

Research Insight

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Genetic Basis of Oil Content in Camellia Species

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Abstract The primary objective of this study was to elucidate the genetic basis of oil content in various *Camellia* species, with a particular focus on identifying key genes and genetic markers associated with oil biosynthesis and fatty acid composition. The study identified several significant genetic markers and differentially expressed genes (DEGs) associated with oil content and quality in *Camellia* species. In *Camellia oleifera*, single nucleotide polymorphisms (SNPs) and insertion-deletion (InDel) markers within key fatty acid desaturase genes were found to be significantly associated with oil content and composition, explaining up to 17.93% of phenotypic variance. Transcriptomic analyses revealed critical genes involved in lipid metabolism and oil accumulation, such as stearyl-ACP desaturases (SADs) and fatty acid desaturase 2 (FAD2), which were differentially expressed during seed development. Additionally, integrative proteomic and transcriptomic analyses identified key metabolites and co-expressed genes involved in oil quality during seed ripening. Comparative studies between high- and low-oil cultivars highlighted the coordinated regulation of upstream and downstream genes essential for high oleic acid accumulation. The findings from this study provide valuable genetic markers and insights into the molecular mechanisms underlying oil biosynthesis in *Camellia* species. These discoveries have significant implications for the genetic improvement of oil content and quality in *Camellia* cultivars through marker-assisted selection and genetic engineering.

Keywords *Camellia oleifera*; Oil biosynthesis; Fatty acid composition; Genetic markers; Transcriptomics

1 Introduction

Camellia species, particularly *Camellia oleifera*, *Camellia lanceoleosa*, and *Camellia chekiangoleosa*, are renowned for their high-quality seed oils, which are rich in unsaturated fatty acids and beneficial secondary metabolites (Lin et al., 2019; Gong et al., 2022; Shen et al., 2022). These species are widely cultivated in regions such as Southern China and Southeast Asia, where they serve as significant sources of edible oil (Ye et al., 2023). The oil extracted from *Camellia* seeds is not only used for culinary purposes but also finds applications in cosmetics and as a lubricant, highlighting its versatility and economic importance (Gong et al., 2020).

The oil content in *Camellia* species is of paramount importance due to its high levels of oleic acid, which is beneficial for human health (Lin et al., 2018). The presence of unsaturated fatty acids makes *Camellia* oil a desirable alternative to other vegetable oils, promoting its use in various industrial applications, including food production and pharmaceuticals (Yao et al., 2016; Lin et al., 2019). Additionally, the genetic diversity and adaptability of *Camellia* species to different environmental conditions enhance their agricultural value, making them a reliable crop for oil production (Barreiro et al., 2021). Recent genomic studies have provided insights into the genes involved in oil biosynthesis, offering potential for genetic improvement and increased oil yield (Lu et al., 2022; Shen et al., 2022).

This study aims to explore the genetic basis of oil content in various *Camellia* species by examining the allelic diversity of key genes associated with oil production. By leveraging recent advancements in genomic and transcriptomic analyses, this study seeks to identify genetic markers and candidate genes that influence oil content and quality. The findings will contribute to the development of marker-assisted selection strategies to enhance oil yield and quality in *Camellia* species, thereby supporting their agricultural and industrial applications.

2 Camellia Species and Oil Composition

2.1 Key camellia species cultivated for oil production

Camellia oleifera and *Camellia sinensis* are two primary species cultivated for oil production. *Camellia oleifera*, commonly known as the tea oil camellia, is extensively grown in China for its seeds, which are a significant source of edible oil rich in unsaturated fatty acids (Zeng et al., 2014; Lin et al., 2018; Lin et al., 2019). *Camellia sinensis*, primarily known for tea production, also contributes to oil production, although it is less prominent compared to *C. oleifera* (Xia et al., 2014).

2.2 Differences in oil composition among species

The oil composition varies significantly among different *Camellia* species. *Camellia oleifera* oil is renowned for its high oleic acid content, which constitutes a substantial portion of its fatty acid profile (Lin et al., 2018; Wu et al., 2019; Gong et al., 2020). This high oleic acid content is attributed to the coordinated expression of genes involved in fatty acid biosynthesis, such as stearoyl-ACP desaturases (SADs) and fatty acid desaturase 2 (FAD2) (Lin et al., 2018; Wu et al., 2019). In contrast, other species like *Camellia sinensis* may have different fatty acid profiles, with varying levels of oleic, linoleic, and palmitic acids (Xia et al., 2014).

2.3 Role of genetics in influencing oil content and quality

Genetics play a crucial role in determining the oil content and quality in *Camellia* species. Studies have identified several key genes associated with oil biosynthesis and fatty acid composition. For instance, in *Camellia oleifera*, genes such as *CoSAD* and *CoFAD2* are critical for the synthesis of oleic acid and other fatty acids (Zeng et al., 2014; Lin et al., 2019; Wu et al., 2019). Single nucleotide polymorphisms (SNPs) and insertion-deletion (InDel) variations within these genes have been linked to variations in oil content and quality (Lin et al., 2019). Transcriptomic analyses have further revealed differentially expressed genes (DEGs) during seed development stages, which are associated with lipid metabolism and oil accumulation (Lin et al., 2018; Gong et al., 2020).

Moreover, the expression levels of genes like *CoFBA* and *CoSAD* have been shown to correlate with oil content, suggesting that enhancing the expression of these genes could improve oil yield and quality in transgenic plants (Zeng et al., 2014). Comparative studies between high- and low-oil cultivars of *C. oleifera* have also highlighted the coordinated regulation of multiple genes that ensure high oleic acid accumulation (Wu et al., 2019).

3 Genetic Determinants of Oil Biosynthesis in Camellia

3.1 Overview of key genes involved in fatty acid biosynthesis

Fatty acid biosynthesis in *Camellia* species is regulated by a variety of genes that play crucial roles in the metabolic pathways leading to oil production. Key genes identified include stearoyl-ACP desaturases (SADs) and fatty acid desaturase 2 (FAD2), which are critical for the synthesis of oleic acid, a major component of *Camellia* oil (Yao et al., 2016; Lin et al., 2018; 2019). SADs are responsible for the desaturation of stearic acid to oleic acid, while FAD2 further desaturates oleic acid to linoleic acid. The expression levels of these genes are tightly regulated during seed development, with higher SAD activity and lower FAD2 activity correlating with increased oleic acid content (Yao et al., 2016; Lin et al., 2018; 2019).

3.2 Analysis of metabolic pathways regulating oil content

The metabolic pathways regulating oil content in *Camellia* species involve complex networks of gene interactions and regulatory mechanisms. Transcriptomic and proteomic analyses have revealed that genes involved in lipid metabolism, such as those encoding enzymes for fatty acid synthesis and modification, are differentially expressed during seed development (Figure 1) (Lin et al., 2018; Gong et al., 2020; Ye et al., 2021). Key metabolic pathways include the glycolysis pathway, which provides precursors for fatty acid synthesis, and the triacylglycerol biosynthesis (TAGBS) pathway, which is crucial for the final assembly of storage lipids (Yao et al., 2016; Li et al., 2022). Additionally, the α -linolenic acid metabolism pathway and glutathione metabolism have been identified as important for oil quality and accumulation (Ye et al., 2021).

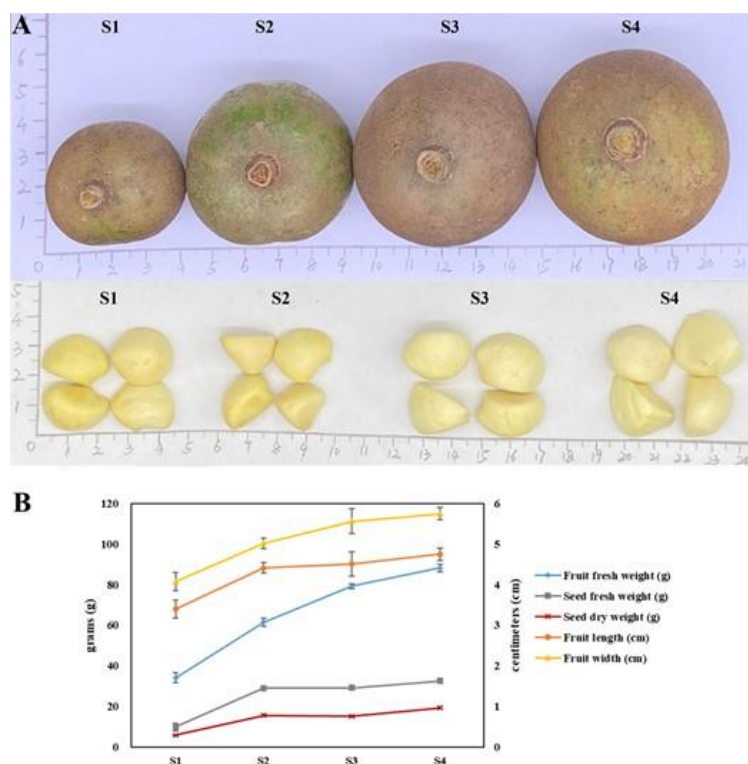


Figure 1 Development of *C. oleifera* seeds. A Phenotypic characterization of *C. oleifera* seeds in four growth periods. S1, nutrition synthesis stage; S2, fat accumulation stage; S3, mature stage; and S4, late mature stage. B Changes in morphological indexes of developing fruits and seeds. Data represent the mean values from three biological replicates, and error bars indicate standard deviations (Adopted from Ye et al., 2021)

3.3 Importance of regulatory genes (e.g., transcription factors) in oil synthesis

Regulatory genes, particularly transcription factors, play a significant role in the regulation of oil biosynthesis in *Camellia* species. MYB transcription factors, for instance, have been identified as key regulators of lipid metabolism and seed maturation (Li et al., 2022). These transcription factors can activate or repress the expression of target genes involved in fatty acid biosynthesis and accumulation. Other important transcription factors include WR11, which interacts with multiple genes encoding enzymes critical for oil synthesis, and ABI3, FUS3, and LEC1, which are associated with seed development and oil accumulation (Wu et al., 2019; Gong et al., 2020). The coordinated expression of these transcription factors ensures the efficient regulation of oil biosynthesis pathways, leading to high oil content in *Camellia* seeds.

4 Genomic Studies on Oil Content Variation

4.1 Summary of genome-wide association studies (GWAS) on oil content in camellia

Genome-wide association studies (GWAS) have been instrumental in identifying genetic variations associated with oil content in various plant species, including *Camellia*. In *Camellia oleifera*, a significant GWAS identified 362 single-nucleotide polymorphisms (SNPs) within four key genes coding for fatty acid desaturases, which are crucial for oil production. This study found 90 significant marker-trait associations, with six SNP markers validated in a hybrid population, explaining up to 17.93% of the phenotypic variance in oil content (Lin et al., 2019). These findings highlight the potential of GWAS in uncovering genetic markers that can be used for marker-assisted selection to improve oil content in *Camellia* species (Ghidoli et al., 2023).

4.2 Insights from QTL mapping in camellia species

Quantitative trait loci (QTL) mapping has provided valuable insights into the genetic control of oil content in *Camellia* species. Although specific QTL mapping studies in *Camellia* are limited, analogous research in related species like *Brassica napus* and *Camelina sativa* has demonstrated the effectiveness of this approach. For instance, in *Brassica napus*, stable QTLs for seed oil content were identified on chromosome A07, with one major QTL,

qA07.SOC, being consistently detected across multiple environments (Zhao et al., 2022). Similarly, in *Camelina sativa*, QTL mapping identified loci associated with oil content and fatty acid composition, aiding in the breeding of high-yielding varieties (Li et al., 2021). These studies suggest that similar QTL mapping efforts in *Camellia* could reveal critical loci for oil content improvement.

4.3 Identification of genetic markers linked to high oil content traits

The identification of genetic markers linked to high oil content traits is crucial for the genetic improvement of *Camellia* species. In *Camellia oleifera*, SNP markers within genes coding for fatty acid desaturases have been linked to oil content and quality. Specifically, six SNP markers from the genes *Cofad2-A*, *CoSAD1*, and *CoSAD2* were validated and found to be significantly associated with oil content traits (Lin et al., 2019). Additionally, transcriptomic analyses have identified differentially expressed genes (DEGs) involved in lipid metabolism and oil biosynthesis, providing further candidate markers for breeding programs (Lin et al., 2018; Gong et al., 2020). These genetic markers and DEGs offer valuable tools for marker-assisted selection and the development of *Camellia* varieties with enhanced oil content.

5 Candidate Genes for Oil Quality and Quantity

5.1 Identification of specific genes associated with oil composition

The identification of specific genes associated with oil composition in *Camellia* species has been a focal point of recent research. In *Camellia oleifera*, key genes such as *CoSAD* and *Cofad2*, which code for fatty acid desaturases, have been linked to oil content and fatty acid composition. These genes were found to contain significant single nucleotide polymorphisms (SNPs) and insertion-deletion (InDel) variations that correlate with oil traits, explaining a substantial proportion of phenotypic variance (Lin et al., 2019). Additionally, transcriptomic analyses have identified differentially expressed genes (DEGs) involved in lipid metabolism, such as stearoyl-ACP desaturases (SADs) and fatty acid desaturase 2 (FAD2), which play crucial roles in the biosynthesis of oleic acid (Lin et al., 2018; Wu et al., 2019).

5.2 Functional analysis of candidate genes in oil accumulation

Functional analysis of candidate genes has provided insights into their roles in oil accumulation. For instance, the coordinated high expression of upstream genes like HAD, EAR, and KASI has been shown to increase the levels of C16:0-ACP, a precursor for oleic acid biosynthesis. Concurrently, the high expression of SAD genes accelerates oleic acid synthesis, while the low expression of downstream genes such as FAD2, FAD3, FAD7, FAD8, and FAE1 reduces the conversion of oleic acid to other fatty acids, ensuring its accumulation (Wu et al., 2019). Proteomic studies have also highlighted the importance of enzymes like diacylglycerol acyltransferase and glyceraldehyde-3-phosphate dehydrogenase in oil biosynthesis, further validating the roles of these candidate genes (Ye et al., 2021; Gong et al., 2022).

5.3 Comparative analysis of gene expression in high vs. low oil-yielding camellia varieties

Comparative transcriptomic analyses between high and low oil-yielding *Camellia* varieties have revealed significant differences in gene expression profiles. High oil-yielding varieties exhibit a coordinated upregulation of genes involved in fatty acid biosynthesis and oil accumulation, such as SAD and WRI1, while low oil-yielding varieties show higher expression of genes involved in fatty acid degradation (Wu et al., 2019; Ye et al., 2020). These studies have identified critical transcription factors, including ABI3, FUS3, LEC1, and WRI1, which regulate the expression of multiple genes associated with oil biosynthesis and accumulation (Wu et al., 2019). Additionally, the expression patterns of lipid biosynthesis genes have been shown to correlate with the stages of seed development, further emphasizing the dynamic regulation of oil content in *Camellia* species (Lin et al., 2018; Gong et al., 2020).

6 Advances in Genomic Selection and Breeding for Oil Content

6.1 Applications of genomic selection techniques to improve oil yield

Genomic selection techniques have significantly advanced the breeding of *Camellia* species for enhanced oil yield. The identification of single nucleotide polymorphisms (SNPs) and insertion-deletion (InDel) markers associated

with oil content and fatty acid composition in *Camellia oleifera* has been a pivotal development. These markers have been validated in various populations, demonstrating their potential for marker-assisted selection to improve oil content and quality (Lin et al., 2019). Additionally, the sequencing and assembly of genomes from multiple oiltea-camellia species have provided a comprehensive understanding of the genetic basis of oil yield, facilitating the identification of key genes related to oil production (Table 1) (Peng et al., 2020; Ye et al., 2023).

Table 1 Comparison of assembled genomes of oiltea-camellia (Adopted from Ye et al., 2023)

Assembly quality	C. Chekiangoleosa	C. Oleifera var. Nanyongensis	C. Lanceoleosa
Genome size (Gb)	2.73	2.89	2.75
N50 of contigs (Mb)	1.92	1.00	1.20
N50 of scaffolds (Mb)	185.30	185.36	186.43
GC content (%)	39.23	37.51	40.55
Sequences anchored to chromosomes (%)	97.4	91.33	91.85
BUSCO (%)	93.6	90.10	95.42
LAI (%)	11.53	-	12.45
Heterozygosity rate (%)	-	2.52	2.20
Number of predicted genes	64608	42426	54172

Note: BUSCO, benchmarking universal single-copy orthologs; LAI, long-terminal-repeat assembly index (Adopted from Ye et al., 2023)

6.2 Recent breeding strategies incorporating genetic insights

Recent breeding strategies have increasingly incorporated genetic insights to enhance oil content in *Camellia* species. For instance, the association analysis of key genes coding for fatty acid desaturases in *Camellia oleifera* has revealed significant marker-trait associations, which can be utilized in breeding programs to select for desirable oil traits (Lin et al., 2019). Moreover, transcriptomic analyses have identified differentially expressed genes (DEGs) involved in fatty acid biosynthesis and metabolism, providing targets for genetic manipulation to improve oil yield (Xia et al., 2014; Xie and Wang, 2018). The integration of multi-omic approaches, including genomics, transcriptomics, and metabolomics, has further accelerated the breeding process by enabling a more precise evaluation of genetic resources and the mining of key genes associated with important traits (Ye et al., 2023).

6.3 Role of CRISPR/Cas9 and other gene-editing tools in optimizing oil traits

CRISPR/Cas9 and other gene-editing tools have revolutionized the optimization of oil traits in *Camellia* species. The CRISPR/Cas9 system has been successfully employed to target and mutate specific genes involved in fatty acid biosynthesis, such as the *FAD2* gene in *Camelina sativa*, resulting in a significant increase in oleic acid content and a decrease in less desirable polyunsaturated fatty acids (Jiang et al., 2017; Morineau et al., 2017; Lee et al., 2021). This gene-editing approach has also been used to create combinatorial mutants in hexaploid *Camelina sativa*, providing a large diversity of lipid profiles and enhancing the genetic variability available for breeding (Aznar-Moreno and Durrett, 2017; Morineau et al., 2017). Furthermore, the identification of potential CRISPR/Cas9 editing sites in the *Camellia sinensis* genome has laid the groundwork for future functional studies and molecular breeding efforts aimed at improving oil traits (Li et al., 2023).

7 Environmental and Epigenetic Influences on Oil Content

7.1 Impact of environmental factors on oil yield in camellia species

Environmental conditions play a significant role in determining the oil yield and composition in *Camellia* species. Studies have shown that factors such as temperature, soil type, and water availability can dramatically influence both the quantity and quality of oil produced. For instance, research on *Camelina sativa*, a close relative of *Camellia*, demonstrated that growing conditions significantly affect oil quantity and fatty acid composition, highlighting the importance of environmental factors in oil biosynthesis (Brock et al., 2020). Similarly, the environmental niche assessment of various *Camelina* species revealed that different environmental conditions lead to significant variations in seed oil content and composition, suggesting that careful management of growing conditions could optimize oil yield in *Camellia* species (Brock et al., 2020).

7.2 Epigenetic modifications affecting gene expression related to oil content

Epigenetic modifications, such as DNA methylation and histone modification, can influence gene expression without altering the DNA sequence, thereby affecting oil content in *Camellia* species. Transcriptomic analyses have identified differentially expressed genes (DEGs) associated with oil biosynthesis at various developmental stages, indicating that epigenetic regulation plays a crucial role in oil accumulation (Zeng et al., 2014; Lin et al., 2018). For example, the expression of key genes involved in lipid metabolism and fatty acid biosynthesis, such as stearoyl-ACP desaturases (SADs) and fatty acid desaturase 2 (FAD2), is tightly regulated during seed development, suggesting that epigenetic mechanisms may modulate these genes to enhance oil production (Zeng et al., 2014; Lin et al., 2018). Additionally, the identification of alternative splicing events and long noncoding RNAs (lncRNAs) in *Camellia oleifera* seeds further supports the role of epigenetic modifications in regulating oil biosynthesis (Gong et al., 2020).

7.3 Interaction between genetics and environmental conditions in oil biosynthesis

The interaction between genetic factors and environmental conditions is critical in determining the oil biosynthesis pathways in *Camellia* species. Genetic studies have identified single nucleotide polymorphisms (SNPs) and insertion-deletion (InDel) variations in key genes associated with oil content and fatty acid composition, which are influenced by environmental factors. For instance, the association analysis of four key genes coding for fatty acid desaturases in *Camellia oleifera* revealed significant marker-trait associations, indicating that both genetic and environmental factors contribute to oil yield (Lin et al., 2019). Moreover, integrative analyses combining transcriptomic and proteomic data have shown that the expression of genes involved in oil biosynthesis is modulated by environmental conditions, such as temperature and nutrient availability, further emphasizing the complex interplay between genetics and the environment (Ye et al., 2021). These findings suggest that optimizing both genetic selection and environmental management could enhance oil production in *Camellia* species.

8 Future Directions and Research Opportunities

8.1 Emerging technologies in genomics and bioinformatics for oil trait analysis

The advent of advanced genomic and bioinformatics technologies has opened new avenues for the analysis of oil traits in *Camellia* species. Techniques such as single-molecule long-read isoform sequencing (Iso-Seq) and RNA-Seq have been instrumental in uncovering the complexity of the transcriptome and identifying key genes involved in oil biosynthesis and accumulation. The integration of these technologies with gas chromatography has provided a comprehensive understanding of the oil biosynthesis pathways at different developmental stages (Gong et al., 2020). Additionally, the use of association genetics to identify single nucleotide polymorphisms (SNPs) related to kernel oil content and quality has shown promise for marker-assisted selection in breeding programs (Lin et al., 2019). The development of chromosome-level genome assemblies, as seen in *Camellia lanceoleosa* and *Camellia chekiangoleosa*, provides valuable resources for understanding genome evolution and the genetic basis of oil traits (Gong et al., 2022; Shen et al., 2022). Future research should focus on leveraging these genomic tools to explore the allelic diversity of key genes and their regulatory networks, which could significantly enhance the efficiency of breeding high oil-yielding *Camellia* varieties.

8.2 Prospective research on understudied camellia species with oil potential

While significant progress has been made in understanding the oil biosynthesis pathways in *Camellia oleifera*, other *Camellia* species with potential oil yield remain understudied. For instance, *Camellia chekiangoleosa* and *Camellia reticulata* have shown promise due to their high-quality seed oil and unique genetic traits (Yao et al., 2016; Xie and Wang, 2018). Comparative transcriptomic analyses have identified genes responsible for fruit count and oil yield, which could be targeted in breeding programs to enhance oil production (Xie and Wang, 2018). Additionally, the first chromosome-level genome sequence of *Camellia chekiangoleosa* provides a foundation for exploring the genetic basis of oil biosynthesis and improving oil traits through genetic manipulation (Shen et al., 2022). Future research should aim to conduct comprehensive genomic and transcriptomic studies on these understudied species to identify novel genes and pathways that contribute to oil accumulation. This could lead to the development of new *Camellia* cultivars with enhanced oil yield and quality.

8.3 Challenges and opportunities in breeding high oil-yielding camellia varieties

Breeding high oil-yielding *Camellia* varieties presents several challenges and opportunities. One of the main challenges is the complex polyploidization and large genome size of *Camellia* species, which complicates genetic analysis and breeding efforts (Gong et al., 2020). However, recent advances in genomic technologies, such as the assembly of reference genomes and multi-omic studies, have provided new insights into the genetic basis of oil traits (Ye et al., 2023). The identification of differentially expressed genes (DEGs) and transcription factors involved in oil biosynthesis and fatty acid accumulation has revealed coordinated mechanisms that regulate these processes (Lin et al., 2018; Wu et al., 2019). Additionally, the use of quantitative proteomics and transcriptomics has highlighted the impact of environmental factors, such as harvesting time, on oil content and quality (Wang et al., 2022). Future breeding programs should focus on integrating these genomic and proteomic data to develop molecular markers for marker-assisted selection and to identify key genes for genetic engineering. By addressing these challenges and leveraging the opportunities presented by emerging technologies, it is possible to accelerate the breeding of high oil-yielding *Camellia* varieties and improve the economic viability of *Camellia* oil production.

9 Conclusioning Remarks

The genetic basis of oil content in *Camellia* species, particularly *Camellia oleifera*, has been extensively studied, revealing several key genetic factors. Transcriptomic and proteomic analyses have identified differentially expressed genes (DEGs) and proteins associated with lipid metabolism and oil biosynthesis. Key genes such as stearoyl-ACP desaturases (SADs) and fatty acid desaturase 2 (FAD2) have been implicated in the regulation of oleic acid levels during seed development. Additionally, MYB transcription factors have been identified as crucial regulators of seed oil biosynthesis, with specific MYB genes showing significant expression during seed maturation. Single nucleotide polymorphisms (SNPs) within genes like CoSAD and CoFAD2 have also been linked to variations in oil content and quality, providing markers for genetic selection. Furthermore, the expression of genes involved in metabolic pathways such as fatty acid metabolism and flavonoid biosynthesis has been shown to correlate with oil accumulation and quality.

The genetic insights gained from these studies have significant implications for *Camellia* breeding programs. The identification of SNP markers associated with high oil content and quality can facilitate marker-assisted selection, enabling the development of superior *Camellia* cultivars with enhanced oil yield and composition. The understanding of key regulatory genes such as MYB transcription factors and their role in lipid metabolism can be leveraged to manipulate gene expression through genetic engineering, potentially increasing oil production. Additionally, the comprehensive transcriptomic and proteomic data provide a valuable resource for identifying candidate genes for targeted breeding and biotechnological interventions aimed at improving oil biosynthesis pathways. The integration of these genetic findings into breeding programs can accelerate the development of high-yielding, high-quality oil-producing *Camellia* varieties, thereby enhancing the economic and nutritional value of *Camellia* oil.

In conclusion, the genetic insights into oil content in *Camellia* species have provided a deeper understanding of the molecular mechanisms underlying oil biosynthesis and accumulation. These findings not only elucidate the complex genetic regulation of oil production but also offer practical applications for improving *Camellia* oil yield and quality through advanced breeding techniques and genetic engineering. The continued exploration of genetic factors and their interactions will be crucial for further advancements in *Camellia* oil production, ultimately contributing to the sustainable development of this valuable oil crop.

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Conflict of Interest Disclosure

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

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