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Identification and Functional Validation of Key Genes Regulating Flowering Time in Tea

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Abstract This study discusses the genetic basis and molecular mechanism of when tea plants flower, and summarizes the progress made in identifying and verifying key genes, such as transcription factors, genes in hormone signaling pathways, and genes that can integrate flowering signals. Research has found that some major regulatory genes, such as *FT*, *SOC1*, *GI* and *CO*, play a key role in integrating light duration and temperature signals. Some non-coding RNAs, such as miRNA and lncRNA, are also involved in the detailed regulation of flowering time. Gene editing tools like CRISPR-Cas9 have also begun to be used to verify the functions of these genes. This study aims to provide a foundation for molecular breeding of tea plants, enabling people to more accurately control the flowering time and thereby increase yield and planting efficiency.

Keywords Tea (*Camellia sinensis*); Flowering time; Gene regulation; Non-coding RNA; Functional validation

1 Introduction

The tea (*Camellia sinensis*) is an important economic crop. When it flowers will directly affect the formation of seeds, the progress of breeding and the yield of tea (Liu, 2024). If the flowering time is appropriate, it can not only balance the growth and fruiting of tea, but also improve the success rate of pollination and increase the number of seeds, thereby making the yield of tea gardens higher (Lin et al., 2022; Naik et al., 2025). However, flowering consumes a lot of water and nutrients. If tea flower too early or too late, it may affect normal growth and eventually lead to a decline in tea quality and yield (Tian et al., 2021; Xu et al., 2022).

Tea is perennial plants, which are different from annual crops. Its flowering time is influenced by many factors, such as genetics, hormone levels, light duration, temperature and nutrition, etc. (Fan et al., 2024; Naik et al., 2025). Weather changes, low temperatures in winter or rain may all cause unstable flowering time of tea, thereby affecting the yield (Lin et al., 2022; Fan et al., 2024). In addition, the flowering of tea is also closely related to the dormancy of winter buds. Currently, scientists are still studying the signals and genes involved (Liu et al., 2022; Xu et al., 2022). Although exogenous hormones or chemical agents can regulate the flowering period, the working principles and safety of these methods are not yet clear (Ionescu et al., 2016; Lin et al., 2022).

This study identified some key genes that affect the flowering time of tea, conducted functional verification on them, and combined transcriptome analysis, hormone signaling pathways and experimental verification to find out the important factors regulating the flowering period. These findings are helpful for better controlling the flowering time of tea. This study aims to provide theoretical support and molecular tools for future breeding and increased production.

2 Biological Basis of Flowering in Tea Plants

2.1 Floral transition phases in *Camellia sinensis*

The flowering process of the tea plant (*Camellia sinensis*) generally includes several stages: flower induction, flower bud differentiation and flower organ differentiation. Through morphological observation, researchers can clearly distinguish the time points of flower induction and flower bud differentiation. The gene expression of different varieties varies at these stages. At present, many genes related to flowering have been identified, such as

PRR7, *GI*, *GID1B*, *GID1C* related to flower induction, and *LFY*, *PNF*, *PNY*, etc. related to flower bud formation (Liu et al., 2020a). There are also some key genes, such as *SOC1*, *HD3A* and *LFY*, which play major roles throughout the flower formation process (Xu et al., 2022). Furthermore, transcriptome analysis also revealed that the expression levels of some transcription factors, such as WRKY, ERF, bHLH, MYB and MADS-box, would increase during flowering period changes, indicating that they are important for flowering period regulation (Liu et al., 2017).

2.2 Seasonal and developmental cues influencing flowering

The flowering of tea plants is jointly influenced by seasonal factors (such as light duration and temperature) and the plant's own hormones. Studies have found that during the development of tea plant flowers, many genes are related to the biological clock and the autonomous flowering pathway. Hormone levels also change significantly during the flowering period. For example, the contents of auxin and gibberellin fluctuate up and down, and the related synthesis and signaling pathway genes also change accordingly (Xu et al., 2022). Some specific genes, such as *CsFLC1* (a member of the MADS-box family), have high expression levels during winter dormancy and flowering periods and may be involved in regulating seasonal flowering (Liu et al., 2022). Furthermore, miR156 controls the flowering time by influencing *SPL-like* genes (such as *CsSPL1*), and the higher the expression of miR156, the later the flowering time. The genes of the PMEI family (such as *CsPMEI2* and *CsPMEI4*) can also accelerate the flowering process, and they function through the autonomous flowering pathway (Wang et al., 2022).

2.3 Anatomical and morphological features of tea flowering

Tea plants have bisexual flowers, which means that the same flower contains both stamens and pistils. The structure of flowers is the same as that of general angiosperms, including sepals, petals, stamens and pistils. During the development of floral organs, many secondary metabolites accumulate, such as flavonoids and anthocyanins. These substances are mainly concentrated in the petals and stamens (Chen et al., 2018). During pollen development, the content changes of certain flavonols (such as derivatives of kaempferol) are highly related to the viability of pollen (Shi et al., 2021). When tea plants flower, nitrogen and sugars in the leaves are redistributed and transported to the flowers, which need these substances to complete development (Fan et al., 2019). In addition, the formation of flowers is also closely related to ethylene, other hormone signals, and the regulation of certain transcription factors (Liu et al., 2020b).

3 Environmental and Hormonal Control of Flowering Time

3.1 Influence of photoperiod and temperature

The flowering time of tea plants is influenced by environmental factors such as the duration of light (photoperiod) and temperature. Research has found that many genes controlling flowering are related to circadian rhythms and autonomous flowering pathways. Among them, the *SOC1* gene plays a very crucial role in the development process of flowers (Xu et al., 2022). There are also *FLC* genes like *CsFLC1*, which have high expression levels during plant dormancy and flowering in winter. This suggests that it may be the key for plants to sense low temperature and control flowering time (Liu et al., 2022). Environmental signals affect proteins like FT through photosensitive proteins and biological clocks. FT moves to the top of plants and initiates flowering (Freytes et al., 2021). Temperature changes and vernalization processes can also regulate these signals, thereby making the flowering time more adaptable to seasonal changes (Lee et al., 2023).

3.2 Roles of phytohormones

During the flowering process of tea plants, the content of hormones in their bodies and the expression of genes related to hormones will also change. Studies have found that more than 200 genes related to hormone synthesis and nearly 200 genes related to hormone signal transduction are involved during flower development (Xu et al., 2022). Hormones, such as gibberellin (GA), abolic acid (ABA), ethylene and auxin (IAA), can affect flower formation by regulating key genes such as *SOC1*, *FT* and *LFY* (Liu et al., 2017; Liu et al., 2022). The use of exogenous hormones can also affect flowering. For example, spraying ethephon can cause some flowers and flower buds to drop and regulate the expression of the ethylene receptor gene *CsETR* (Zhang et al., 2022). In addition, the use of hydrocyanamide in tea oil tea can make it flower earlier. This effect is related to hormones, MAPK pathway, oxygen metabolism, etc. in the plant (Lin et al., 2022).

3.3 Environmental stressors and their impact on flowering

When the environment is not ideal, such as drought, high salt content or reduced soil nutrients, the flowering time of tea will also be affected. These pressures can alter the flowering process by regulating photoperiod and hormone signaling pathways (Lee et al., 2023). Under difficult conditions, plants may flower earlier or later to increase the success rate of reproduction (Cho et al., 2017). These environmental signals and photoperiodic control mechanisms are interconnected, and genes like *FT* act as the “bridge” in the middle, simultaneously participating in responding to stress and controlling flowering (Riboni et al., 2014). In addition, environmental stress may also indirectly affect the expression of genes related to flowering by altering glucose metabolism, reactive oxygen species levels, etc. within plants (Liu et al., 2017; Cho et al., 2018; Lin et al., 2022).

4 Identification of Flowering Time Genes in Tea

4.1 Genome and transcriptome resources for gene discovery

In recent years, genomic information and a large amount of transcriptome data of the tea (*Camellia sinensis*) have laid the foundation for identifying the genes that control the flowering time. By conducting transcriptome sequencing on tea plants of different varieties and at different developmental stages, researchers identified a total of 92 core genes related to flower development, covering the entire process from flower bud formation to full flower opening (Xu et al., 2022). Meanwhile, through genomic alignment, they also identified 401 and 356 genes related to flowering respectively from small-leaf and large-leaf tea plants, all of which are candidates for subsequent functional studies (Liu et al., 2020a).

4.2 Homology-based identification using model species

Researchers also identified multiple homologous genes in tea plants by leveraging known flowering genes in model plants such as Arabidopsis thaliana and rice. For instance, *CsFLC1* in tea plants belongs to the MADS-box gene family. It is very similar to *FLC* in *Arabidopsis thaliana*. Experimental results show that it can affect the flowering time of tea plants and is also related to the dormancy of buds in winter (Figure 1) (Liu et al., 2022). In addition, *CsWRKY7* is also very similar to *AtWRKY7* and *AtWRKY15* of *Arabidopsis thaliana*. Overexpression of it will cause delayed flowering of plants and reduce the expression of key genes such as *FT*, *AP1* and *LFY* at the same time (Chen et al., 2019). The regulatory modules miR156 and SPL also have similar functions in tea plants. For example, Csn-miR156d can regulate FT, AP1, FUL and SOC1 by targeting CsSPL1, thereby delaying the flowering time.

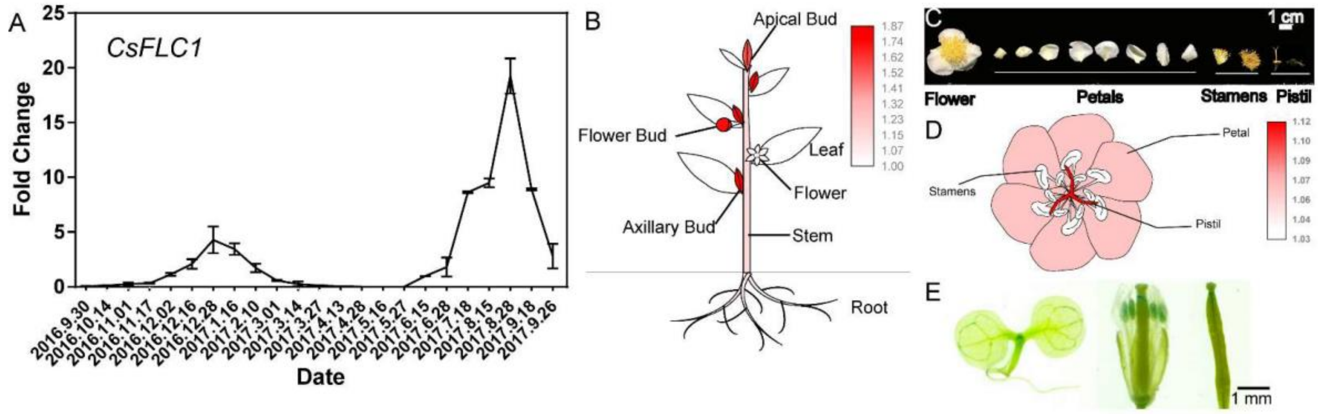

Figure 1 Expression patterns of *CsFLC1* (Adopted from Liu et al., 2022)

Image caption: (A) Expression of *CsFLC1* in axillary or flower buds of tea plant throughout the year. (B) Different tissue expression of *CsFLC* in tea plant. (C) Various parts of flowers of tea plant. (D) Expression patterns of *CsFLC1* in different parts of flowers in tea plant. (E) GUS staining of *pCsFLC1::GUS* transgenic *Arabidopsis thaliana* (Adopted from Liu et al., 2022)

4.3 High-throughput screening strategies (RNA-seq, WGCNA, GWAS)

Nowadays, high-throughput technologies such as RNA-seq and WGCNA have been widely used to screen genes related to flowering in tea plants. Researchers analyzed transcriptome data of different developmental stages and different varieties and found that genes such as *SOC1*, *LFY*, *GI* and *PRR7* showed obvious expression trends at the flower induction and flower bud differentiation stages (Liu et al., 2020a). Furthermore, differential expression analysis also identified hundreds of genes related to hormone synthesis and signal transduction, constituting a relatively complex hormone regulatory network. It is speculated that genes such as *MYC*, *FT*, *SOC1* and *LFY* are the cores among them (Xu et al., 2022). Although GWAS methods are not widely used in tea plants, previous studies, through genome-wide association analysis combined with functional validation, have discovered genes like *CsMADS27* that play an important role in the dormancy and germination processes of tea plants (Hao et al., 2024).

5 Key Gene Families Involved in Flowering Regulation

5.1 CONSTANS-like and FT/TFL1 family genes

CONSTANS (*CO*) and *FLOWERING LOCUS T* (*FT*) are very important regulatory genes in the photoperiodic pathway. Research has found that in tea plants and their close relatives, these two genes and their similar genes play a key role in the regulatory network of circadian rhythms and photcycles, and can regulate flower bud differentiation and flowering time. For instance, *Unigene0001842* (that is, CO) and *Unigene0084708* (that is, FT) have been identified as the core genes regulating the flowering time of tea plants. They can also work together with genes such as *GI* and *PRR* that regulate circadian rhythms to help initiate flower bud differentiation (Guo et al., 2022). In addition, genes like *HD3A* in the FT/TFL1 family also occur during the flower development process of tea plants, while *SOC1*, as a downstream integration factor, plays a leading role throughout the flowering process (Xu et al., 2022).

5.2 MADS-box genes and floral integrators

The MADS-box gene is also very important in the regulation of flowering in tea plants. *CsFLC1* is a gene similar to FLC in the MADS-box family, and its expression level is very high when plants are dormant and preparing to flower in winter. It can affect the expression of flower-related genes such as *SOC1*, *AGL42*, *SEP3* and *AP3*, and can also change the flowering time by regulating hormone signals (Liu et al., 2022). There is another key gene, *CsMADS27*, which also belongs to the MADS-box family. It can control the dormancy and germination of tea plants. This gene is regulated by *CsCBF1* and *CsZHD9*, and controls the expression of downstream *CsDJC23* (Hao et al., 2024). These MADS-box genes can also work together with transcription factors such as WRKY, MYB, and bHLH to jointly regulate flower development and secondary metabolism (Liu et al., 2017; Sun et al., 2019).

5.3 Circadian clock and vernalization-related genes

The flowering of tea plants is also regulated by some genes in the circadian rhythm and vernalization pathway. Genes such as *PRR7*, *GI* and *LHY* are closely related to flower bud differentiation, and their expression levels increase under stress (Liu et al., 2020a; Guo et al., 2022). *CsFLC1* can not only control flowering but also regulate the dormancy of tea plants in winter, indicating that the spring pathway also plays an important role in tea plants (Liu et al., 2022). Furthermore, flowering integration genes such as *SOC1* and *LFY*, like an intersection point, can integrate various signals from photoperiod, hormones and vernalization, and ultimately precisely control when flowering occurs (Xu et al., 2022).

6 Regulatory Networks and Molecular Pathways

6.1 Integrative regulatory models in tea flowering

When tea plants flower is determined by many levels of molecular mechanisms. These mechanisms include miRNA, transcription factors, hormone signals and energy metabolism, etc. miR156 and miR172 can control the expression of key genes such as *SPL* and *AP2*, thereby affecting the expression of *SOC1*. This forms two main pathways: miR156-SPL and miR172-AP2, which jointly participate in the regulation of flowering time (Wang, 2014; Fan et al., 2024). In addition, genes such as *PRR*, *LHY*, *GI*, *CO* and *FT* can receive light and temperature signals in the environment and pass on this information to promote flower bud formation (Guo et al., 2022). The flowering of tea plants also requires a large amount of energy and carbohydrates. These substances, in combination with hormone signals, jointly construct a very complex regulatory network (Tang et al., 2023).

6.2 Crosstalk between hormone signaling and gene expression

Different plant hormones play different roles in the flowering process of tea plants. Some hormone levels increase, such as zeaxanthin (cZ), brassinolide (BL), salicylic acid (SA), ACC and jasmonic acid (JA), which can accelerate flowering. Hormones such as ABA, tZR, dh-Z and IP can delay flowering (Fan et al., 2024). These hormones can also interact with some key genes, helping to control the process of flower bud differentiation and flowering. The study also found that hormones in old leaves can guide flower bud development by regulating energy metabolism and rhythm genes (Guo et al., 2022). When the bud begins to grow, zeaxin plays a core role. It can activate many growth-promoting factors and help the bud grow rapidly (Tang et al., 2023).

6.3 Epigenetic mechanisms and chromatin remodeling

In addition to genes and hormones, epigenetics and chromatin conditions can also affect the flowering of tea plants. Small RNA molecules like miR156 and miR172 can participate in epigenetic regulation by controlling the genes they target (Wang, 2014; Fan et al., 2024). In addition, some transcription factors, such as bHLH, MYB and NAC families, also regulate the expression of genes related to secondary metabolism and flowering, change the structure of chromatin, and thereby affect the activity level of genes (Tai et al., 2018). These mechanisms work together to ensure that tea plants can enter the flowering stage at the appropriate time (Li et al., 2015; Wang et al., 2025).

7 Case Study: Functional Characterization of *CsaFT1* in Tea Flowering Regulation

7.1 Identification and cloning of *CsaFT1*

CsaFT1 is a FLOWERING gene in tea plants. It belongs to the FT (FLOWERING LOCUS T) family and is an important member that regulates the flowering time of plants. Researchers identified this gene by analyzing the genome and transcriptome of the tea plant and obtained its complete cDNA sequence using molecular cloning technology. In multiple studies, *FT* genes are considered to play a key role in the development of tea plant flowers and are expressed at different developmental stages, indicating that they are involved in flower bud initiation and the formation of floral organs (Figure 2) (Liu et al., 2020a; Xu et al., 2022).

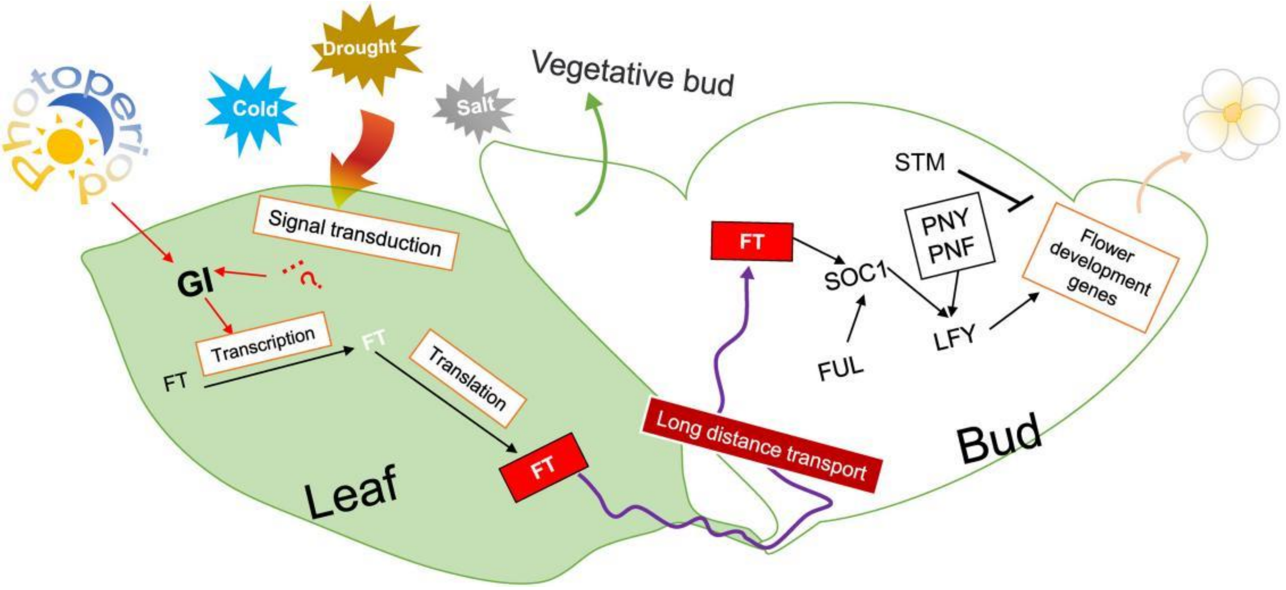

Figure 2 Putative gene regulatory network of flowering in tea plants (Adopted from Liu et al., 2020a)

Image caption: Arrows indicate positive control, perpendicular lines indicate negative control, orange frames indicate physiological processes, other frames indicate proteins, white letters without frames indicate mRNA and black letters without frames indicate genes (Adopted from Liu et al., 2020a)

7.2 Expression pattern and functional assays

The expression level of *CsaFT1* in tea plants is significantly increased before flowering and during the flower bud formation stage. Functional tests show that after introducing *CsaFT1* into *Arabidopsis thaliana*, the plants can flower earlier and also increase the expression levels of flower-related genes such as *SOC1* and *LFY*. These results suggest that *CsaFT1* can indeed promote plant flowering (Liu et al., 2020a). Furthermore, some plant hormones, such as gibberellin and abscisic acid, also affect the expression of *CsaFT1*, indicating that it is also involved in the hormone-regulated flowering mechanism (Xu et al., 2022).

7.3 Implications for breeding early- or late-flowering cultivars

The research on *CsaFT1* provides a new direction for regulating the flowering time of tea plants. By controlling the expression of this gene, it is possible to achieve breeding of early or late flowering traits, thereby growing more suitable tea varieties in different regions or seasons. This not only helps balance the vegetative growth and flowering of tea plants, but also increases the yield and quality of tea (Liu et al., 2020a; Xu et al., 2022). In the future, *CsaFT1* can be used as a molecular marker to breed new tea varieties that adapt to different climates and tea-picking times, bringing a more sustainable development path to the tea industry.

8 Applications in Tea Breeding and Crop Improvement

8.1 Marker-assisted selection for flowering traits

With the sequencing of the tea genome and the pan-genome completed, scientists have identified many important genes and allelic variations related to flowering time. These achievements have laid the foundation for the development of molecular markers and the realization of label-assisted selection (MAS). By combining genotype and phenotype analysis, researchers can more accurately identify early-flowering or late-flowering varieties, thereby accelerating the breeding progress and improving the breeding efficiency (Chen et al., 2023; Li et al., 2023).

8.2 Molecular breeding strategies for climate adaptation

Nowadays, climate change is becoming increasingly obvious, which also has an impact on the growth and flowering time of tea. Molecular breeding methods, such as genomic selection, genetic modification and gene editing, can help breed new varieties that are more adaptable to extreme weather conditions like drought and high temperatures. By screening genes related to stress resistance and flowering time and combining genomic breeding technology, scientists are expected to cultivate high-yield and high-quality tea varieties more quickly (Mukhopadhyay et al., 2015; Lubanga et al., 2022; Ramakrishnan et al., 2023).

8.3 Integration with phenology-based cultivation practices

If these molecular breeding achievements are combined with the planting and management methods of tea gardens, the flowering time can be better controlled. For instance, by using molecular markers to identify early-flowering or late-flowering varieties and combining them with local weather and growth records, more reasonable planting and tea-picking times can be arranged, thereby enhancing the yield and quality of tea. Meanwhile, this method can also help tea gardens better cope with climate change and maintain stable production (Ranatunga, 2019; Li et al., 2023; Zakir et al., 2023).

9 Concluding Remarks

In recent years, research on the molecular mechanism of when tea flower has made rapid progress. Scientists have identified many key genes, such as *CsFLC1* and *CsMADS27* in the MADS-box family, which play a significant role in regulating flowering time, winter dormancy and germination. Through genomic and transcriptomic analysis, classic flowering genes such as *SOC1*, *LFY*, *FT*, *GI*, and *PRR7* were also discovered. The combination of miR156d and *CsSPL1* is also closely related to the flowering time and the development of flower organs. In addition, hormones such as gibberellin, abolic acid and ethylene, along with their signaling pathways, also affect flowering and dormancy. These hormones, together with transcription factors (such as MYB, WRKY, bHLH, etc.), form a complex regulatory network.

However, it is still not very clear how tea integrates external signals (such as light duration and temperature) to regulate flowering. The specific expression and function of these genes in different varieties, at different developmental stages or under environmental pressure still require more experiments to verify. In particular, there are still many questions that have not been clarified regarding how key genes interact with each other, how hormones and transcription factors work together, and the role of epigenetics in the regulatory process.

Nowadays, with the increasing amount of tea genomic data and the maturation of gene editing tools like CRISPR, it is expected that in the future, the genes that control the flowering time can be precisely regulated. This will help regulate the growth rhythm of tea and increase the yield. In the future, new tea varieties that are more adaptable to climate and have better control over flowering time can be bred through molecular marker breeding, gene transformation or editing, thereby promoting the efficient and sustainable development of the tea industry.

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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.

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