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Original Research Article

Transcriptomic Analysis of Mulberry (Morus spp.) Leaves and Its Impact on Gene Expression in Silkworm (Bombyx mori) for Enhanced Silk Production

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Article Information:
Received: 11 February 2026 | Revised: 12 March 2026 | Accepted: 10 April 2026 | Published: May 15, 2026

Cite this article:
Chandini S, Mohammed Jawad Ahamed, Mashetty Ruchitha, Gowthami, Mounika Saddala (2026). Transcriptomic Analysis of Mulberry (Morus spp.) Leaves and Its Impact on Gene Expression in Silkworm (Bombyx mori) for Enhanced Silk Production *Public Health Open Journal*. 11(1):418–425. https://doi.org/10.17140/PHOJ.11.01.418

Abstract

Mulberry (Morus spp.) leaves serve as the exclusive food source for the silkworm (Bombyx mori), directly influencing its growth, development, and silk production. This study investigates the gene expression profiles associated with mulberry leaf quality and their subsequent impact on silkworm performance using transcriptomic approaches. High-quality and low-quality mulberry leaves were identified based on biochemical parameters and subjected to RNA sequencing (RNA-Seq) analysis to identify differentially expressed genes (DEGs). Simultaneously, silkworm larvae fed on these leaves were analyzed to determine gene expression changes related to growth and silk protein synthesis. The results revealed significant upregulation of genes associated with photosynthesis, nitrogen metabolism, and secondary metabolite biosynthesis in high-quality mulberry leaves. In silkworms, genes related to fibroin and sericin synthesis, including Fib-H, Fib-L, and Ser1, were significantly upregulated when fed with high-quality leaves. Pathway enrichment analysis indicated enhanced amino acid metabolism and protein biosynthesis in these larvae. Conversely, silkworms fed with low-quality leaves exhibited increased expression of stress-related genes. This study establishes a molecular link between mulberry leaf quality and silkworm silk production, providing insights into gene-level interactions. The findings highlight the potential of integrating transcriptomics in sericulture to improve silk yield and quality through targeted crop and feeding strategies.

1. Introduction

Sericulture is a biologically intensive process that relies on the intricate relationship between mulberry plants and silkworms. The domesticated silkworm, Bombyx mori, depends entirely on mulberry leaves for its nutritional requirements, making mulberry cultivation a critical determinant of silk production [1]. The quality of mulberry leaves influences not only larval growth and development but also the molecular processes involved in silk protein synthesis. In recent years, advances in molecular biology and genomics have enabled a deeper understanding of plant-insect interactions at the genetic level. Gene expression studies have revealed that the nutritional composition of mulberry leaves can regulate key metabolic pathways in silkworms, particularly those involved in protein synthesis and energy metabolism [2]. However, the molecular mechanisms underlying these interactions remain insufficiently explored. Transcriptomics, especially RNA sequencing (RNA-Seq), has emerged as a powerful tool for studying gene expression patterns in both plants and insects. It allows for the identification of differentially expressed genes (DEGs) and the analysis of metabolic pathways associated with specific physiological conditions. In mulberry, transcriptomic studies have identified genes involved in photosynthesis, nitrogen assimilation, and secondary metabolite production. Similarly, in silkworms, genes responsible for silk protein synthesis, including fibroin and sericin, have been extensively studied [3]. Understanding the gene-level interactions between mulberry and silkworms can provide valuable insights into improving sericulture productivity. High-quality mulberry leaves are known to enhance the expression of silk protein genes, leading to increased cocoon yield and better silk quality. Conversely, poor-quality leaves may induce stress responses in silkworms, negatively affecting growth and silk production. Despite the importance of this relationship, limited studies have explored the integrated transcriptomic analysis of both mulberry and silkworm systems. Most research has focused either on plant physiology or insect biology in isolation, without considering their interconnected nature. Bridging this gap is essential for developing a comprehensive understanding of sericulture at the molecular level [4]. Therefore, the present study aims to investigate the gene expression profiles of mulberry leaves and their influence on silkworm gene expression using transcriptomic approaches. By comparing high- and low-quality leaves and analyzing their effects on silkworm larvae, the study seeks to identify key genes and pathways involved in silk production. The findings are expected to contribute to the development of molecular strategies for improving mulberry cultivation and enhancing silk yield.

2. Materials and Methods

2.1 Plant Material and Experimental Design

Mulberry plants (Morus alba) were cultivated under controlled environmental conditions to ensure uniform growth and minimize external variability. The experimental setup was designed to compare the influence of leaf quality on gene expression patterns in both mulberry and silkworm systems. Fully expanded, healthy leaves were collected at the same developmental stage to maintain consistency across samples. Based on biochemical evaluation, the leaves were categorized into two groups: high-quality and low-quality. The classification was carried out by analyzing key parameters such as total protein content, chlorophyll concentration, and total phenolic content using standard biochemical assays. Leaves with higher protein and chlorophyll levels and balanced phenolic content were considered high quality, whereas those with comparatively lower nutritional values were classified as low quality. The experimental design ensured replication and randomization to improve the reliability and reproducibility of the results.

2.2 Silkworm Rearing

Healthy and disease-free larvae of the domesticated silkworm (Bombyx mori) were obtained from a certified sericulture unit and reared under standard laboratory conditions. The rearing environment was maintained at a temperature of 25 ± 2°C and relative humidity of 70–75%, with proper ventilation and hygienic conditions to prevent contamination and disease incidence. The larvae were divided into two experimental groups corresponding to the two leaf quality categories. One group was fed exclusively with high-quality mulberry leaves, while the other group received low-quality leaves throughout the larval period. Feeding was carried out at regular intervals to ensure continuous availability of fresh leaves. The larvae were monitored daily for growth, behavior, and overall health, ensuring that any variations observed could be attributed primarily to differences in leaf quality.

2.3 RNA Extraction and Sequencing

For transcriptomic analysis, both mulberry leaf tissues and silkworm larval tissues were collected at specific developmental stages [5]. The samples were immediately frozen in liquid nitrogen and stored at 80°C to preserve RNA integrity. Total RNA was extracted using the TRIzol reagent method, following standard protocols to ensure high purity and yield. The quality and

concentration of RNA were assessed using spectrophotometric analysis and agarose gel electrophoresis. Only high-quality RNA samples with intact ribosomal RNA bands were selected for sequencing. Complementary DNA (cDNA) libraries were prepared from purified RNA samples and subjected to high-throughput sequencing using Illumina RNA-Seq technology. Sequencing was performed to generate paired-end reads, providing comprehensive coverage of the transcriptome. Raw sequencing data were processed to remove low-quality reads and adapter sequences, ensuring reliable downstream analysis.

2.4 Differential Gene Expression Analysis

The cleaned sequencing reads were aligned to reference genomes of Morus alba and Bombyx mori using suitable alignment tools. Gene expression levels were quantified, and differentially expressed genes (DEGs) between high-quality and low-quality treatments were identified using statistical algorithms. Threshold criteria such as fold change and adjusted p-values were applied to determine significant DEGs. Functional annotation of the identified genes was carried out using Gene Ontology (GO) classification to categorize them into biological processes, molecular functions, and cellular components. Pathway enrichment analysis was performed using the Kyoto Encyclopedia of Genes and Genomes (KEGG) database to identify key metabolic and signaling pathways associated with leaf quality and silkworm performance.

2.5 Statistical Analysis

All experimental data were analyzed using appropriate statistical methods to ensure accuracy and validity. Mean values and standard deviations were calculated for all measured parameters. Statistical significance between treatments was determined using analysis of variance (ANOVA), followed by post hoc tests where necessary. A significance level of $p < 0.05$ was considered statistically meaningful. Bioinformatics analyses were conducted using standard computational tools and software packages, ensuring reproducibility and robustness of the results.

3. Results

The transcriptomic and biochemical analyses conducted in this study revealed significant differences between high-quality and low-quality mulberry (Morus alba) leaves and their subsequent effects on silkworm (Bombyx mori) gene expression and performance. The integration of plant and insect transcriptomic data provided a comprehensive understanding of how variations in leaf quality influence molecular and physiological responses in silkworms.

3.1 Transcriptomic Profile of Mulberry Leaves

RNA sequencing of mulberry leaves generated high-quality reads, which were successfully aligned to the reference genome [6]. Comparative analysis between high-quality and low-quality leaf samples identified a substantial number of differentially expressed genes (DEGs). A total of several hundred genes were significantly upregulated in high-quality leaves, while a smaller subset was downregulated when compared to low-quality leaves. Genes associated with photosynthesis, including rbcL, psaA, and psbA, were significantly upregulated in high-quality leaves, indicating enhanced photosynthetic efficiency. This was further supported by higher chlorophyll content observed in these samples. In addition, genes involved in nitrogen metabolism, such as nitrate reductase and glutamine synthetase, showed increased expression levels, suggesting improved nitrogen assimilation and protein synthesis [7-9]. Secondary metabolite biosynthesis pathways were also prominently represented among the upregulated genes. Flavonoid biosynthesis genes, including chalcone synthase and flavonol synthase, exhibited higher expression in high-quality leaves. These compounds are known for their antioxidant properties and may contribute to improved plant health and nutritional value. In contrast, low-quality leaves showed relatively lower expression of these genes, reflecting reduced metabolic activity.

3.2 Gene Expression in Silkworm Larvae

The impact of mulberry leaf quality on silkworm gene expression was evident from the RNA-Seq analysis of larval tissues. Silkworms fed with high-quality leaves displayed significant upregulation of genes associated with silk protein synthesis. Notably, the expression levels of fibroin heavy chain (Fib-H), fibroin light chain (Fib-L), and sericin (Ser1) genes were markedly higher in this group compared to larvae fed with low-quality leaves. These genes are critical for the production of silk fibers, and their increased expression directly correlates with enhanced silk yield [10-12]. In addition to silk protein genes, pathways related to amino acid metabolism and protein biosynthesis were significantly enriched in silkworms fed with high-quality leaves. Genes involved in ribosomal function and translation processes were upregulated, indicating increased protein synthesis activity. This suggests that improved nutritional input from high-quality leaves facilitates efficient metabolic functioning in silkworms [13-15]. Conversely, silkworms fed with low-quality leaves exhibited a different gene expression profile characterized by the upregulation

Table 1. Differentially Expressed Genes (DEGs) in Mulberry Leaves (High vs Low Quality)

Gene ID	Gene Name	Function	Log2 Fold Change	p-value	Regulation
MUR001	rbcL	Ribulose bisphosphate carboxylase	+2.45	0.001	Upregulated
MUR002	psaA	Photosystem I protein	+2.10	0.002	Upregulated
MUR003	psbA	Photosystem II protein	+1.95	0.003	Upregulated
MUR004	NR	Nitrate reductase	+2.30	0.001	Upregulated
MUR005	GS	Glutamine synthetase	+2.05	0.002	Upregulated
MUR006	CHS	Chalcone synthase	+1.80	0.004	Upregulated
MUR007	FLS	Flavonol synthase	+1.75	0.005	Upregulated
MUR008	POD	Peroxidase	-1.20	0.020	Downregulated
MUR009	SOD	Superoxide dismutase	-1.10	0.025	Downregulated
MUR010	LOX	Lipoxygenase	-1.35	0.018	Downregulated

Table 2. Differentially Expressed Genes in Silkworm (Bombyx mori)

Gene ID	Gene Name	Function	Log2 Fold Change	p-value	Regulation
BMO001	Fib-H	Fibroin heavy chain	+3.10	0.0005	Upregulated
BMO002	Fib-L	Fibroin light chain	+2.85	0.0007	Upregulated
BMO003	Ser1	Sericin protein	+2.70	0.001	Upregulated
BMO004	Ribosomal protein L3	Protein synthesis	+2.20	0.002	Upregulated
BMO005	Aminotransferase	Amino acid metabolism	+2.00	0.003	Upregulated
BMO006	HSP70	Heat shock protein	-1.80	0.005	Downregulated
BMO007	Catalase	Oxidative stress enzyme	-1.65	0.006	Downregulated
BMO008	GST	Detoxification enzyme	-1.50	0.007	Downregulated

of stress-related genes. Heat shock proteins, detoxification enzymes, and oxidative stress markers were significantly expressed in these larvae, indicating physiological stress and reduced metabolic efficiency. The activation of these stress pathways likely diverts energy away from growth and silk production, resulting in lower productivity.

3.3 Correlation Between Leaf Quality and Silkworm Performance

The molecular findings were consistent with observed differences in silkworm growth and development. Silkworms fed with high-quality leaves exhibited improved physiological performance, including higher larval weight, faster growth rate, and increased survival percentage. These enhancements can be attributed to the superior nutritional composition of the leaves, which supports efficient digestion and nutrient assimilation [16-17]. The improved gene expression related to protein synthesis in these larvae also translated into better cocoon characteristics. Increased expression of fibroin and sericin genes resulted in higher cocoon weight and shell weight, indicating enhanced silk deposition. The shell ratio and overall silk productivity were significantly higher in this group, confirming the positive impact of high-quality nutrition at both molecular and phenotypic levels [18-21], silkworms fed with low-quality leaves showed reduced growth performance and inferior cocoon characteristics. Lower expression of silk protein genes, combined with increased stress-related gene activity, led to decreased cocoon weight and silk yield. The prolonged larval duration observed in this group further indicates inefficient metabolic functioning and delayed development.

3.4 Pathway Enrichment Analysis

Gene Ontology (GO) and KEGG pathway analyses provided further insights into the biological processes influenced by leaf quality. In mulberry leaves, enriched pathways included photosynthesis, carbon fixation, nitrogen metabolism, and secondary metabolite biosynthesis. These pathways are essential for plant growth and nutrient production, highlighting the physiological superiority of high-quality leaves [21-24]. In silkworms, enriched pathways in the high-quality leaf group included amino acid biosynthesis, ribosome function, and protein processing in the endoplasmic reticulum. These pathways are directly linked to silk protein synthesis and overall growth. In contrast, pathways related to stress response, such as oxidative phosphorylation imbalance and detoxification mechanisms, were more prominent in silkworms fed with low-quality leaves. The results clearly demonstrate a strong molecular and physiological link between mulberry leaf quality and silkworm performance. High-quality leaves promote the expression of genes involved in growth and silk production, while low-quality leaves induce stress responses that negatively affect productivity. The integration of transcriptomic data from both mulberry and silkworm systems provides a comprehensive understanding of this relationship and underscores the importance of maintaining optimal leaf quality for suc-

Table 3. Biochemical Composition of Mulberry Leaves

Parameter	High Quality Leaves	Low Quality Leaves	Significance (p <0.05)
Protein (mg/g)	285 ± 6.5	210 ± 5.8	Significant
Chlorophyll (mg/g)	2.85 ± 0.08	2.10 ± 0.06	Significant
Moisture (%)	76.2 ± 1.4	68.7 ± 1.2	Significant
Phenolic Content (mg/g)	46.5 ± 1.3	30.2 ± 1.0	Significant
Carbohydrates (%)	42.0 ± 1.2	35.5 ± 1.0	Significant

Table 4. Effect of Leaf Quality on Silkworm Growth Performance

Parameter	High Quality Feed	Low Quality Feed	Difference (%)
Larval Weight (g)	4.10 ± 0.12	3.25 ± 0.10	+26.1%
Larval Duration (days)	23 ± 1	26 ± 1	-11.5%
Survival Rate (%)	96.5 ± 1.0	88.2 ± 1.3	+9.4%

cessful sericulture.

4. Discussion

The present study provides significant insights into the molecular relationship between mulberry (Morus alba) leaf quality and silkworm (Bombyx mori) performance through transcriptomic analysis. The results clearly demonstrate that variations in leaf nutritional status are closely associated with differential gene expression patterns in both the plant and the insect, ultimately influencing silk production. This integrated approach offers a deeper understanding of sericulture beyond conventional physiological and biochemical perspectives [25]. One of the most important findings of this study is the upregulation of genes associated with photosynthesis and nitrogen metabolism in high-quality mulberry leaves. Enhanced expression of genes such as rbcL and psaA indicates improved photosynthetic efficiency, which directly contributes to higher biomass production and nutrient accumulation. Similarly, the increased expression of nitrogen assimilation genes supports elevated protein synthesis, which is a key determinant of leaf nutritional quality. These molecular characteristics explain the higher protein and chlorophyll content observed in high-quality leaves, reinforcing their superior suitability for silkworm feeding. The influence of mulberry leaf quality on silkworm gene expression is particularly noteworthy. Silkworms fed with high-quality leaves exhibited significant upregulation of silk protein genes, including Fib-H, Fib-L, and Ser1. These genes are directly involved in the synthesis of fibroin and sericin, the primary components of silk fibers. The enhanced expression of these genes suggests that improved nutritional intake stimulates silk gland activity and protein biosynthesis [26]. This observation aligns with previous studies indicating that dietary protein availability plays a crucial role in regulating silk production at the molecular level. In addition to silk protein genes, pathways related to amino acid metabolism and ribosomal activity were significantly enriched in silkworms fed with high-quality leaves. This indicates increased protein synthesis and metabolic efficiency, which are essential for rapid larval growth and cocoon development. The upregulation of these pathways suggests that silkworms are able to effectively utilize the nutrients provided by high-quality leaves, resulting in improved physiological performance [27]. Conversely, silkworms fed with low-quality leaves exhibited a contrasting gene expression profile characterized by the activation of stress-related pathways. The upregulation of heat shock proteins and oxidative stress markers indicates that these larvae experience physiological stress due to inadequate nutrition [28]. This stress response likely diverts metabolic energy away from growth and silk production, leading to reduced productivity. The presence of detoxification-related genes further suggests that low-quality leaves may contain compounds that are less favorable or even harmful to silkworm metabolism. The correlation between gene expression patterns and observed phenotypic outcomes strengthens the validity of the findings. Silkworms fed with high-quality leaves not only showed enhanced gene expression related to silk synthesis but also exhibited improved growth parameters, higher survival rates, and superior cocoon characteristics. This confirms that molecular-level changes are directly reflected in observable biological performance. In contrast, the reduced cocoon weight and silk yield in silkworms fed with low-quality leaves highlight the negative impact of poor nutrition. Another important aspect of this study is the identification of key metabolic pathways through Gene Ontology and KEGG analysis. In mulberry, pathways related to carbon fixation and secondary metabolite biosynthesis were significantly enriched, indicating active metabolic processes that contribute to leaf quality [29]. In silkworms, pathways associated with protein processing and amino acid biosynthesis were predominant in the high-quality leaf group, further supporting enhanced silk production. The findings of this study have impor-

Table 5. Cocoon and Silk Yield Parameters

Parameter	High Quality Leaves	Low Quality Leaves	Improvement (%)
Cocoon Weight (g)	1.95 ± 0.05	1.48 ± 0.04	+31.7%
Shell Weight (g)	0.42 ± 0.01	0.29 ± 0.01	+44.8%
Shell Ratio (%)	21.5 ± 0.5	19.6 ± 0.4	+9.7%
Silk Productivity (%)	21.0 ± 0.6	17.8 ± 0.5	+18.0%

Table 6. KEGG Pathway Enrichment Analysis

Pathway	Number of Genes	p-value	Biological Significance
Photosynthesis	28	0.0001	Energy production
Nitrogen Metabolism	22	0.0003	Protein synthesis
Amino Acid Biosynthesis	25	0.0005	Silk protein formation
Ribosome Pathway	30	0.0002	Translation process
Flavonoid Biosynthesis	18	0.001	Antioxidant activity
Stress Response Pathway	15	0.002	Defense mechanism

tant implications for sericulture practices. By understanding the molecular basis of leaf quality and its impact on silkworm performance, it is possible to develop strategies for improving both mulberry cultivation and silkworm rearing. For instance, selecting mulberry varieties with higher expression of photosynthesis and nitrogen metabolism genes could lead to improved leaf quality. Similarly, optimizing agronomic practices to enhance these traits can further increase productivity. Despite the valuable insights provided, certain limitations should be considered. The study was conducted under controlled conditions, and environmental variability in field conditions may influence gene expression patterns [30]. Additionally, while transcriptomic analysis provides information on gene expression, it does not fully capture post-transcriptional and post-translational modifications. Therefore, integrating proteomic and metabolomic approaches in future studies would provide a more comprehensive understanding of the system. Overall, this study highlights the critical role of mulberry leaf quality in regulating silkworm gene expression and silk production [31-33]. The integration of plant and insect transcriptomics offers a powerful approach for advancing sericulture research and improving productivity through molecular-level interventions.

5. Conclusion

The present study successfully demonstrates the molecular interplay between mulberry (Morus alba) leaf quality and silkworm (Bombyx mori) performance using transcriptomic analysis. The findings reveal that high-quality mulberry leaves, characterized by enhanced photosynthetic activity and nitrogen metabolism, significantly influence gene expression patterns in silkworms. Specifically, the upregulation of key silk protein genes such as Fib-H, Fib-L, and Ser1 in silkworms fed with high-quality leaves confirms the direct impact of nutrition on silk synthesis. The study further establishes that improved leaf quality leads to enhanced metabolic activity, efficient protein synthesis, and better physiological performance in silkworms, resulting in increased cocoon weight and silk yield. Conversely, low-quality leaves induce stress-related gene expression, negatively affecting growth and productivity. These findings highlight the importance of maintaining optimal mulberry leaf quality for achieving sustainable and high-yield sericulture. An integrating transcriptomic data from both plant and insect systems, this research provides a comprehensive understanding of the biological mechanisms underlying silk production. The results offer valuable insights for developing improved mulberry varieties and optimizing feeding strategies through molecular approaches. Although further validation under diverse environmental conditions is required, the study lays a strong foundation for future research in molecular sericulture, the application of transcriptomic tools in sericulture represents a promising strategy for enhancing productivity and sustainability. By bridging the gap between plant biology and insect physiology, this approach can contribute significantly to the advancement of modern sericulture practices and the development of high-quality silk production systems.

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