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Original Article

The up-regulation of photosynthetic gene expression promotes flowering in kiwifruit

Tingchang Liu[1], Shiming Han[1*], Yuexia Wang[1,2], Yumei Fang[1], Lina Guo[1], Yuxin Wang[1], Jihong Dong[2]
[1]School of Biological Science and Technology, Liupanshui Normal University, Guizhou, Liupanshui, China
[2]School of Public Administration, China University of Mining and Technology, Xuzhou, Jiangsu, China

**Corresponding author's email:* hanshiliang888@163.com
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Abstract

China has rich genetic resources of kiwifruit (*Actinidia chinensis*), the flowering time of kiwifruit is crucial for the yield, quality, and economic benefits, and the mechanisms underlying the earlier flowering time of kiwifruit need to explore. It is unclear for the mechanism of flowering time of kiwifruit to now. A new kiwifruit variety Minihong 1 (M) was approved in 2025, with a flowering time is about ten days earlier than the other two varieties Hanhong (H) and Guichang (G). We selected the folded, unfolded, mature leaves, alabastrum and full-flowering stages of the above three varieties for RNA-seq, and conducted Venn diagram analysis of the high-expression genes (FPKM value > 100) in the alabastrum of these three varieties, and found that 381 genes specifically highly expressed in the early-flowering variety M. Further analysis, it includes 42 genes related to photosynthesis, and most of these genes particularly high expressing in M from the vegetative growth period to the early reproductive growth stage (alabastrum stage). We speculate that the high expression of photosynthetic genes in M leads to increase accumulation of photosynthetic products, which promotes its flowering earlier. This study proposes possible factors that determine the flowering period of kiwifruit, laying a theoretical foundation for the regulation of kiwifruit flowering in the future.

Keywords: Kiwifruit, *Actinidia chinensis,* Photosynthesis, Flowering time

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Introduction

Kiwifruit (*Actinidia chinensis*) is a plant that belongs to Magnoliopsida (flowering plants): Ericales:Actinidiaceae (Nishiyama, 2007). There are 54 species of Actinidia worldwide, with 52 species in China, and the mainly cultivated varieties breeding from delicious Actinidia and the Chinese Actinidia at present (Wu et al., 2003). Kiwifruit and its extracts have significant nutritional and economic value (Li et al, 2025). For example, improving cardiac function (Pam et al., 2024), stomach cancer, colon cancer, cirrhosis with ascites, chronic hepatitis, leukemia, rectal prolapse, hernia and uterine prolapse (Wang et al., 2022).

Plant photosynthesis is highly responsive to fluctuations in environmental cues (Zuo, 2025), and has a significant influence on growth and development (organogenesis, mitosis, accumulation of biomass), biochemical processes (intensity of photosynthesis, antioxidant status and intensity of lipid peroxidation processes) (Perfileva et al., 2025). Studies on photosynthetic populations in crops such as wheat (Yang et al., 2010) and corn (Tang et al., 2014) have shown that photosynthetic rate positively linked with yield. The net photosynthetic rate of leaves at the podding stage was significantly positively correlated with yield in hybrid soybeans. The influence of photosynthetic rate on rapeseed seedlings is primarily linked agronomic traits and yield, during the flowering period mainly affects the yield by influencing the number of effective pods per plant, and during the alabastrum stage has a significant impact on quality-related traits (Li, 2014). The photosynthetic rate of wheat is significantly correlated with stomatal conductance and transpiration rate (Zhang et al., 2012). The net photosynthetic rate of rapeseed at the seedling stage is negatively correlated with intercellular CO_2 concentration, while at the full-flowering stage is positively correlated with transpiration rate, intercellular CO_2 concentration and stomatal conductance, especially with stomatal conductance (Ju, 2013).

Flowering is an important developmental transition from the vegetative to the reproductive phase in plants (Zhao et al., 2025), and the flowering time of plants is regulated by both the external environment and internal genetics. Photoperiod is an important inducing factor for plant flowering (Wang et al., 2025). Flowering is accelerated by exposure to long-day conditions in long-day plants, and by exposure to short-day conditions in short-day plants (Song, 2015); High-temperature-induced FKF1 accumulation promotes flowering (Lee et al., 2025); heat-induced reactive oxygen species (ROS) to modulate tomato flowering (Verma and Moschou, 2025); Nutrient cues control flowering time in plants (Cho et al., 2025); The application of plant growth regulators can regulate the flowering period of mangoes under low-temperature stress (Xiao, 2023); microRNAs miR156 and miR157 controls transitions from juvenile to adult vegetative phase and from adult to reproductive phase (Roggen et al., 2025); SHORT VEGETATIVE PHASE (SVP) family MiSVP1 and MiSVP2 regulated the flowering time by regulating the expression of FLOWERING LOCUS T (FT) gene (Mo et al., 2025). AP2/ERF genes could be key regulators in flower development in *A. eriantha*., two of them (AeAP2/ERF061, AeAP2/ERF067) may play a crucial role in plant flower development regulation and flower tissue forming (Jiang et al., 2022); Two modules consisting of 237 TFs were correlated with floral bud and flower development (Brian et al., 2021); MADS-box plays a key role in plant floral organ differentiation, AcMADS-box genes are mainly associated with light and phytohormone responsiveness, and most genes of them were highly expressed in flowers (Ye et al., 2022). kiwifruit PEBP (phosphatidylethanolamine-binding protein) gene has a function on regulation of kiwifruit vegetative and reproductive phenologies (Voogd et al., 2017). AcPHYB, AcPHYA and AcCRY2 are photoreceptor genes which significantly highly expressed from late flower development until full-flowering and fitting with floral evocation (Ferradás et al., 2017); multiple kiwifruit CENTRORADIALIS (CEN)-like genes have been identified as potential repressors of flowering, and mutation of these genes transformed a climbing woody perennial into a compact plant with rapid terminal flower and fruit development (Varkonyi-Gasic et al., 2019). At present, there are few studies on the regulatory mechanism of kiwifruit flowering time. This paper proposes that early-flowering kiwifruit increase the products of photosynthesis by up-regulating multiple photosynthetic genes, thereby advancing the flowering time of kiwifruit, providing a new idea for the study of flowering mechanism in kiwifruit.

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Material and Methods

Plant material

The Minihong 1 (M) used in this study is a new plant variety approved and granted by the Planting Management Department of the Ministry of Agriculture and Rural Affairs of the People's Republic of China in 2025 (https://zys.moa.gov.cn/gsgg/202504/t20250421_6473411.htm), Hanhong (H) is a high-yield, disease-resistant (gray mold, bacterial canker) and yellow-fleshed variety originated from Lushan Mountain in Jiangxi Province and Guichang (G) is a variety widely cultivated in Guizhou province with high yield and good storage stability (Jin, 2005). The M and H are diploid varieties, the G is a hexaploid variety, the alabastrum period of the early-flowering kiwifruit variety M is ten days earlier than that of H and G (Table 1).

Table-1. The alabastrum and full-flowering stages of different kiwifruit varieties.

	Alabastrum	full-flowering
Minihong 1(M)	March 14th	April 3rd
Hanhong (H)	March 24th	April 11th
Guichang (G)	March 24th	April 15th

RNA-seq and gene annotation

All samples were collected from the kiwifruit planting orchard in Mucheng, Liupanshui City, Guizhou Province, under same grown conditions, the samples of kiwifruitt at alabastrum, full-flowering, folded, unfolded, and mature leaves stages were frozen in liquid nitrogen and stored at -80℃, each sample has three biological replicates in each period, and send to Novogene for transcriptome sequencing and assembly to obtain unigene sequences. RNA is extracted from tissues or cells using standard extraction methods, and the quality of extracted RNA was strictly controlled by the Agilent 2100 bioanalyzer method, total RNA was used as input material for the RNA sample preparations. Briefly, mRNA was purified from total RNA using Poly-T oligo-attached magnetic beads. Fragmentation was carried out using divalent cations under elevated temperature in First Strand Synthesis Reaction Buffer (5X). First strand cDNA was synthesized using random hexamer primer and M-MuLV Reverse Transcriptase, then used RNaseH to degrade the RNA. Second strand cDNA synthesis was subsequently performed using DNA Polymerase I and dNTP. Remaining overhangs were converted into blunt ends via exonuclease/polymerase activities. After adenylation of 3' ends of DNA fragments, adaptor with hairpin loop structure were ligated to prepare for hybridization. To select cDNA fragments of preferentially 370~420 bp in length, the library fragments were purified with AMPure XP system (Beckman Coulter, Beverly, USA), then PCR was performed with Phusion High-Fidelity DNA polymerase. Gene expression analysis was performed using inter-library FPKM normalization methods (Hagel et al., 2015), and clustering of data was performed using OrthoMCL, a program designed for the scalable construction of orthologous groups across multiple eukaryotic taxa (Li and Godzik, 2006.)

The differentially expressed genes (DEGs) with the threshold of $|\log2(FoldChange)| > 1$ & $padj < 0.05$ were analyzed via R package "DESeq2" and GO enrichment and KEGG pathways were run in R software, and gene annotation of the above transcriptome dates were proceeding by different databases: NR Description, NT Description, Swissprot Description, PFAM description, BP Description, MF Description, and CC Description.

GO and KEGG enrichment analysis of differentially expressed genes

Gene Ontology (GO) enrichment analysis of differentially expressed genes was implemented by the clusterProfiler R package, in which gene length bias was corrected. GO terms with corrected P value less than 0.05 were considered significantly enriched by differential expressed genes. KEGG is a database resource for understanding high-level functions and utilities of the biological system, such as the cell, the organism and the ecosystem, from molecular-level information, especially large-scale molecular datasets generated by genome sequencing and other high-through put experimental technologies (http://www.genome.jp/kegg/). We used

clusterProfiler Rpackage to test the statistical enrichment of differential expression genes in KEGG pathways.

Venn diagram construction

Previous studies have defined highly expressed genes with the FPKM value of expression level > 100 times (Kao et al., 2002; Li et al., 2018; Lüli et al., 2021), Venn diagrams were drawn using the package *VennDiagram* to screen the above three varieties for highly expressed genes (Chen and Boutros, 2011).

Heat map construction

Heat map of the expression of photosynthesis-related genes of three kiwifruit varieties M, H, and G under in different leaf and flower stages were performed using the software GraphPad_Prism_8.0.2.263. According to the previous study (Hagel et al., 2015), some modifications have been made as follows: The logarithm of the FPKM values calculated by taking two as the base was obtained. The average values of the logarithms of the selected candidate genes for each sample were calculated, and the correction value = ((log (FPKM values, 2) - Max(Average)) / Min(Average).

Results

The early-flowering kiwifruit variety M has 381 specifically highly expressed genes

Three kiwifruit varieties M, H and G as experimental materials in this study, and the accuracy of transcriptome sequencing for the above three varieties at different stages were all greater than 96%. To explore the reasons for the early flowering of M, we analyzed transcriptome sequencing on the alabastrum of the kiwifruit varieties M, H, and G. Venn plots were drawn for the highly expressed genes (FPKM value > 100) of the above three varieties. The results indicated that 381 genes specifically and highly expressed in the early-flowering variety M (Figure 1).

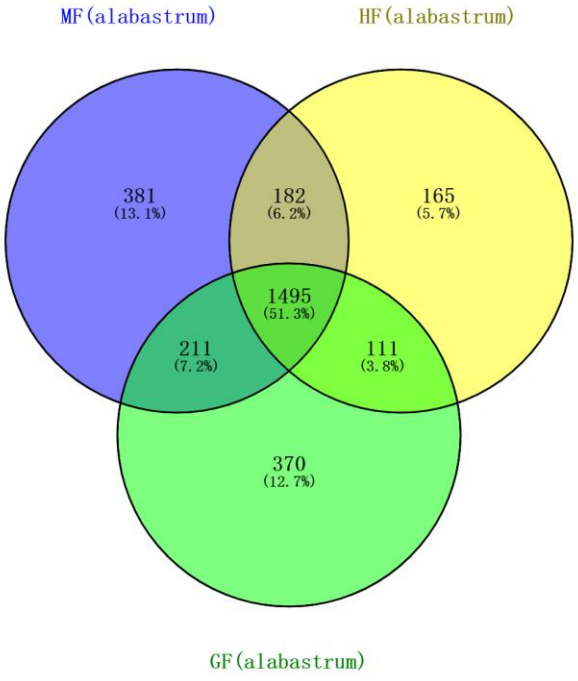

Figure-1. the Venn figure of flower-organ genes expression in kiwifruit varieties at different flowering periods. MF refers to the flower organ of variety M, HF refers to the flower organ of variety H, and GF refers to the flower organ of variety G.

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There are 42 photosynthesis-related genes highly expressed in the flower of the early-flowering kiwifruit variety M

To analyze the characteristics of the highly expressed genes of the early-flowering variety M, we conducted functional gene annotations on different date bases. The results indicate that there are 42 genes related to photosynthesis, accounting for 11% of all highly expressed genes (Table 2).

Table-2. The specific highly expressed genes related to photosynthesis in the early-flowering kiwifruit variety M at alabastrum stage.

Gene_id	NR Description
Cluster-34428.95203	Magnesium-chelatase subunit ChlI like [Actinidia chinensis var. chinensis]
Cluster-34428.96848	Magnesium-chelatase subunit ChlH like [Actinidia chinensis var. chinensis]
Cluster-34428.94631	Magnesium-protoporphyrin IX monomethyl ester [oxidative] cyclase [Actinidia chinensis var. chinensis]
Cluster-34428.96724	Chlorophyll a-b binding protein 37precursor [Actinidia chinensis var. chinensis]
Cluster-34428.99698	Photosystem II protein like [Actinidia chinensis var. chinensis]
Cluster-34428.92911	Ribulose-phosphate 3-epimerase [Actinidia chinensis var. chinensis]
Cluster-34428.109438	Pyridoxal 5'-phosphate synthase subunit PDX1.3 like [Actinidia chinensis var. chinensis]
Cluster-34428.100148	Protein CURVATURE THYLAKOID 1A like [Actinidia chinensis var. chinensis]
Cluster-34428.94252	ATP synthase subunit b' like [Actinidia chinensis var. chinensis]
Cluster-34428.103288	photosystem I reaction center subunit N, chloroplastic [Ricinus communis]
Cluster-34428.94079	Magnesium-chelatase subunit ChlI like [Actinidia chinensis var. chinensis]
Cluster-34428.86747	Magnesium-chelatase subunit ChlH like [Actinidia chinensis var. chinensis]
Cluster-34428.93992	Magnesium protoporphyrin IX methyltransferase [Actinidia chinensis var. chinensis]
Cluster-35618.0	Chlorophyll a-b binding protein 4, chloroplastic [Capsicum chinense]
Cluster-34428.94072	Photosynthetic NDH subunit of lumenal location 5 like [Actinidia chinensis var. chinensis]
Cluster-34428.94429	Photosynthetic NDH subunit of lumenal location 5 like [Actinidia chinensis var. chinensis]
Cluster-34428.97835	Plastidic ATP/ADP-transporter like [Actinidia chinensis var. chinensis]

Cluster-34428.96792	Triose phosphate/phosphate translocator TPT like [Actinidia chinensis var. chinensis]
Cluster-34428.89550	V-type proton ATPase subunit E like [Actinidia chinensis var. chinensis]
Cluster-34428.101080	ATP synthase subunit beta like [Actinidia chinensis var. chinensis]
Cluster-34428.108038	GDP-mannose 3,5-epimerase [Actinidia chinensis var. chinensis]
Cluster-34428.90931	NADH dehydrogenase [ubiquinone] 1 alpha subcomplex subunit 8-B like [Actinidia chinensis var. chinensis]
Cluster-34428.95242	beta-xylosidase/alpha-L-arabinofuranosidase 2-like [Camellia sinensis]
Cluster-34428.92877	Beta-glucosidase like [Actinidia chinensis var. chinensis]
Cluster-34428.99052	malate dehydrogenase [Actinidia chinensis var. chinensis]
Cluster-34428.94118	NADH dehydrogenase [ubiquinone] iron-sulfur protein like [Actinidia chinensis var. chinensis]
Cluster-34428.99168	Photosynthetic NDH subunit of lumenal location 5 like [Actinidia chinensis var. chinensis]
Cluster-34428.124792	NADH dehydrogenase [ubiquinone] 1 alpha subcomplex subunit like [Actinidia chinensis var. chinensis]
Cluster-34428.97265	PREDICTED: triose phosphate/phosphate translocator, non-green plastid, chloroplastic-like [Nicotiana sylvestris]
Cluster-34428.86240	Fasciclin-like arabinogalactan protein [Actinidia chinensis var. chinensis]
Cluster-34428.105205	NADH dehydrogenase [ubiquinone] 1 alpha subcomplex subunit 9 like [Actinidia chinensis var. chinensis]
Cluster-34428.89358	Oxidoreductase, N-terminal protein [Actinidia chinensis var. chinensis]
Cluster-34428.83249	NADH-ubiquinone oxidoreductase [Actinidia chinensis var. chinensis]
Cluster-34428.102752	RuBisCO large subunit-binding protein subunit beta like [Actinidia chinensis var. chinensis]
Cluster-34428.91281	Glucan 1,3-alpha-glucosidase [Actinidia chinensis var. chinensis]
Cluster-34428.92415	V-type proton ATPase subunit d2 [Actinidia chinensis var. chinensis]
Cluster-34428.92124	Aconitate hydratase [Actinidia chinensis var. chinensis]
Cluster-34428.104452	Phosphatidylinositol-3-phosphatase [Actinidia chinensis var. chinensis]
Cluster-34428.79168	Glucan endo-1,3-beta-glucosidase [Actinidia chinensis var. chinensis]

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Cluster-34428.103747	Plastidial pyruvate kinase [Actinidia chinensis var. chinensis]
Cluster-34428.90368	Triosephosphate isomerase [Actinidia chinensis var. chinensis]
Cluster-34428.72476	Glucan endo-1,3-beta-glucosidase [Actinidia chinensis var. chinensis]

According to gene annotation, most of these genes encode catalytic enzymes in the process of photosynthesis. We conducted GO analysis in combination with the genes expressed at the full-flowering stage, and the results showed that the enzymes with catalytic activity accounted for the largest proportion, with 6,403 genes, and the significance was $2.03e^{-19}$, and it is consistent with the relatively high proportion of genes encoding photosynthetic catalytic enzymes at the alabastrum stage of kiwifruit variety M (Figure 2).

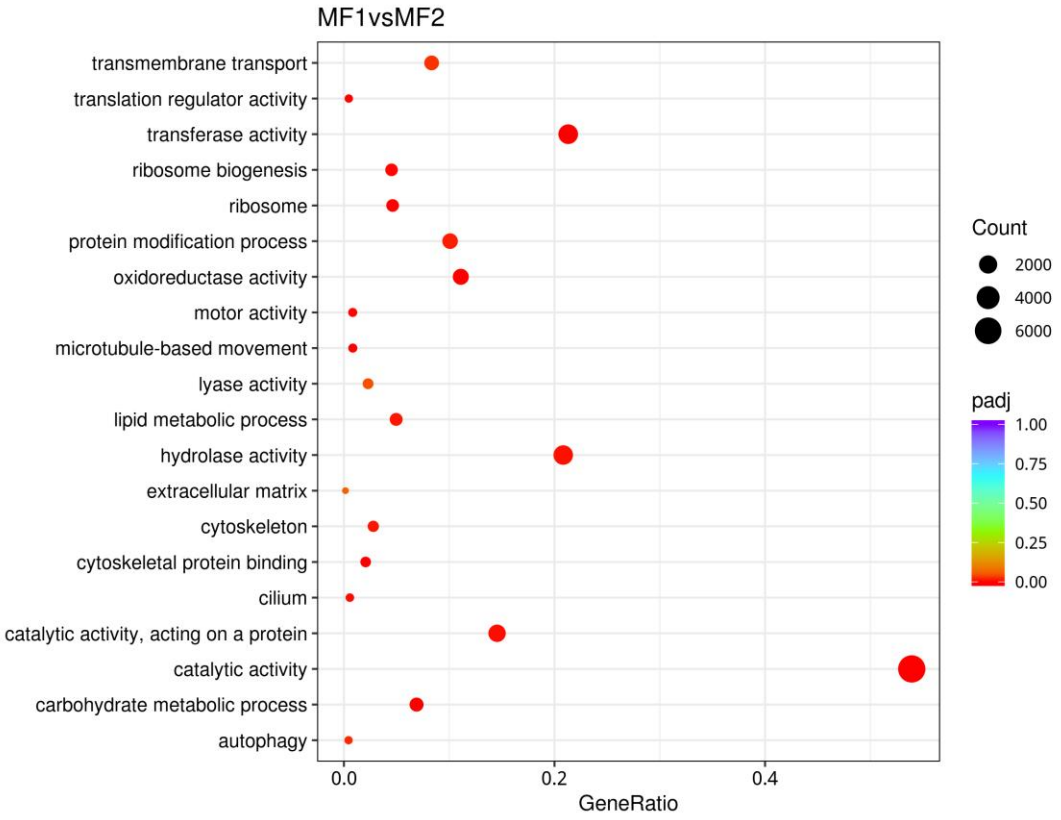

Figure-2. GO analysis of expressed genes of kiwifruit variety M at alabastrum and full-flowering stages.

The photosynthesis-related genes are mainly highly expressed during the alabastrum of the early-flowering variety M

To clarify the expression of photosynthesis-related genes in the flowers of kiwifruit varieties, we used heat maps to analyze the expression levels of the flowers of the above three varieties M, H, and G during the alabastrum and full-flowering stages. The results indicate that during the alabastrum stage, the expression levels of photosynthetic genes in the early-flowering variety M were all higher than those in the varieties H and G. During the full-flowering stage, the expression levels of photosynthesis-related genes in the above three varieties showed no evident pattern (Figure 3).

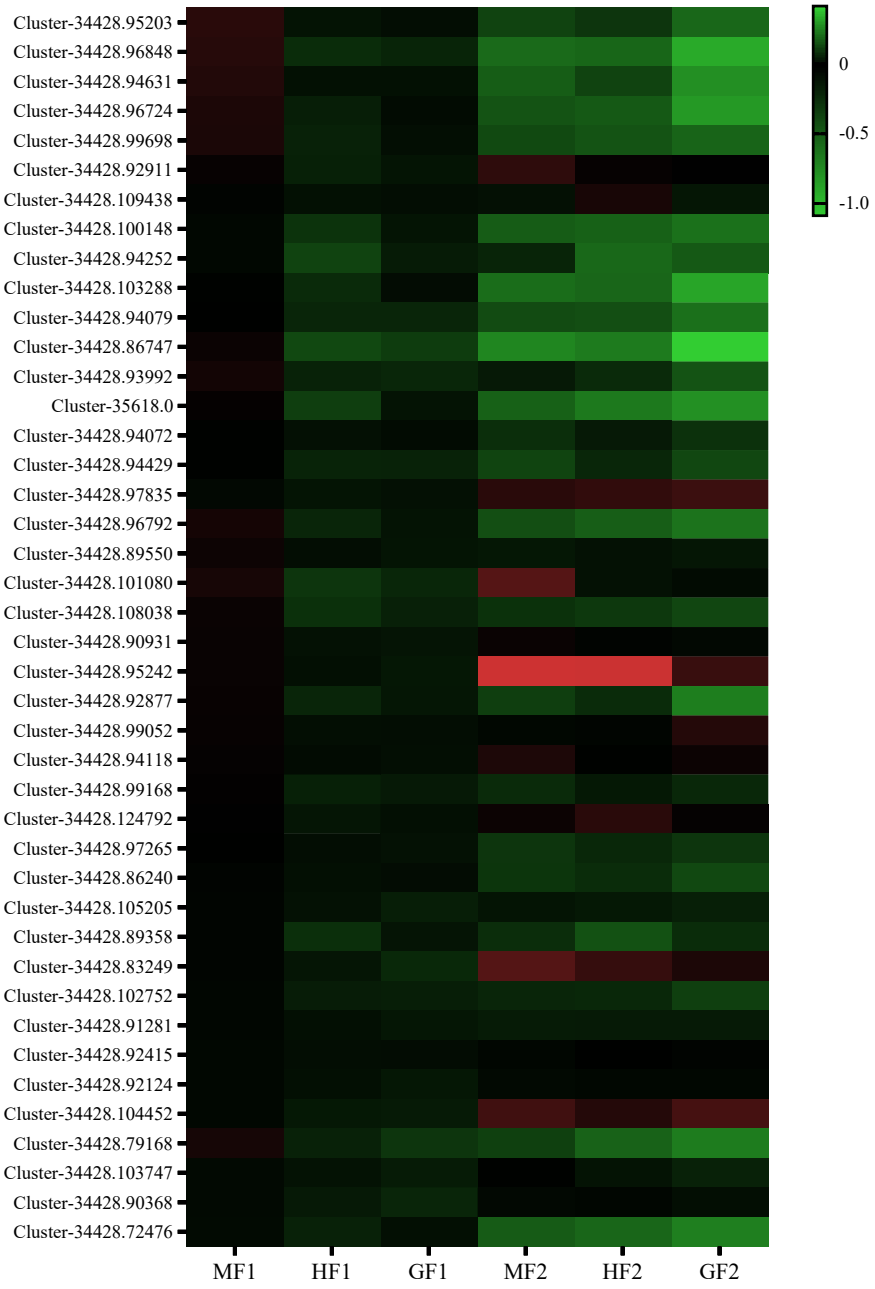

Figure-3. Heat map of highly expressed genes related to photosynthesis in different kiwifruit varieties at alabastrum and full-flowering stages.

MF1 refers to the alabastrum stage of variety M, HF1 refers to the alabastrum stage of variety H, GF1 refers to the alabastrum stage of variety G, MF2 refers to the full-flowering stage of variety M, HF2 refers to the full-flowering stage of variety H, and GF2 refers to the full-flowering stage of variety G.

To further confirm that the flowering time of kiwifruit is mainly determined by the expression of photosynthetic genes during the alabastrum stage. We conducted a KEGG pathway enrichment analysis on the expressed genes of the early-flowering kiwifruit variety M and the results showed that the statistically significant level difference of genes related to photosynthetic antenna was the highest, reaching $1.19981707186e^{-10}$, and the number of differentially expressed genes on KEGG terms was 67 (Figure 4). The trend was consistent with the kiwifruit varieties H and G.

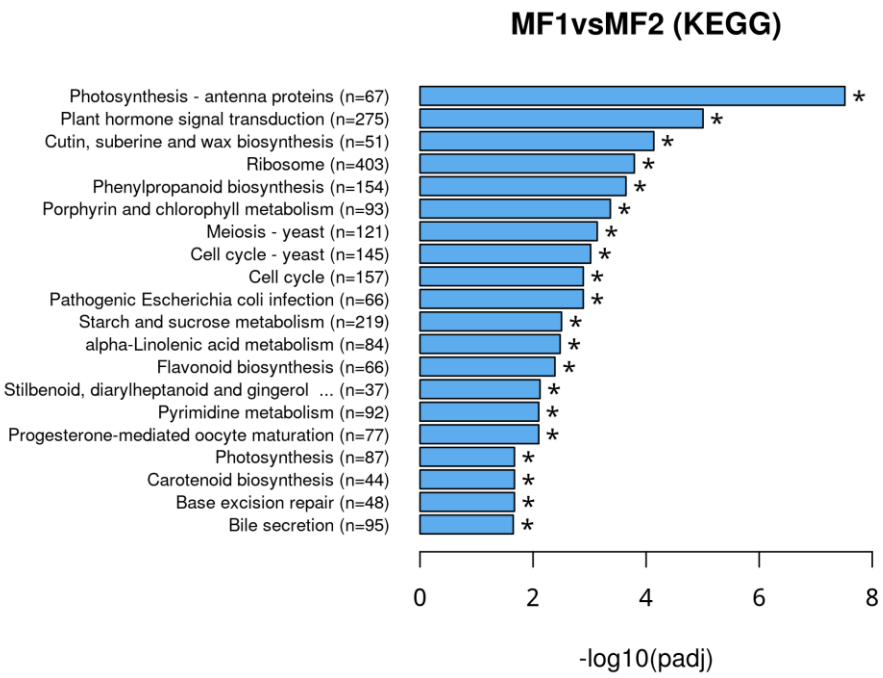

Figure-4. KEGG analysis of expressed genes of kiwifruit variety M at alabastrum and full- flowering stages.
HF1 refers to the alabastrum stage of variety H, MF2 refers to the full-flowering stage of variety M.

The photosynthesis-related genes were generally highly expressed in the early-flowering variety M at different leaf stages

The accumulation of photosynthetic products in the early growth stage of plants can determine the flowering time in the reproductive stage (Leipner et al., 2008). Increasing the expression levels of photosynthesis-related genes can often enhance the rate of photosynthesis and increase the content of photosynthetic products such as sucrose and starch (Xia et al., 2009; Uematsu et al., 2012; Chen et al., 2020). To verify that the reason for the early flowering of the kiwifruit variety M is due to the high expression of photosynthesis-related genes during the vegetative growth period, the folded, unfolded, and mature leaves were performed by RNA-seq of the above three kiwifruit varieties respectively, and a heat map was drawn for the photosynthesis-related highly expressive in the early flowering variety M, and the result shows that during the three different vegetative growth periods, the expression levels of most photosynthesis-related genes in the early-flowering variety M were higher than those in the other two varieties, which is consistent with the expression patterns of photosynthesis-related genes in the alabastrum of the above three varieties (Figure 5).

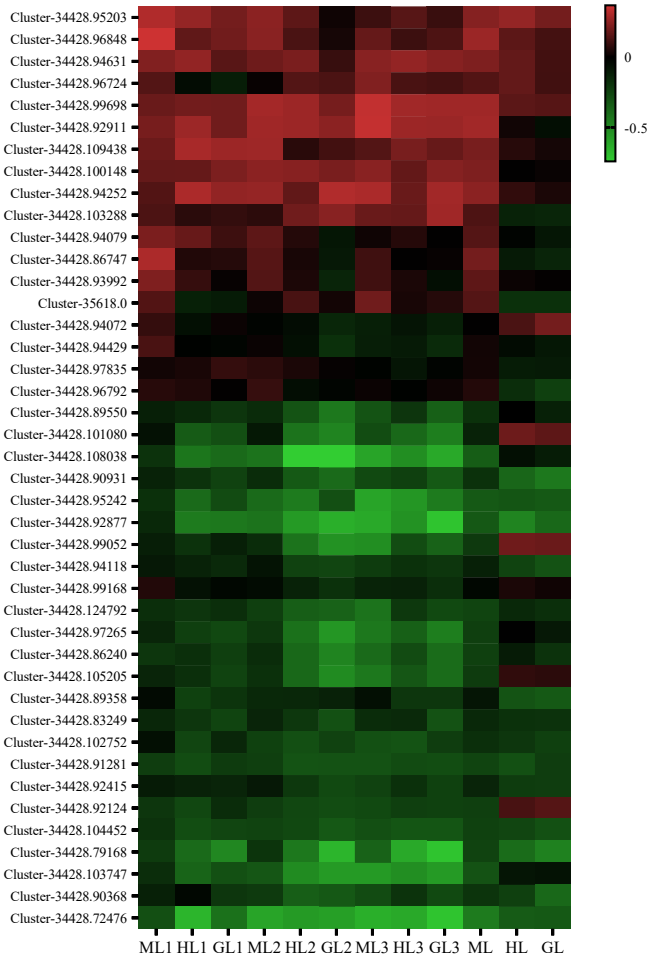

Figure-5. Heat map of high-expression genes related to photosynthesis in leaves of different kiwifruit varieties at different growth stages.

ML1 refers to the folded leaves of variety M, HL1 refers to the folded leaves of variety H, GL1 refers to the folded leaves of variety G, ML2 refers to the unfolded leaves of variety M, HL2 refers to the unfolded leaves of variety H, GL2 refers to the unfolded leaves of variety G, and ML3 refers to the mature leaves of variety M, HL3 refers to the mature leaves of the variety H, GL3 refers to the mature leaves of the variety G, ML refers to the average value of the leaves of variety M at the above three periods, HL refers to the average value of the leaves of variety H at the above three periods, and GL refers to the average value of the leaves of the variety G at three periods.

Discussion

Previous studies have shown that enhanced photosynthesis can improve plant flowering (Leipner et al., 2008; Khan et al., 2015; Heberling et al., 2018; Zhang et al., 2023; Wingler and Soualiou, 2025). M has an exceptionally high expression of 42 genes related to photosynthesis compared to H and G. Among them, Cluster-34428.94079, Cluster-34428.93992, Cluster-34428.101080, Cluster-34428.99168 and Cluster-34428.79168 are important candidate genes. Moreover, the expression level of these genes is relatively high in different leaf stages of M. We speculate that the high expression of photosynthetic genes from the vegetative growth period to the early reproductive growth stage (alabastrum stage) of M leads to increase accumulation of photosynthetic products, which promotes its flowering earlier. We can use early-flowering kiwi variety M as a crossbreeding parent, to improve the flowering period of other late-flowering varieties in the future.

Although most of the genes that are particularly highly expressed during the alabastrum stage of M have

similar expressions at different leaf stages, there are also some genes that are highly expressed in H and G, such as genes Cluster-34428.94631, Cluster-34428.99698, Cluster-34428.92911, Cluster-34428.109438, Cluster-34428.100148, Cluster-34428.94252, Cluster-34428.103288 Cluster-34428.104452. Both Cluster-34428.94631 and Cluster-34428.99698 are related to the regulation of magnesium utilization. Cluster-34428.92911 is a ribulose phosphate 3-epimerase. Cluster-34428.109438 encodes Pyridoxal 5'-phosphate synthase subunit PDX1.3 like protein, Cluster-34428.100148 encodes CURVATURE THYLAKOID 1A like Protein. Cluster-34428.94252 and ATP are related to synthase subunit b like (ATP synthase beta subunit). Cluster-34428.103288 and Cluster-34428.101080 are photosystem I reaction center subunit N in the chloroplast. Cluster-34428.99052 is malate dehydrogenase, and Cluster-34428.94072 is a Photosynthetic NDH subunit of luminal location 5-like protein. Among of them, only two photosynthetic genes (Cluster-34428.109438, Cluster-34428.94252) had significantly higher expression levels in H compared to M, and one photosynthetic genes (Cluster-34428.94252) had significantly higher expression levels in G compared to M. However, among the 34 photosynthetic genes which M is highly expressed compared to H and G, 23 are significantly higher than H, and 26 are significantly higher than G. Photosynthesis is a complex process involving multiple genes (Huang et al., 2025; Williams et al., 2022). The above-mentioned exceptional genes indicate that, when the expression levels of most photosynthetic genes are relatively low, in order to maintain normal flowering and fruiting of plants, plants need to compensatorily up-regulate other genes that can increase photosynthesis.

Conclusions

As of now, the mechanism of flowering time of kiwifruit is unclear. In this study we proposed a new model, that the high expression of photosynthetic genes in early-flowering kiwifruit variety leads to increased accumulation of photosynthetic products, which promote its flowering earlier. This study proposes a possible regulation mechanism of kiwifruit flowering.

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Disclaimer: None.

Conflict of Interest: None.

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Contribution of Authors

Han S, Liu T, Wang Y & Fang Y: Conceived idea, planned the experiments, interpreted data and revised & edited the final draft.

Liu T, Han S, Guo L & Dong J: Reviewed literature, interpreted data and contributed to drafting the manuscript.

Liu T & Wang Y: Performed the experiments, collected & analyzed the data and prepared the initial draft of the manuscript.

All authors read and approved the final draft of the manuscript.

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