Case Study Open Access

Epigenetic Variation and Oil Accumulation in *Camellia oleifera*: A Case from High- and Low-Altitude Regions

Jianmin Zheng, Lian Chen, Chuchu Liu
Institute of Life Sciences, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China
Corresponding email: chuchu.liu@jicat.org

Tree Genetics and Molecular Breeding, 2025, Vol.15, No.3 doi: 10.5376/tgmb.2025.15.0015
Received: 19 May, 2025
Accepted: 21 Jun., 2025
Published: 30 Jun., 2025

Preferred citation for this article:
Zheng J.M., Chen L., and Liu C.C., 2025, Epigenetic variation and oil accumulation in *Camellia oleifera*: a case from high- and low-altitude regions, Tree Genetics and Molecular Breeding, 15(3): 128-137 (doi: 10.5376/tgmb.2025.15.0015)

Abstract This study mainly summarizes the relationship between oil accumulation and epigenetics in *Camellia oleifera* at different altitudes, analyzes common epigenetic mechanisms such as DNA methylation and histone modification, and examines how they affect the expression of genes related to fatty acid synthesis and oil metabolism. It also discusses how environmental stress at high and low altitudes alters the structure of the epigenome. To regulate the yield and quality of oils, a comparative analysis was conducted on *Camellia oleifera* populations from different altitudes. It was found that *Camellia oleifera* can adapt to environmental changes by adjusting its epigenetic state. This "plasticity" may play an important role in the development and ecological adaptation of plants. This study aims to provide some useful theoretical references for the genetic improvement of woody oil crops and the breeding of new high-quality oil varieties in the future.

Keywords *Camellia oleifera*; Woody oil crops; Altitudinal variation; Epigenetic regulation; Oil accumulation

1 Introduction

Camellia oleifera is one of the important oil trees in China and around the world (Yao et al., 2024). It contains a lot of unsaturated fatty acids, is healthy to eat and can also be used as medicine. Therefore, it is called "Oriental olive Oil". *Camellia* oil has significant uses in food, medicine and industry, and also brings considerable economic benefits (Gong et al., 2020; Lin et al., 2024).

The altitude and related environmental conditions, such as temperature, sunlight and humidity, will significantly affect the oil content and quality of *Camellia oleifera*. At different altitudes, the oil content, fatty acid types and some metabolites of *Camellia oleifera* seeds will vary. These changes are closely related to the regulation of gene expression during the development of seeds (Wu et al., 2019; Ye et al., 2021; Yang et al., 2024).

Nowadays, an increasing number of studies are focusing on the role of epigenetics in the formation of plant traits and metabolites. Epigenetic patterns such as DNA methylation, histone modification and non-coding RNA can affect the expression of key genes. These regulatory methods will further affect the synthesis of oils, the development of seeds, and the response of plants to the external environment. These findings provide a new perspective for understanding the oil accumulation mechanism of *Camellia oleifera* in different ecological environments (Gong et al., 2020; Liu et al., 2023).

This study compared the epigenetic differences and oil accumulation of *Camellia oleifera* germplasm at different altitudes and found that environmental factors can regulate the process of oil synthesis by influencing epigenetic methods. This research aims to provide scientific basis and theoretical support for the high-quality and high-yield breeding and resource utilization of *Camellia oleifera* in the future.

2 Oil Biosynthesis Pathways in *Camellia oleifera*

2.1 Overview of lipid metabolic pathways

The oil in *Camellia oleifera* seeds mainly exists in the form of triacylglycerol (TAG). The lipid metabolism process includes the synthesis, modification and formation of fatty acids. The synthesis of fatty acids begins in the chloroplasts and requires the participation of multiple enzymes, such as acetyl-CoA carboxylase (ACCase), several β-ketoacyl-ACP synthetases (KAS I/II/III), hydroxyacyl-ACP dehydrogenase (HAD) and enoyl-ACP reductase (EAR). These synthesized fatty acids are then activated by long-chain acyl-CoA synthetase (LACS) and then transferred to the endoplasmic reticulum, where they are further modified and finally assembled into TAG. Key synthases also include triglyceride synthase (DGAT) and phosphatidylcholine:diacylglycerol acyltransferase (PDAT) (Figure 1) (Gong et al., 2020; Ye et al., 2020; Yang et al., 2024; Zhu et al., 2024).

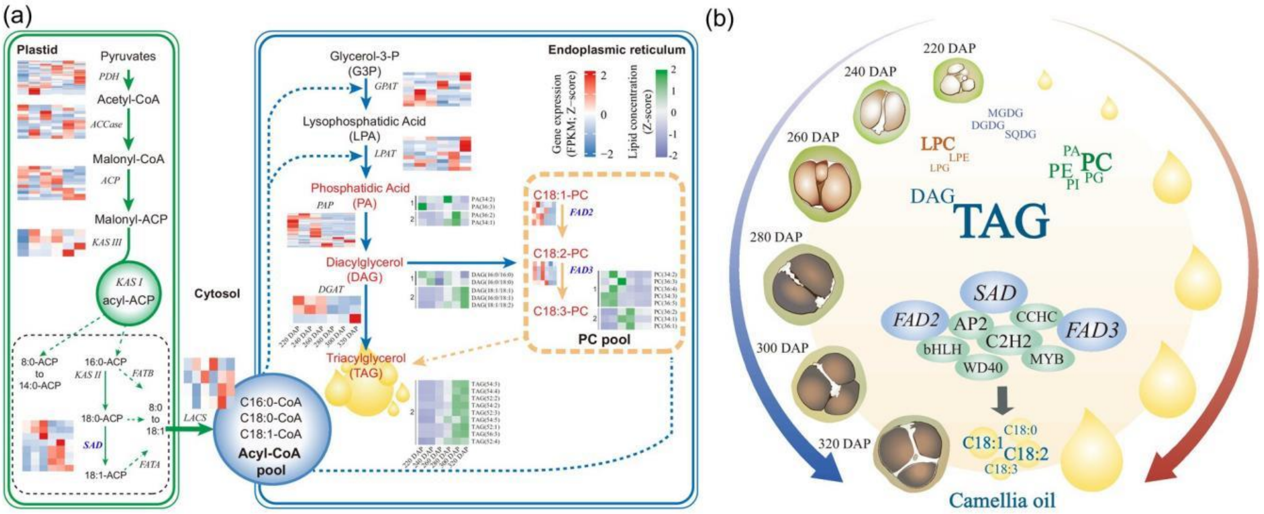

Figure 1 The regulatory network of key lipid metabolites in Changlin40 (Adopted from Zhu et al., 2024)

Image caption: (a) The metabolic pathway for lipid. The red-blue heatmap represents the expression levels of corresponding catalytic genes at different seed kernel developmental stages, while the green-purple heatmap represents the content of corresponding metabolites at different seed kernel developmental stages. PDH, Pyruvate dehydrogenase; ACCase, Acetyl-CoA carboxylase; ACP, Acyl carrier protein; KASIII, Beta-ketoacyl-(acyl-carrier-protein) synthase III; FATB, Fatty acyl-ACP thioesterase B; KASII, Beta-ketoacyl-(acyl-carrier-protein) synthase II; SAD, Stearoyl-ACP desaturase; FATA, Fatty acyl-ACP thioesterase A; LACS, Long-chain Acyl-CoA synthetase; GPAT, Glycerol-3-phosphate acyltransferase; LPAT, Lysophosphatidic acid acyltransferase; PAP, Purple acid phosphatase; DGAT, Diacylglycerol acyltransferase; FAD2, Fatty acid desaturase 2; FAD3, Fatty acid desaturase 3. (b) Schematic of *Camellia* oil biosynthesis in Changlin40 seed kernel (Adopted from Zhu et al., 2024)

2.2 Key genes and enzymes involved in triacylglycerol formation

Throughout the entire process of oil synthesis, many key genes and enzymes play significant roles. Through the joint study of transcriptome and proteome, it was found that in the later stage of seed maturation, the expressions of genes such as *ACCase*, KAS family, *SAD*, *FAD2/3*, *LPAAT*, *DGAT* and *PDAT* were all very high. All of these contribute to the massive accumulation of oils and fats (Ye et al., 2020; Yang et al., 2024). In addition, studies have also found that WRI1 transcription factors can interact with 17 enzymes related to lipid synthesis, and transcription factors such as MYB and ZIP also play a role in the regulatory process (Gong et al., 2020; Li et al., 2022). Population genome studies have pointed out that genes such as *SAD* and *KAS III* were selected by humans to have better alleles during the domestication process of *Camellia oleifera*, which helps to increase the yield and quality of oil (Lin et al., 2022; Zhu et al., 2024).

2.3 Tissue-specific and developmental regulation of oil content

The accumulation of oil is also related to the stage of seed development and different tissue parts. When seeds enter the mature stage, the oil content increases rapidly, and at this time, the expression of some key synthetic genes also rises simultaneously (Zhang et al., 2021; Yang et al., 2024). The expression levels of genes such as *SAD* and *FAD2* vary among different varieties and different parts, which leads to differences in lipid composition and content (Lin et al., 2018; Zhu et al., 2024). Furthermore, transcription factors such as MYB are specifically expressed at different developmental stages of seeds, and they can regulate lipid metabolism and the maturation process of seeds (Li et al., 2022). Through multiple omics studies, it has also been found that the expression of these genes and proteins is finely regulated by developmental stage and tissue type (Ye et al., 2020; Ye et al., 2021).

3 Epigenetic Regulation in Plants

3.1 DNA methylation: types, functions, and measurement

DNA methylation is one of the most important mechanisms in the epigenetic regulation of plants. It mainly occurs on the two bases of cytosine (C) and adenine (A). Methylation often occurs in the CG, CHG and CHH sequences (where H stands for A, T or C). It can prevent genes from being transcribed, thereby affecting gene expression and transposon activity (Liang et al., 2019). The changes in DNA methylation are regulated by two types of enzymes: methyltransferases are responsible for adding methyl groups, while demethylases remove them. This change is reversible (Chang et al., 2019; Tresas et al., 2025). DNA methylation often plays a key role during plant development, environmental adaptation or coping with adverse conditions (Abdulraheem et al., 2024). At present, researchers usually use some techniques to detect DNA methylation, such as methylation-sensitive digestion, methylation-specific PCR, and whole-genome methylation sequencing (Liang et al., 2019; Da Costa et al., 2024).

3.2 Histone modifications and chromatin remodeling in gene expression

In addition to DNA methylation, histone modification is also an important regulatory approach. It includes types such as methylation, acetylation and ubiquitination. These modifications are like a kind of “code” that can change the structure of chromatin and thereby affect whether genes are activated. For instance, methylation on H3K4 and H3K36 often makes genes more easily expressed, while methylation on H3K9 and H3K27 may silence genes (Xu et al., 2018). The activities of these modification enzymes can also be affected by the external environment or intracellular metabolism, thereby helping plants respond quickly to stress and even generate “memory” responses (Kumar et al., 2020). Furthermore, chromatin remodeling complexes can further affect whether genes are easily readable by moving the position of nucleosomes or changing their number (Tresas et al., 2025).

3.3 Non-coding RNAs and their roles in epigenetic signaling

Non-coding RNAs (ncRNAs) also play a significant role in epigenetic regulation. They include small interfering RNA (siRNA) and microRNA (miRNA), etc. siRNA can guide DNA methylation or silence certain genes after transcription, which can prevent transposon activity and also regulate gene expression (Ramirez-Prado et al., 2018). miRNA participates in regulating development and response to stress by cutting mRNA or blocking protein translation (Xu et al., 2018). These non-coding RNAs often work together with DNA methylation and histone modification to construct a complex regulatory network.

4 Environmental Effects on Epigenetic Marks

4.1 Altitude-related environmental changes: temperature, UV, and oxygen availability

The increase in altitude brings about some environmental pressures, such as lower temperatures, stronger ultraviolet rays, and less oxygen in the air. These changes can induce epigenetic modifications in the plant genome, such as DNA methylation and histone modifications. These modifications can regulate gene expression and help plants adapt to new environments (Baduel et al., 2024; Bogan and Yi, 2024). For instance, temperature changes can regulate gene activity by influencing the structure of chromatin. Ultraviolet rays may cause DNA damage, thereby bringing about epigenetic changes. And changes in oxygen concentration can also regulate genes related to REDOX (Varotto et al., 2020; Ali et al., 2022). These changes enable plants like *Camellia oleifera* to exhibit different traits at different altitudes and survive better (Miryeganeh, 2021; Bogan and Yi, 2024).

4.2 Stress-induced epigenetic responses in perennial woody plants

For perennial woody plants like *Camellia oleifera*, in the face of repeated or long-term stresses such as drought, low temperature and strong light, they will also regulate the expression of related genes by means such as DNA methylation, histone acetylation or methylation (Ali et al., 2022; Bogan and Yi, 2024). These changes not only enable plants to respond quickly to the environment, but also allow them to “remember” these stresses. When plants encounter similar conditions again, they can react faster and more effectively (He and Li, 2018; Baduel et al., 2024). This mechanism is more flexible than gene mutations, enabling plants to adapt more easily to complex environments and facilitating long-term survival (Varotto et al., 2020; Miryeganeh, 2021).

4.3 Transgenerational epigenetic memory and adaptation potential

Some epigenetic markers caused by the environment do not only function within a single plant but can also be passed between cell divisions or generations, which is called “epigenetic memory” (He and Li, 2018; Sobral and Sampedro, 2022; Baduel et al., 2024). In plants such as *Camellia oleifera*, this memory enables the next generation to perform better in similar environments, such as stronger growth ability or higher oil content (Anastasiadi et al., 2021; Brukhin and Albertini, 2021). However, whether this kind of memory is stable and hereditary is still influenced by many factors. Some epigenetic markers are “reset to zero” during sexual reproduction, but some studies have found that under asexual reproduction or specific conditions, some markers can be stably passed on (Radford, 2018; Anastasiadi et al., 2021; Jo and Nodine, 2024). This intergenerational transmission ability provides a new direction for the breeding and adaptability improvement of economic crops such as *Camellia oleifera*.

5 Altitude and Oil Accumulation in *Camellia oleifera*

5.1 Comparative oil profiles from high- and low-altitude plantations

In high-altitude areas, the fruit traits and oil quality of *Camellia oleifera* show significant differences. For instance, an analysis of 48 *Camellia oleifera* germplasm samples from the high-altitude areas in eastern Guizhou Province revealed significant variations in traits such as single fruit weight, fruit peel thickness, and the yields of fresh and dry seeds. Among them, the content of seed kernel oil has a significant positive correlation with the contents of palmitic acid and linoleic acid, but a negative correlation with the content of 11-eicosenoic acid. Some excellent individuals in high-altitude areas (such as QD-33, QD-34, QD-48) have high lipid content and good quality, and are very promising materials for breeding (Wan et al., 2024). In addition, by comparing the high-oil and low-oil *Camellia oleifera* seeds, it was found that there were also significant differences between the two in terms of oil content and fatty acid composition. Oleic acid accumulates more in high-oil seeds, which may be due to the coordinated work of multiple related genes, promoting the synthesis of oleic acid (Wu et al., 2019).

5.2 Influence of temperature and light on oil yield and quality

Temperature and light are important environmental factors affecting the oil accumulation and quality of *Camellia oleifera* seeds. Research has found that the expression of the LEA gene family is enhanced in the later stage of embryonic development, and a large amount of LEA protein accumulates. These proteins not only participate in seed development and oil accumulation, but also respond to stresses such as drought and shading. qPCR analysis further indicated that the expression of some *LEA* genes would increase under simulated drought or different light conditions. This indicates that changes in temperature and light may alter lipid synthesis and accumulation by affecting the expression of related genes (Liu et al., 2023).

5.3 Potential links between altitude-specific stress and epigenetic change

In high-altitude environments, low temperatures and strong ultraviolet rays are often present. These factors may affect the expression of genes related to oil synthesis, and thus also influence the final accumulation of oils. The expression changes of the *LEA* gene under drought and light variations also suggest that this regulatory process may involve epigenetic mechanisms, such as DNA methylation or histone modification. These mechanisms can help *Camellia oleifera* adapt to environmental stress and regulate oil accumulation simultaneously (Liu et al., 2023). Furthermore, the situation of multi-gene co-expression in high-oil *Camellia oleifera* also indicates that epigenetic regulation is likely to play an important role in this process (Wu et al., 2019).

6 Epigenetic Modifications Associated with Oil Traits

6.1 Differential DNA methylation regions (DMRs) related to fatty acid biosynthesis genes

DNA methylation is an important epigenetic mode for regulating gene expression. Fatty acids are the main components of oils and fats, and their synthesis process is controlled by related genes. The methylation status of these genes will directly affect the accumulation of fats. Studies have found that different types of fatty acids, such as polyunsaturated fatty acids and short-chain fatty acids, can affect the methylation levels of these genes, thereby altering gene expression (Chung and Kim, 2024; Ediriweera and Sandamalika, 2024). In oil crops, key genes in the fatty acid synthesis pathway exhibit Differential DNA methylation regions (DMRs), which are closely related to the content and composition of oils. This also provides molecular-level evidence for explaining the differences in lipid properties between high-altitude and low-altitude *Camellia oleifera*.

6.2 Expression changes in oil-related genes mediated by epigenetic variation

In addition to DNA methylation, histone modification can also affect lipid synthesis. Epigenetic modifications can control the synthesis and accumulation of fats by regulating the expression of important transcription factors and metabolic enzymes. For instance, histone H3 lysine 4 trimethylation (H3K4me3) is associated with some regulatory factors of fatty acid synthesis, including WRINKLED1, ABI3 and FUS3, which regulate glycolysis and fatty acid synthesis pathways and thereby affect lipid accumulation (Moreno-Pérez et al., 2021). In addition, fatty acids themselves can in turn regulate the epigenetic state of genes, thus forming the mutual influence between metabolism and epigenetics (Chung and Kim, 2024; Ediriweera and Sandamalika, 2024).

6.3 Integration of methylome, transcriptome, and lipidome data

To gain a comprehensive understanding of the relationship between epigenetics and lipid traits, a combined multi-omics analysis is highly effective. Combining the data of the methylome, transcriptome and lipidome can more systematically identify the key methylation regions, differentially expressed genes and metabolites related to lipid accumulation (Moreno-Pérez et al., 2021; Wang and Yamaguchi, 2024). For instance, through the joint analysis of the methylome and transcriptome, the relationship between the methylation status of certain fatty acid synthesis genes and their expression levels can be directly observed. Lipidome data, on the other hand, can reveal the final accumulation of lipids. This integrated analysis method provides a new idea for studying the molecular mechanism of oil differences in *Camellia oleifera* under different altitude conditions.

7 Techniques for Studying Epigenetics in Woody Oil Crops

7.1 Bisulfite sequencing and whole-genome methylome profiling

Bisulfite sequencing (BS-seq for short) is currently one of the most commonly used and highest-resolution methods for studying DNA methylation. After treatment with bisulfite, the unmethylated cytosine will transform into uracil, while the methylated cytosine will remain unchanged. This method can help us detect the changes at every methylation site across the entire genome. Using it to analyze the methylation patterns of oil woody plants in different environments (such as high altitude and low altitude) can provide valuable data to study the relationship between epigenetic regulation and oil accumulation (Mladenov et al., 2021; Agius et al., 2023; Singh et al., 2023). In addition to BS-seq, there are also methods such as MSAP (methylation-sensitive amplification polymorphism) that can be used to detect methylation differences between different populations or families (Albaladejo et al., 2019).

7.2 ATAC-seq, ChIP-seq and their limitations in tree species

ATAC-seq and ChIP-seq are two other commonly used high-throughput technologies. ATAC-seq can quickly determine where the chromatin is open. ChIP-seq can be used to locate specific histone modification regions or identify the positions where transcription factors bind to DNA. These techniques are widely used in model plants and some crops. However, in woody oil crops, experiments and data analysis have become more difficult because samples are not easy to obtain, and there are many cell types and complex tissues (Chachar et al., 2022; Xue et al., 2025). Furthermore, the cell walls of woody plants are very thick, making it difficult to extract cell nuclei and perform chromatin immunoprecipitation, which also affects the promotion of these techniques.

7.3 Emerging single-cell and third-generation epigenomic tools

In recent years, single-cell omics (such as single-cell transcriptomics and single-cell epigenomics) and third-generation sequencing technologies (such as nanopore sequencing and single-molecule real-time sequencing) have begun to be used in the epigenetic research of woody plants. Single-cell technology can clearly observe the differences among different cells in the same tissue and is helpful for understanding how complex traits such as lipid accumulation are regulated at the cellular level (Figure 2) (Liang et al., 2023; Xue et al., 2025). The third-generation sequencing technology can directly read the methylation information of long DNA fragments, making up for the drawback that the second-generation sequencing can only view short fragments. This provides a new tool for studying the epigenetic mechanisms in the complex genomes of woody plants (Yang et al., 2022). Although these technologies are not yet mature, their application prospects in woody oil crops like *Camellia oleifera* are worth looking forward to.

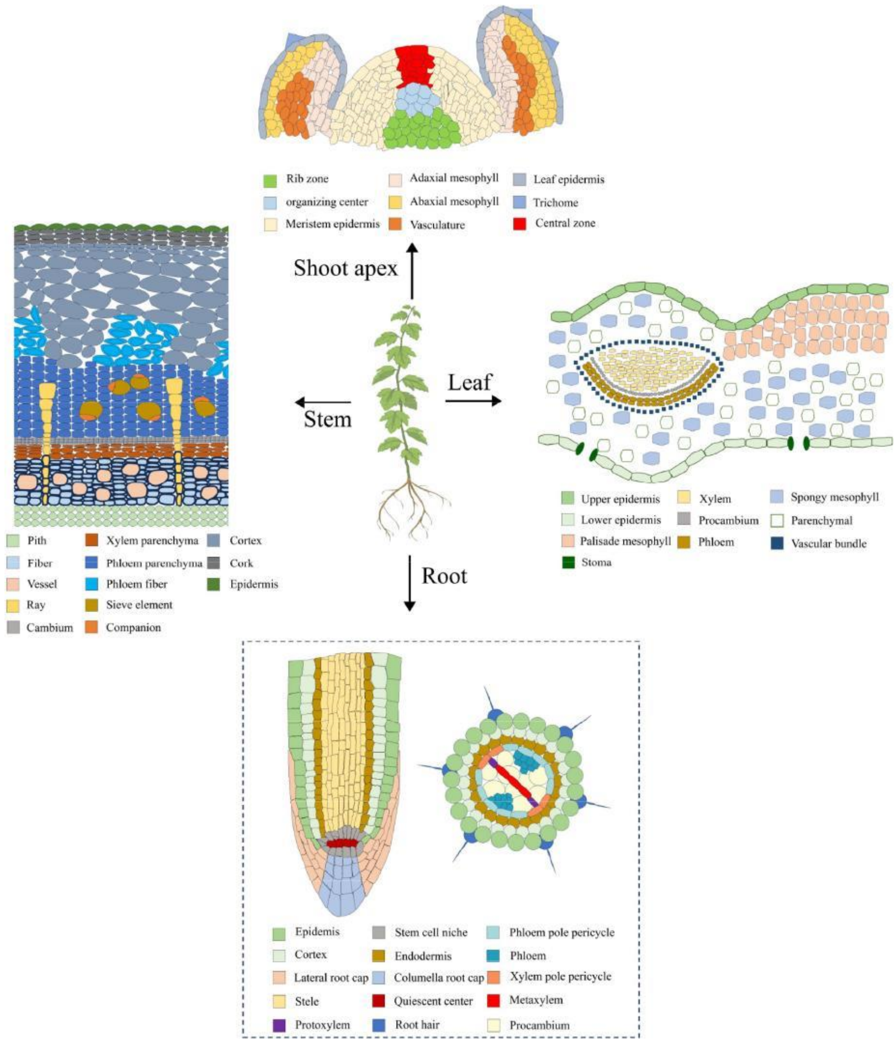

Figure 2 Cell types of roots, stems, leaves, and shoot apexes. The dotted lines indicate the absence of reported studies in woody plants (Adopted from Liang et al., 2023)

8 Case Study: Comparative Epigenomic Analysis of High- vs. Low-Altitude *Camellia oleifera*

8.1 Field sampling and phenotypic description of populations

The research team selected some natural populations of *Camellia oleifera* from both high-altitude and low-altitude areas, systematically collected seed samples, and recorded phenotypic data such as the growth status of the plants, fruit size, and seed oil content. It was found that *Camellia oleifera* under different ecological environments showed significant differences in fruit development, oil accumulation and seed maturation. *Camellia oleifera* populations in high-altitude areas generally have higher oil content and more ideal fatty acid composition (Yang et al., 2024; Kong et al., 2025).

8.2 Key findings on methylation patterns and gene expression differences

Through the analysis of whole-genome transcriptome and other multi-omics data, it was found that there were a large number of genes with significant expression differences in the early, middle and late stages of seed development in both high-oil and low-oil varieties. These genes were involved in multiple directions such as fatty acid synthesis, lipid accumulation and hormone signaling pathways (Wu et al., 2019; Yang et al., 2024). Among the varieties with high oil content, upstream genes such as *HAD*, *EAR* and *KASI* are continuously highly expressed, providing sufficient precursors for oleic acid synthesis. The expression level of the *SAD* gene is also relatively high, which is conducive to the accumulation of oleic acid. The expression of downstream genes such as *FAD2* and *FAD3* is relatively low, reducing the transformation and consumption of oleic acid (Wu et al., 2019; Yang et al., 2024). In addition, some transcription factors such as MADS-box and bHLH also show specific expression patterns in lipid synthesis regulation.

8.3 Epigenetic signatures linked to superior oil accumulation in highland trees

The *Camellia oleifera* population in high-altitude areas also exhibits epigenetic characteristics associated with high oil content accumulation. Joint multi-omics analysis revealed that transcription factors such as WRI1, MYB, and ZIP could regulate the expression of key lipid synthesis genes, and these expression activities were also closely related to certain specific DNA methylation modifications and transcriptional variations (Gong et al., 2020; Ye et al., 2021). Furthermore, through QTL mapping and association analysis, researchers also found that some specific SNP loci on genes such as *SAD* and *FAD2* were significantly associated with the high oil trait, and these loci could be used as markers in molecular breeding (Lin et al., 2019; Lin et al., 2024). That is to say, these epigenetic and gene-level changes work together to create the excellent oil accumulation capacity of high-altitude *Camellia oleifera*.

9 Applications and Breeding Implications

9.1 Epigenetic markers for oil yield trait selection

In recent years, genomic and transcriptomic studies have identified many key genes related to lipid accumulation, such as *SAD*, *FAD2* and *WRI1*, etc. (Wu et al., 2019; Gong et al., 2020; Yang et al., 2024). Through genome-wide association study (GWAS) and QTL mapping, researchers identified some SNP and InDel variations closely related to oil content and fatty acid composition. These variations can be used as molecular markers for screening *Camellia oleifera* materials with high oil content and high-quality fatty acids (Lin et al., 2019; Lin et al., 2024). Furthermore, transcriptional variations and alternative splicing also provide new epigenetic marker resources (Gong et al., 2020). The application of these markers can improve the efficiency of molecular marker-assisted selection (MAS) and cultivate *Camellia oleifera* varieties with high oil yield more precisely.

9.2 Integration of epigenetics into molecular breeding programs

Multiomics studies such as transcriptomics, proteomics and metabolomics have shown that the process of lipid accumulation involves the joint regulation of multiple genes (Wu et al., 2019; Ye et al., 2021; Yang et al., 2024). If epigenetic information such as DNA methylation, histone modification, and non-coding RNA is also incorporated, a more comprehensive understanding of the genetic mechanism of lipid accumulation can be achieved (Gong et al., 2020). By integrating the QTL mapping results, candidate genes and epigenetic regulatory networks, truly important regulatory factors can be screened out. This is very helpful for promoting gene editing and precision breeding in *Camellia oleifera*, and can also accelerate the breeding speed of superior varieties (Ye et al., 2023; Lin et al., 2024).

9.3 Potential for environment-specific oil crop improvement

Different ecological environments such as high altitude and low altitude have significant effects on lipid accumulation and the expression of related genes (Wu et al., 2019; Ye et al., 2021; Yang et al., 2024). Epigenetic variation is an important way for plants to adapt to the environment, and it can provide theoretical support for breeding *Camellia oleifera* varieties adapted to specific environments (Liu et al., 2023; Ye et al., 2023). If the epigenetic markers and regulatory genes related to environmental response can be identified, there is hope to breed new types of *Camellia oleifera* that are adapted to different ecological regions and have stronger oil accumulation capacity, and achieve targeted improvement and regionalized efficient cultivation of *Camellia oleifera*.

10 Concluding Remarks

Epigenetic variations such as DNA methylation and histone modification can regulate gene expression, thereby influencing the external traits of plants and their ability to adapt to the environment. In *Camellia oleifera*, the expression of genes related to oil accumulation and lipid metabolism is closely related, and the expression of these genes is affected by environmental factors, such as altitude and climate. Epigenetic mechanisms provide a possible molecular basis for *Camellia oleifera* to regulate lipid synthesis in different altitude environments, and also help explain the reasons for the differences in lipid content and fatty acid composition.

Although epigenetic regulation has great potential in crop improvement, its practical application in woody crops such as *Camellia oleifera* still faces many difficulties. For instance, it remains uncertain whether epigenetic modifications can be stably inherited, and the interaction between the environment and the genome is also very complex. Currently, there is a lack of a unified research method. Moreover, under field conditions, it is also difficult to assess whether these apparent effects are stable. To transform the research achievements in the laboratory into practical breeding applications, it is also necessary to address the issues of stability and controllability across generations and in different environments.

Future research can focus on developing more efficient and standardized detection and editing technologies to precisely regulate the epigenetic status of genes related to lipid synthesis. Through epigenomic editing technology, it is possible to breed new varieties of *Camellia oleifera* that are more adaptable to climate change and "climate-smart", which can not only increase yields but also improve the quality of oils. Further promoting the application of epigenetic markers in *Camellia oleifera* breeding can also provide new solutions for addressing global climate change and ensuring oil supply.

Acknowledgments

The authors appreciate the modification suggestions from two anonymous peer reviewers on the manuscript of this study.

Conflict of Interest Disclosure

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

References

Abdulraheem M., Xiong Y., Moshood A., Cadenas-Pliego G., Zhang H., and Hu J., 2024, Mechanisms of plant epigenetic regulation in response to plant stress: recent discoveries and implications, Plants, 13(2): 163.
https://doi.org/10.3390/plants13020163

Agius D., Kapazoglou A., Avramidou E., Baránek M., Carneros E., Caro E., Castiglione S., Cicatelli A., Radanović A., Ebejer J., Gackowski D., Guarino F., Gulyás A., Hidvégi N., Hoenicka H., Inácio V., Johannes F., Karalija E., Lieberman-Lazarovich M., Martinelli F., Maury S., Mladenov V., Morais-Cecílio L., Pečinka A., Tani E., Testillano P., Todorov D., Valledor L., and Vassileva V., 2023, Exploring the crop epigenome: a comparison of DNA methylation profiling techniques, Frontiers in Plant Science, 14: 1181039.
https://doi.org/10.3389/fpls.2023.1181039

Albaladejo R., Parejo-Farnés C., Rubio-Pérez E., Nora S., and Aparicio A., 2019, Linking DNA methylation with performance in a woody plant species, Tree Genetics and Genomes, 15: 15.
https://doi.org/10.1007/s11295-019-1325-x

Ali S., Khan N., and Tang Y., 2022, Epigenetic marks for mitigating abiotic stresses in plants, Journal of Plant Physiology, 275: 153740.
https://doi.org/10.1016/j.jplph.2022.153740

Anastasiadi D., Venney C., Bernatchez L., and Wellenreuther M., 2021, Epigenetic inheritance and reproductive mode in plants and animals, Trends in Ecology and Evolution, 36(12): 1124-1140.
https://doi.org/10.1016/j.tree.2021.08.006

Baduel P., Sammarco I., Barrett R., Coronado-Zamora M., Crespel A., Díez-Rodríguez B., Fox J., Galanti D., González J., Jueterbock A., Wootton E., and Harney E., 2024, The evolutionary consequences of interactions between the epigenome, the genome and the environment, Evolutionary Applications, 17(7): e13730.
https://doi.org/10.1111/eva.13730

Bogan S., and Yi S., 2024, Potential role of DNA methylation as a driver of plastic responses to the environment across cells, organisms, and populations, Genome Biology and Evolution, 16(2): evae022.
https://doi.org/10.1093/gbe/evae022

Brukhin V., and Albertini E., 2021, Epigenetic modifications in plant development and reproduction, Epigenomes, 5(4): 25.
https://doi.org/10.3390/epigenomes5040025

Chachar S., Chachar M., Riaz A., Shaikh A., Li X., Li X., Guan C., and Zhang P., 2022, Epigenetic modification for horticultural plant improvement comes of age, Scientia Horticulturae, 292: 110633.
https://doi.org/10.1016/j.scienta.2021.110633

Chang Y., Zhu C., Jiang J., Zhang H., Zhu J., and Duan C., 2019, Epigenetic regulation in plant abiotic stress responses, Journal of Integrative Plant Biology, 62(5): 563-580.
https://doi.org/10.1111/jipb.12901

Chung M., and Kim B., 2024, Fatty acids and epigenetics in health and diseases, Food Science and Biotechnology, 33(14): 3153-3166.
https://doi.org/10.1007/s10068-024-01664-3

Da Costa G., Cerqueira A., De Brito C., Mielke M., and Gaiotto F., 2024, Epigenetics regulation in responses to abiotic factors in plant species: a systematic review, Plants, 13(15): 2082.

Ediriweera M., and Sandamalika W., 2024, The epigenetic impact of fatty acids as DNA methylation modulators, Drug Discovery Today, 30(2): 104277.
https://doi.org/10.1016/j.drudis.2024.104277

Gong W., Song Q., Ji K., Gong S., Wang L., Chen L., Zhang J., and Yuan D., 2020, Full-length transcriptome from *Camellia oleifera* seed provides insight into the transcript variants involved in oil biosynthesis, Journal of Agricultural and Food Chemistry, 68(49): 14670-14683.
https://doi.org/10.1021/acs.jafc.0c05381

He Y., and Li Z., 2018, Epigenetic environmental memories in plants: establishment, maintenance, and reprogramming, Trends in Genetics, 34(11): 856-866.
https://doi.org/10.1016/j.tig.2018.07.006

Jo L., and Nodine M., 2024, To remember or forget: Insights into the mechanisms of epigenetic reprogramming and priming in early plant embryos, Current Opinion in Plant Biology, 81: 102612.
https://doi.org/10.1016/j.pbi.2024.102612

Kong Q., Chen T., Wang H., Zheng S., Wang H., Liang H., Zhou L., Yang H., Jiang X., Ding C., and Feng S., 2025, Variation of *Camellia oleifera* fruit traits and nutritional constituents in seed oil during development and post-harvest, Scientia Horticulturae, 339: 113903.
https://doi.org/10.1016/j.scienta.2024.113903

Kumar R.M.S., Wang Y., Zhang X., Cheng H., Sun L., He S., and Hao F., 2020, Redox components: key regulators of epigenetic modifications in plants, International Journal of Molecular Sciences, 21(4): 1419.
https://doi.org/10.3390/ijms21041419

Li S., Huang H., Ma X., Hu Z., Li J., and Yin H., 2022, Characterizations of MYB transcription factors in *Camellia oleifera* reveal the key regulators involved in oil biosynthesis, Horticulturae, 8(8): 742.
https://doi.org/10.3390/horticulturae8080742

Liang S., Li Y., Chen Y., Huang H., Zhou R., and Ma T., 2023, Application and prospects of single-cell and spatial omics technologies in woody plants, Forestry Research, 3: 27.
https://doi.org/10.48130/FR-2023-0027

Liang Z., Riaz A., Chachar S., Ding Y., Du H., and Gu X., 2019, Epigenetic modifications of mRNA and DNA in plants, Molecular Plant, 13(1): 14-30.
https://doi.org/10.1016/j.molp.2019.12.007

Lin P., Chai J., Wang A., Zhong H., and Wang K., 2024, High-density genetic map construction and quantitative trait locus analysis of fruit- and oil-related traits in *Camellia oleifera* based on double digest restriction site-associated DNA sequencing, International Journal of Molecular Sciences, 25(16): 8840.
https://doi.org/10.3390/ijms25168840

Lin P., Wang K., Wang Y., Hu Z., Yan C., Huang H., Ma X., Cao Y., Long W., Liu W., Li X., Fan Z., Li J., Ye N., Ren H., Yao X., and Yin H., 2022, The genome of oil-Camellia and population genomics analysis provide insights into seed oil domestication, Genome Biology, 23: 14.
https://doi.org/10.1186/s13059-021-02599-2

Lin P., Wang K., Zhou C., Xie Y., Yao X., and Yin H., 2018, Seed transcriptomics analysis in *Camellia oleifera* uncovers genes associated with oil content and fatty acid composition, International Journal of Molecular Sciences, 19(1): 118.
https://doi.org/10.3390/ijms19010118

Lin P., Yin H., Yan C., Yao X., and Wang K., 2019, Association genetics identifies single nucleotide polymorphisms related to kernel oil content and quality in *Camellia oleifera*, Journal of Agricultural and Food Chemistry, 67(9): 2547-2562.
https://doi.org/10.1021/acs.jafc.8b03399

Liu L., Xu J., Chen J., Yang B., Yang C., Yang Y., Wang K., Zhuo R., and Yao X., 2023, The *LEA2* gene sub-family: characterization, evolution, and potential functions in *Camellia oleifera* seed development and stress response, Scientia Horticulturae, 322: 112392.
https://doi.org/10.1016/j.scienta.2023.112392

Miryeganeh M., 2021, Plants' epigenetic mechanisms and abiotic stress, Genes, 12(8): 1106.
https://doi.org/10.3390/genes12081106

Mladenov V., Fotopoulos V., Kaiserli E., Karalija E., Maury S., Baránek M., Segal N., Testillano P., Vassileva V., Pinto G., Nagel M., Hoenicka H., Miladinović D., Gallusci P., Vergata C., Kapazoglou A., Abraham E., Tani E., Gerakari M., Sarri E., Avramidou E., Gašparović M., and Martinelli F., 2021, Deciphering the epigenetic alphabet involved in transgenerational stress memory in crops, International Journal of Molecular Sciences, 22(13): 7118.
https://doi.org/10.3390/ijms22137118

Moreno-Pérez A., Santos-Pereira J., Martins-Noguerol R., DeAndrés-Gil C., Troncoso-Ponce M., Venegas-Calerón M., Sánchez R., Garcés R., Salas J., Tena J., and Martínez-Force E., 2021, Genome-wide mapping of histone H3 lysine 4 trimethylation (H3K4me3) and its involvement in fatty acid biosynthesis in sunflower developing seeds, Plants, 10(4): 706.
https://doi.org/10.3390/plants10040706

Radford E., 2018, Exploring the extent and scope of epigenetic inheritance, Nature Reviews Endocrinology, 14: 345-355.
https://doi.org/10.1038/s41574-018-0005-5

Ramirez-Prado J., Abulfaraj A., Rayapuram N., Benhamed M., and Hirt H., 2018, Plant immunity: from signaling to epigenetic control of defense, Trends in Plant Science, 23(9): 833-844.

Singh V., Ahmed S., Saini D., Gahlaut V., Chauhan S., Khandare K., Kumar A., Sharma P., and Kumar J., 2023, Manipulating epigenetic diversity in crop plants: techniques, challenges and opportunities, Biochimica et Biophysica Acta- General subjects, 1868(2): 130544.
https://doi.org/10.1016/j.bbagen.2023.130544

Sobral M., and Sampedro L., 2022, Phenotypic, epigenetic, and fitness diversity within plant genotypes, Trends in Plant Science, 27(9): 843-846.
https://doi.org/10.1016/j.tplants.2022.06.008

Tresas T., Isaioglou I., Roussis A., and Haralampidis K., 2025, A brief overview of the epigenetic regulatory mechanisms in plants, International Journal of Molecular Sciences, 26(10): 4700.
https://doi.org/10.3390/ijms26104700

Varotto S., Tani E., Abraham E., Krugman T., Kapazoglou A., Melzer R., Radanović A., and Miladinović D., 2020, Epigenetics: possible applications in climate-smart crop breeding, Journal of Experimental Botany, 71(17): 5223-5236.
https://doi.org/10.1093/jxb/eraa188

Wan X., Sun D., Nie Y., Wang Q., Zhang T., Wang R., Li F., Zhao X., and Gao C., 2024, Analysis and evaluation of *Camellia oleifera* Abel. germplasm fruit traits from the high-altitude areas of East Guizhou Province, China, Scientific Reports, 14: 18440.
https://doi.org/10.1038/s41598-024-69454-9

Wang X., and Yamaguchi N., 2024, Cause or effect: probing the roles of epigenetics in plant development and environmental responses, Current Opinion in Plant Biology, 81: 102569.
https://doi.org/10.1016/j.pbi.2024.102569

Wu B., Ruan C., Han P., Ruan D., Xiong C., Ding J., and Liu S., 2019, Comparative transcriptomic analysis of high- and low-oil *Camellia oleifera* reveals a coordinated mechanism for the regulation of upstream and downstream multigenes for high oleic acid accumulation, 3 Biotech, 9: 257.
https://doi.org/10.1007/s13205-019-1792-7

Xu Y., Zhang L., and Wu G., 2018, Epigenetic regulation of juvenile-to-adult transition in plants, Frontiers in Plant Science, 9: 1048.
https://doi.org/10.3389/fpls.2018.01048

Xue Y., Cao X., Chen X., Deng X., Deng X., Ding Y., Dong A., Duan C., Fang X., Gong L., Gong Z., Gu X., He C., He H., He S., He X., He Y., He Y., Jia G., Jiang D., Jiang J., Lai J., Lang Z., Li C., Li Q., Li X., Liu B., Liu B., Luo X., Qi Y., Qian W., Ren G., Song Q., Song X., Tian Z., Wang J., Wang Y., Wu L., Wu Z., Xia R., Xiao J., Xu L., Xu Z., Yan W., Yang H., Zhai J., Zhang Y., Zhao Y., Zhong X., Zhou D., Zhou M., Zhou Y., Zhu B., Zhu J., and Liu Q., 2025, Epigenetics in the modern era of crop improvements, Science China Life sciences, 68: 1570-1609.

Yang D., Wang R., Lai H., He Y., Chen Y., Xun C., Zhang Y., and He Z., 2024, Comparative transcriptomic and lipidomic analysis of fatty acid accumulation in three *Camellia oleifera* varieties during seed maturing, Journal of Agricultural and Food Chemistry, 72(32): 18257-18270.
https://doi.org/10.1021/acs.jafc.4c03614

Yang L., Zhang P., Wang Y., Hu G., Guo W., Gu X., and Pu L., 2022, Plant synthetic epigenomic engineering for crop improvement, Science China Life Sciences, 65(11): 2191-2204.
https://doi.org/10.1007/s11427-021-2131-6

Yao X.Z., Tang H., Jiao Y.J., He Y.M., and Lu L.T., 2024, Genomic insights into the evolutionary history of the *Camellia* genus: comprehensive analysis of phylogenetic relationships, speciation, and adaptive evolution, Journal of Tea Science Research, 14(1): 64-78.
https://doi.org/10.5376/jtsr.2024.14.0007

Ye C., He Z., Peng J., Wang R., Wang X., Fu M., Zhang Y., Wang A., Liu Z., Jia G., Chen Y., and Tian B., 2023, Genomic and genetic advances of oiltea-camellia (*Camellia oleifera*), Frontiers in Plant Science, 14: 1101766.

Ye Z., Wu Y., Muhammad Z., Yan W., Yu J., Zhang J., Yao G., and Hu X., 2020, Complementary transcriptome and proteome profiling in the mature seeds of *Camellia oleifera* from Hainan Island, PLoS One, 15(2): e0226888.
https://doi.org/10.1371/journal.pone.0226888

Ye Z., Yu J., Yan W., Zhang J., Yang D., Yao G., Liu Z., Wu Y., and Hou X., 2021, Integrative iTRAQ-based proteomic and transcriptomic analysis reveals the accumulation patterns of key metabolites associated with oil quality during seed ripening of *Camellia oleifera*, Horticulture Research, 8: 157.
https://doi.org/10.1038/s41438-021-00591-2

Zhang F., Li Z., Zhou J., Gu Y., and Tan X., 2021, Comparative study on fruit development and oil synthesis in two cultivars of *Camellia oleifera*, BMC Plant Biology, 21: 348.
https://doi.org/10.1186/s12870-021-03114-2

Zhu H., Wang F., Xu Z., Wang G., Hu L., Cheng J., Ge X., Liu J., Chen W., Li Q., Xue F., Liu F., Li W., Wu L., Cheng X., Tang X., Yang C., Lindsey K., Zhang X., Ding F., Hu H., Hu X., and Jin S., 2024, The complex hexaploid oil-Camellia genome traces back its phylogenomic history and multi- omics analysis of Camellia oil biosynthesis, Plant Biotechnology Journal, 22(10): 2890-2906.
https://doi.org/10.1111/pbi.14412