteine protease cathepsin propeptide inhibitor domain
DN7998_c1_g1	1/1006	Down-regulated	Acid phosphatase activity	Hydrolysis of cAMP to 5'-AMP	Purple acid phosphatase	Calcineurin, Purple acid phosphatase N-terminal domain

FnM, Function not matched.

Rate) ≤ 0.01 , a total of 1,908 differentially expressed genes (DEGs) with significant ($p < 0.05$) expression differences were identified. Among these, 1,116 genes were up-regulated and 792 were down-regulated in XZ-XB compared to XZ-3. In the up-regulated DEGs, *DN721_c0_g1*, *DN9098_c0_g1*, *DN7103_c0_g1*, and *DN11078_c0_g1* exhibited expression levels in XZ-XB approximately 10,000 times higher than those in Xiangzhu 3, specifically 17,508-fold, 12,396-fold, 11,266-fold, and 9,735-fold, respectively. Among the down-regulated DEGs, *DN41995_c0_g1*, *DN5624_c0_g2*, *DN8330_c0_g5*, and *DN7998_c1_g1* showed expression levels in XZ-3 only about 1/1000 of those in XZ-XB, specifically 1/2793, 1/1630, 1/1218, and 1/1006-fold, respectively (Table 3).

3.3 Functional annotation of differentially expressed unigenes

Table 3 presents the functional annotations of the top four unigenes with the most significant differential expression between XZ-XB and XZ-3. Among the significantly up-regulated genes in XZ-XB compared to XZ-3, only *DN9098_c0_g1* has a relatively well-defined function, primarily associated with cysteine protease activity in plants. The functions of the other three genes remain largely uncharacterized. The gene of *DN721_c0_g1* was annotated in the Swiss-Prot and Pfam databases as involved in the formation and

function of RNA polymerase. Among the significantly down-regulated genes, the function of *DN41995_c0_g1* remains unknown. *DN5624_c0_g2* is primarily involved in the synthesis of transmembrane transport proteins. *DN8330_c0_g5* mainly affects the synthesis and function of plant cysteine proteases, and *DN7998_c1_g1* is associated with the regulation of phosphatase activity.

KEGG functional annotation analysis of the differentially expressed unigenes (Figure 2) revealed that 185 up-regulated and 116 down-regulated unigenes were mapped. They were assigned to five major functional categories: metabolic processes, cellular processes, organismal systems, genetic information processing, and environmental information processing. In terms of metabolic processes, the down-regulated genes were associated with: amino acid metabolism (11 unigenes), biosynthesis of other secondary metabolites (10 unigenes), carbohydrate metabolism (17 unigenes), energy metabolism (7 unigenes), terpenoid and polyketide metabolism (9 unigenes), lipid metabolism (4 unigenes), metabolism of cofactors and vitamins (4 unigenes), metabolism of other amino acids (4 unigenes), and nucleotide metabolism (1 unigene). The up-regulated genes were involved in the same nine subcategories as above, with unigene counts of 12, 11, 23, 15, 7, 8, 10, 12, and 2, respectively, and were additionally associated with glycan biosynthesis and metabolism (1 unigene). Among all metabolic process-related genes, those affecting carbohydrate metabolism were the most abundant, with 23 up-regulated and 17 down-regulated unigenes. For genetic information

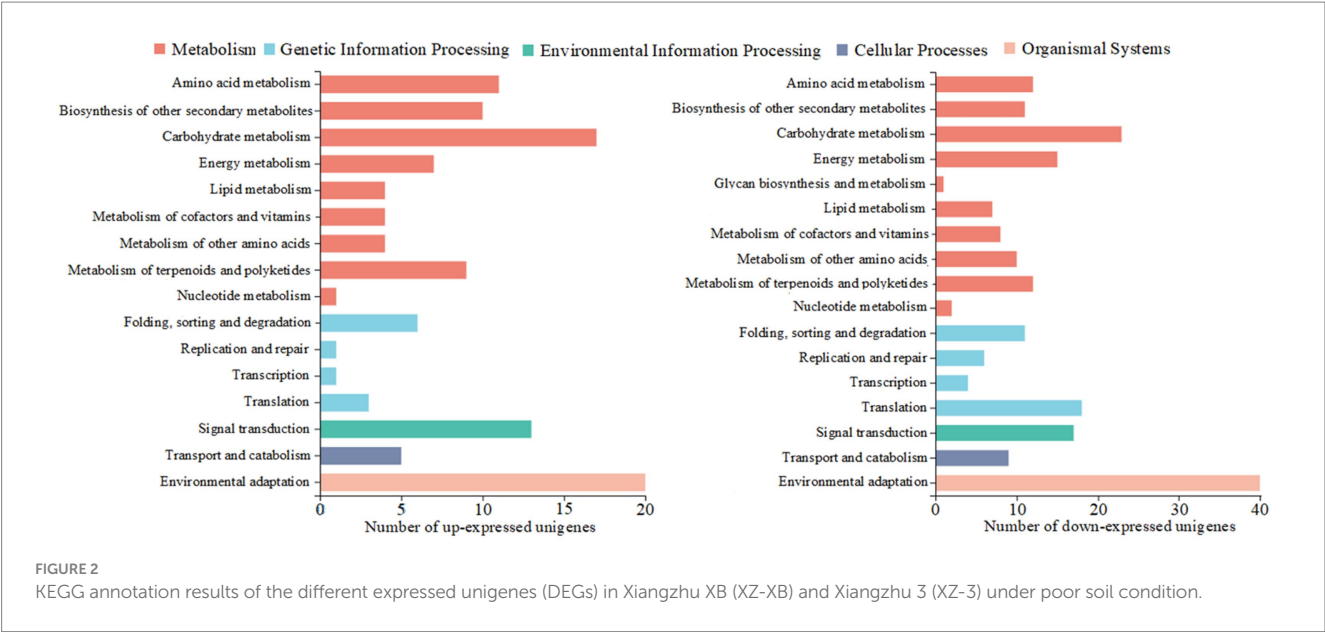


TABLE 4 Function of *environment adaption* related unigenes between Xiangzhu XB (XZ-XB) and Xiangzhu 3 (XZ-3).

Unigene function of NR description	Up-expressed unigenes (XZ-XB/XZ-3)	Down-expressed unigenes (XZ-XB/XZ-3)
NB-ARC & LRR domain containing protein	DN17704_c0_g1, DN6646_c0_g2, DN10746_c0_g3, DN17991_c0_g1, DN3772_c0_g1, DN13857_c0_g1, DN1120_c0_g1, DN1918_c0_g1, DN25266_c1_g2, DN16371_c0_g3, DN17991_c0_g5, DN7764_c0_g1, DN10000_c0_g2, DN206_c0_g1, DN28971_c0_g2	DN6646_c0_g1, DN27420_c0_g1, DN12765_c0_g2, DN12161_c0_g1, DN5665_c0_g2, DN35326_c0_g1, DN35326_c0_g2, DN19854_c1_g1, DN10000_c0_g1, DN19854_c0_g1, DN3511_c0_g1, DN25528_c0_g1
Disease resistance protein	DN25328_c0_g2, DN9287_c0_g2, DN1954_c0_g1, DN9439_c0_g2, DN28971_c0_g3	DN25334_c0_g1
Death- associated protein kinase	Not available	DN23138_c0_g1
Cyclic nucleotide-gated ion channel	Not available	DN20183_c0_g3, DN712_c0_g1
Pathogenesis related protein	Not available	DN13478_c0_g2
Cysteine proteinase	Not available	DN37443_c0_g1
Calcium- binding protein	DN7728_c0_g1, DN17002_c0_g1, DN20795_c0_g1, DN2710_c0_g1, DN8538_c0_g2, DN4394_c0_g1, DN4555_c0_g1	DN19122_c0_g1
Parvalbumin	DN10131_c0_g1, DN16338_c0_g1, DN6474_c0_g1, DN15518_c0_g1	Not available
WRKY transcription factor	DN13125_c0_g1, DN4382_c0_g1, DN788_c0_g1	DN21479_c0_g1
Hypothetical protein	DN10985_c0_g1 (FN43), DN33116_c0_g1 (F8388)	Not available
Calcium-dependent protein kinase	DN13170_c0_g1	Not available
Pathogenesis-related genes transcriptional activator	DN1117_c0_g1	Not available
Polcalcin	DN38256_c0_g1	Not available

processing, the DEGs were annotated to the following functional subcategories: folding, sorting, and degradation (11 vs. 6 unigenes), replication and repair (6 vs. 1 unigene), transcription (4 vs. 1 unigene), translation (18 vs. 3 unigenes). Notably, translation-related genes were the most abundant among up-regulated unigenes (18), while folding, sorting, and degradation were most represented among down-regulated unigenes (6). Within the remaining three functional categories, only one specific function was annotated in each: environmental information

processing (signal transduction), cellular processes (transport and catabolism), organismal systems (environmental adaptation). Overall, environmental adaptation contained the highest number of unigenes, including 40 up-regulated and 20 down-regulated genes.

Further in-depth analysis of the differentially expressed genes related to environmental adaptation is presented in Table 4. The results indicate that the highest number of DEGs were associated with the synthesis of proteins containing NB-ARC and LRR domains, including 15

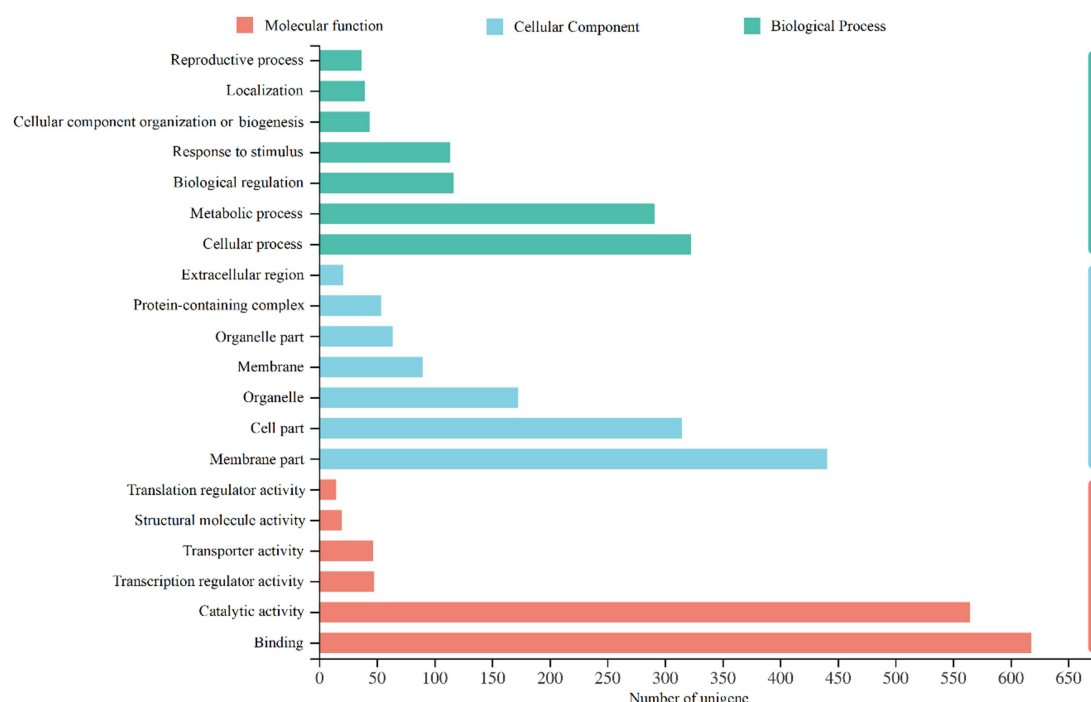


FIGURE 3

GO annotation results of the different expressed unigenes (DEGs) in Xiangzhu XB (XZ-XB) and Xiangzhu 3 (XZ-3) under poor soil condition.

up-regulated and 12 down-regulated genes. This was followed by genes related to calcium-binding proteins and disease resistance proteins, with 7 and 5 up-regulated DEGs, respectively, and only one down-regulated gene in each category. In addition to the above genes that were both up- and down-regulated, three genes were exclusively up-regulated. These are involved in the functions of calcium-dependent protein kinase (*DN13170_c0_g1*), transcription activator of pathogenesis-related genes (*DN1117_c0_g1*), calneurin (*DN38256_c0_g1*). Furthermore, five genes were exclusively down-regulated, functioning in death-associated protein kinase (*DN23138_c0_g1*), cyclic nucleotide-gated ion channels (*DN20183_c0_g3*, *DN712_c0_g1*), pathogenesis-related protein (*DN13478_c0_g2*), and cysteine protease (*DN37443_c0_g1*).

GO functional annotation analysis of the DEGs (Figure 3) revealed that among the 1,908 differentially expressed genes, multiple unigenes were co-annotated in the categories of molecular function, biological process, and cellular component. Overall, the largest number of DEGs were annotated in molecular function (1,356), followed by cellular component (1,196) and biological process (1,006). Within the molecular function category, the most annotated terms were “binding” and “catalytic activity,” with 618 and 565 unigenes, respectively. The other four functions (translation regulator activity, structural molecule activity, transporter activity, and transcription regulator activity) had relatively fewer annotated unigenes, ranging between 15 and 50. In the biological process category, the most annotated term was “cellular process” (323 unigenes), followed by “metabolic process” (291 unigenes). The number of unigenes annotated as “response to stimulus” and “biological regulation” were nearly identical, with 114 and 117, respectively. Terms such as “reproduction,” “cellular localization,” and “cellular component organization or biogenesis” had relatively fewer unigenes, each numbering around 40. For the cellular component category, the term “membrane part” contained the highest number of unigenes (441), followed by “cell part” (315). The remaining terms

included “organelle” (173), “membrane” (90), “organelle part” (64), “protein-containing complex” (54), and “extracellular region” (21).

3.4 Results of qRT-PCR detection

While transcriptome sequencing reflects the overall trend in gene expression, it may not perfectly capture the expression dynamics of every single gene. In contrast, qRT-PCR measures the actual expression levels of specific genes. To validate the accuracy of transcriptome sequencing results, it is common practice to select a subset of genes for verification using qRT-PCR. Consistency in expression trends between the two methods is generally considered successful validation. To assess the reliability of the transcriptome sequencing results in this study, four genes with substantial expression differences were selected for qRT-PCR analysis using the Actin gene as the internal reference. The results are presented in Table 5. Although the fold changes in gene expression detected by qRT-PCR differed somewhat from those obtained in the transcriptome sequencing analysis, the overall expression trends were consistent. The strong correlation between RNA-seq and qRT-PCR results (Table 5) validates the reliability of our transcriptomic data for identifying DEGs.

4 Discussion

4.1 The ramie transcriptome characteristics under poor soil conditions

The number of unigenes assembled in this study was significantly higher than the number of expressed genes obtained in the transcriptome study of ramie by Liu et al. (2013). This discrepancy may

TABLE 5 qRT-PCR checking results of the four screened genes.

Unigene name	Fold Change (XZ-XB/XZ-3) of PCR test	Fold change (XZ-XB/XZ-3) of transcriptome sequencing
TRINITY_DN9098_c0_g1	2,616	12,396
TRINITY_DN41995_c0_g1	1/1504	1/2793
TRINITY_DN721_c0_g1	11,754	17,508
TRINITY_DN11078_c0_g1	1789	9,735

be attributed to the induction of gene expression under poor soil stress that is not activated under normal growth conditions (as in the experimental setup of Liu's study). However, compared to the 77.7% unigene functional annotation rate reported in Liu's study, the highest annotation rate achieved in this study was only 53.71%. As a non-model plant without a publicly available reference genome, functional annotation of unigenes relies solely on information from related species in public databases (Chen et al., 2014; Ma et al., 2017). Previous studies on plant responses to abiotic stress have largely focused on drought, salinity, alkali, and heavy metal tolerance, while mechanisms underlying adaptation to nutrient-poor conditions remain poorly explored (Wu et al., 2016). This has resulted in a scarcity of genetic information related to poor soil tolerance in existing databases, ultimately leading to the limited functional annotation of many expressed genes in this study.

4.2 The contribution of DEGs in helping ramie adapting to poor soil conditions

Among the annotated differentially expressed genes identified in this study, *DN5624_c0_g2* is associated with ABC transporters. As a superfamily of proteins involved in the transmembrane transport of nutrients, photosynthetic products, and hormones, ABC transporters play a positive role in promoting root absorption of nutritional elements (Rentsch et al., 2007; Courty et al., 2015). For example, the orthologs of the ABC transports G subfamily in white lupin (*Lupinus albus*), such as *L.albABCG29*, are crucial for enhancing phosphorus accumulation under low-phosphorus conditions and have been linked to improved plant growth through mechanisms like promoted root development and rhizosphere formation (Aslam et al., 2021). Similarly, in maize (*Zea mays* L.), a set of Zm ABC genes such as *ZmABC012*, 013, 031, contribute to lead stress tolerance (Guo et al., 2022). However, the up-regulation of *DN5624_c0_g2* in the poor soil-sensitive variety XZ-3 suggests that it may act as a suppressor of ABC transporter synthesis or its function might be specific to transporting compounds that are detrimental under nutrient-deficient stress. This highlights the complex and sometimes contradictory roles of transporter families, necessitating functional validation in ramie.

Another highly up-regulated gene in XZ-3, *DN8330_c0_g5*, is annotated with functions related to pentatricopeptide repeat (PPR) proteins and senescence-specific cysteine proteases. The PPR proteins influence RNA metabolism through editing, splicing, and other

mechanisms, primarily promoting RNA translation (Huang and Huang, 2018). Cysteine proteases, widely involved in various physiological processes, induce or participate in both natural and stress-induced senescence (Liu et al., 2018). The co-upregulation of these functional domains strongly suggests that under poor soil condition, *DN8330_c0_g5* in the sensitive variety promotes the translation of RNA associated with senescence-specific cysteine proteases, leading to increased production of senescence-promoting enzymes and accelerating plant aging and death. This mechanism is conserved across species. For example, in creeping bentgrass (*Agrostis stolonifera*), heat stress induces general protease activities that accelerate leaf senescence (Rossi and Huang, 2024). This indicates that *DN8330_c0_g5* represents a promising target for gene silencing or knockout to delay stress-induced senescence and enhance poor soil tolerance in ramie.

Additionally, *DN7998_c1_g1*, which is highly expressed in XZ-3, may function as an inhibitor of purple acid phosphatases (PAPs). The PAPs enhance the activation of organic phosphorus, thereby helping plants adapt to low-phosphorus environments (Liu et al., 2019). Their function has been validated in several plants, including Arabidopsis (Wang et al., 2011), rice (Lu et al., 2016), and common bean (Wu et al., 2018). As a member of the cysteine protease family, papain-like cysteine proteases are primarily associated with programmed cell death in plants (Liu et al., 2018; Ueda et al., 2000). Previous studies have shown that under environmental stresses such as drought and salinity, plants accumulate papain-like cysteine proteases to promote senescence (Cilliers et al., 2018; Havé et al., 2018). Therefore, the highly expressed *DN8330_c0_g5* in XZ-3 may be a key gene regulating the synthesis of papain-like cysteine proteases in ramie, while the highly expressed *DN9098_c0_g1* in XZ-XB may act as a suppressor. This presents a direct breeding application: selecting for alleles of *DN7998_c1_g1* that confer low expression could be a strategy to enhance phosphorus scavenging capacity in new ramie varieties.

4.3 The potential mechanisms underlying ramie tolerance to poor soil stress

Through functional enrichment analysis of differentially expressed genes, this study found that the largest number of genes were associated with carbohydrate metabolism and environmental adaptation. This suggests that ramie varieties with strong adaptability to poor soil conditions may mitigate the impact of nutrient deficiency on photosynthetic product accumulation (i.e., carbohydrates) by regulating specific genes, while also modulating environment adaptation-related genes to reduce the effects of nutrient scarcity on plant growth.

Among the differentially expressed genes involved in environmental adaptation, annotated functions were primarily associated with the synthesis and activity of death-associated protein kinases, pathogenesis-related proteins, and cysteine proteases (which induce plant senescence). Thus, it can be inferred that ramie germplasms with high tolerance to poor soil reduce the expression of genes that promote senescence and cell death, thereby alleviating the damage caused by nutrient stress and enhancing adaptation to poor environments.

Among the genes positively correlated with ramie's adaptability to poor soil, functions were related to critical proteins such as

calcium-dependent protein kinases and calcineurin. Calcium-dependent protein kinases transduce environmental stress signals and defense responses (Ni and Wei, 2002) but rely on calcium signaling. Calcineurin maintains high calcium ion concentrations to ensure the activity of calcium-dependent protein kinases, thereby facilitating signal transduction. Therefore, the ability to rapidly and sensitively recognize poor soil signals and transmit them to the plant for swift defensive responses represents a key mechanism enabling ramie germplasms with high poor soil tolerance to adapt to nutrient-deficient environments.

4.4 Agroecological benefits derived by the ramie cultivation on degraded lands

Soil degradation, particularly of arable land, is mainly driven by some interconnected factors as soil erosion, structural deterioration from intensive tillage, and ecological imbalance caused by the excessive use of fertilizers, pesticides, and plastic mulch (Oliveira et al., 2022; Dadzie et al., 2023). The development of stress-tolerant ramie varieties offers a dual-benefit strategy: enabling productive utilization of degraded land while concurrently restoring soil health through agroecological mechanisms.

As a perennial, ramie requires only a single establishment, but provides repeated harvests over 5–10 years or more. This long-term growth habit minimizes soil disturbance, thereby reducing structural damage and erosion risk. Its well-developed root and rhizome system enhances soil stabilization, while the dense canopy effectively intercepts rainfall (Wang et al., 2021). Together, these traits enable ramie to offer soil and water conservation benefits comparable to those of 5–6 year-old regenerating forests or perennial grasslands (Liao et al., 2011). Breeding ramie for improved adaptation to poor soils can further reduce reliance on synthetic fertilizer. This not only improves nutrient use efficiency within ramie systems, but also helps mitigate the acidification and compaction often associated with the chemical fertilizer application in conventional crop production (Pahalvi et al., 2021). Moreover, the practice of leaf stripping during harvesting, coupled with natural root turnover, continuously returns organic matter to the soil (Bene et al., 2011). This, together with root exudates supply, builds stable organic carbon, which is vital energy to soil microbiota, significantly enhancing microbial diversity and activity (Zhu et al., 2018).

In summary, ramie serves as a multifunctional crop for sustainable land management. Its cultivation on degraded or marginal lands can simultaneously improve soil structure, enhance fertility, and reactivate soil biological communities—all while maintaining economic returns through sustainable fiber production.

4.5 Implications of the screened genes for molecular breeding

The DEGs identified in this study provide a valuable resource for molecular breeding of ramie with enhanced adaptation to nutrient-deficient soils. The highly expressed genes in XZ-XB (the poor soil tolerant germplasm), such as *DN721_c0_g1*, *DN9098_c0_g1*, can be used as molecular markers for marker-assisted selection. Breeders

can screen germplasm collections for these favorable alleles to rapidly introgress the tolerance trait. Conversely, the genes highly expressed in the sensitive XZ-3 (e.g., *DN8330_c0_g5* and *DN7998_c1_g1*) are targets for gene editing. Using gene editing tools such as CRISPR-Cas9 to knock out these genes in elite but sensitive varieties could directly convert them into nutrient-efficient cultivars. Furthermore, the suite of DEGs related to carbohydrate metabolism, calcium signaling, and defense responses provides a foundation for developing multi-gene selection models, enabling the pyramiding of several advantageous transcriptional alleles for robust and durable tolerance to poor soil.

5 Conclusion

This study identified key genes involved in ramie's adaptation to poor soil condition through transcriptome analysis. A total of 1,908 differentially expressed genes (DEGs) were detected, among which seven unigenes showed large expression differences (>1,000-fold change). Functional annotation linked these DEGs to the functions of nutrient transport, senescence, and stress signaling. Results uncovered here provide valuable genetic resources and candidate targets to breed advanced ramie varieties that are genetically equipped to thrive in poor soil condition. The development of such varieties could transform ramie cultivation from conventional cropping system into an integrated agroecological solutions. This ramie production system simultaneously contributes to fiber production, soil restoration, and alleviates competition between food and fiber crops for arable land.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

SW: Data curation, Formal analysis, Visualization, Writing – original draft. HJ: Visualization, Writing – review & editing. HX: Conceptualization, Writing – review & editing. YJ: Conceptualization, Project administration, Supervision, Writing – review & editing.

Funding

The author(s) declare that financial support was received for the research and/or publication of this article. This work was financially supported by the Yuelushan Laboratory Breeding Project (YLS-2025-ZY02056), Natural Science Foundation of China (32071940 and 31872877), and the National Science and Technology Resource Sharing Service Platform Project (NCGRC-2025-48).

Acknowledgments

We acknowledge all those who contributed to this work but are not named as authors.

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