Combined treatment of calcium chloride and ε-polylysine maintains postharvest storage quality of dandelions (*Taraxacum antungense* Kitag.) by regulating phenylpropanoid metabolism

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Abstract

As a leafy vegetable, dandelion (*Taraxacum antungense* Kitag.) leaves are subject to senescence, such as yellowing and even decay, during postharvest storage. Calcium chloride ($CaCl_2$) and ε-polylysine (ε-PL) treatments can safely and effectively improve the postharvest quality of fruits and vegetables. To improve the storage quality, dandelions were treated with 0.5% (w/v) $CaCl_2$ and 0.9 g/L ε-PL and stored at 4±0.5 ºC. The results showed that the combination treatment of $CaCl_2$ and ε-PL ($CaCl_2$+ε-PL treatment) could effectively delay the yellowing and chlorophyll content decline, as well as reduce the browning index, when compared with those of the control and single treatments. The $CaCl_2$+ε-PL treatment also enhanced the synthesis and accumulation of secondary metabolites. The combination treatment could significantly enhance the enzyme activities of phenylalanine ammonia-lyase (PAL), 4-coumarate-CoA ligase (4CL), and cinnamate 4-hydroxylase (C4H) in phenylpropanoid metabolism and up-regulate the expression levels of *TaPAL*, *Ta4CL*, and *TaC4H*. Meanwhile, ε-PL treatment was more effective than $CaCl_2$ treatment in promoting the expression of these genes. Correlation analysis indicates that the transcription levels and activities of the three enzymes, as well as the contents of secondary metabolites, are linked to the quality changes of dandelions treated with $CaCl_2$ + ε-PL during cold storage. Principal component analysis (PCA) was used to assess the storage quality of dandelions during cold storage, and the results showed the following rankings: $CaCl_2$+ε-PL>ε-PL>$CaCl_2$>control. These findings suggest that $CaCl_2$+ε-PL treatment can improve the postharvest storage quality of dandelions by modulating the phenylpropane metabolic pathway.

Keywords: dandelions; calcium chloride; ε-polylysine; phenylpropanoid metabolism; storage quality.

1. Introduction

Dandelions (*Taraxacum* spp.) are perennial herbs that have long been utilized as functional food and medicine (Liu et al., 2019a). As a leafy vegetable, the physiological metabolism of postharvest dandelions is still active, and their leaves are highly susceptible to yellowing, water loss, browning, and rotting, resulting in short shelf life and poor quality. However, there has been little research on the postharvest preservation of dandelions. Due to the high nutritional value of dandelions, which are rich in trace elements, minerals, and vitamins (Zhao et al., 2025), and effective active ingredients such as chlorogenic acid, total flavonoids, and total phenolics (Yan et al., 2024), the medicinal value of dandelions is now widely studied, and the active ingredients of their extracts have been applied in the treatment of various diseases (Chen et al., 2021; Deng et al., 2025; El-Refaiy, et al., 2025; Liu et al., 2025a). Dandelion leaves can be eaten fresh directly (more than 80% edible), as in vegetable salad, blanched and served cold, or processed into different foods, and have wide potential for market development (Lis et al., 2019). In order to improve the storage quality of fresh dandelions, Dermesonluoglu et al. (2016) developed and verified a predictive model for the impact of storage temperature on microbial spoilage and quality deterioration of pre-packaged dandelions. Calcium chloride ($CaCl_2$) and ε-polylysine (ε-PL) treatments have been reported to be effective and safe in enhancing the postharvest storage quality of fruits and vegetables, but fewer studies have been conducted on the application of these two treatments to leafy vegetables. In order to efficiently improve the nutritional value and fresh food quality of postharvest dandelions, the present study combined $CaCl_2$ and ε-PL treatments and verified their application.

Calcium is a cell wall component and acts as a sequestering agent to prevent the structure of the cell wall from being broken down by enzymes (Ribeiro, et al., 2020; Hocking et al., 2016). It has been shown that calcium can enhance the structure of the cell wall by interacting with free carboxyl groups that are released during pectin de-esterification to generate insoluble calcium pectinate (Wehr et al., 2004; Toivonen et al., 2008). $CaCl_2$ plays a significant role in maintaining the postharvest quality of fruits and vegetables. Nigro et al. (2006) reduced the incidence of grey mold on table grapes by pre-harvest $CaCl_2$ treatment. Ultrasound combined with $CaCl_2$ slightly acidic electrolyzed water treatment better inhibited microbial growth and delayed the quality decline of onions in terms of color, hardness, etc. (Yang et al., 2025). Combined treatment of chitosan and $CaCl_2$ effectively delayed browning, inhibited microbial growth, and improved the quality of postharvest fresh-cut honeydew melon (Chong et al., 2015). By modulating antioxidant capacity, phenylpropanoid metabolism, and phytohormone signaling, $CaCl_2$ treatment can effectively alleviate chilling injury in postharvest nectarines (Liu et al., 2024a). The postharvest quality of broccoli was maintained by the combined application of kojic acid and $CaCl_2$, which reduced the breakdown of chlorophyll (Chl) and induced the gene expression and activities of antioxidant enzymes (Yan et al., 2020). Similarly, combined treatment with 2,4-epibrassinolide and $CaCl_2$ could also maintain total Chl content and antioxidant level and maintain the postharvest quality of baby mustard (Di et al.,2024).

ε-PL is a natural and safe food preservative (Hiraki, et al.,2003; Li et al.,2019). Many studies have demonstrated the potential application of ε-PL in postharvest storage and preservation of fruits and vegetables. It has been confirmed that the combination treatment of ε-PL and ultrasound improves the storage quality of fresh-cut lettuce by controlling microbial growth during the storage period (Fan et al., 2019). The postharvest energy content increased, and the postharvest quality of *Volvariella volvacea* was maintained after combined ε-PL and 1-methylcyclopropene (1-MCP) treatment (Chen et al., 2024). Liu et al. (2024c) used ε-PL treatment on 'Jinxiu' yellow peach and found that ε-PL treatment could effectively delay peach fruit senescence, reduce internal browning of the pulp, enhance antioxidant enzyme activity, and improve peach fruit quality. The application of ε-PL had a positive effect on the quality of apples during storage by increasing the activities of defense-related enzymes such as phenylalanine ammonia-lyase (PAL), increasing the phenolic content, and ultimately improving the antioxidant capacity of apples (Zheng et al., 2022). Similarly, Zhang et al. (2023a) found that the application of ε-PL improved citrus disease resistance by enhancing the activities of phenylpropanoid metabolism enzymes and promoting the synthesis of phenolics.

Phenylpropanoid metabolism is an important secondary metabolic pathway in plants, which is the synthesis pathway of lignin, flavonoid, and phenolic compounds (Zhang et al., 2015). Phenolic compounds are crucial for human health because of their antibacterial, anti-inflammatory, and antioxidant properties (Ding et al.,2024). In addition, this pathway improves cell wall strength and plant disease resistance by controlling the production of lignin, flavonoid, and phenolic compounds, which are indispensable antimicrobial agents found in abundance in plants (Wang et al., 2024; Dong et al., 2021). It has been shown that acibenzolar-S-methyl treatment can increase the activities of PAL and polyphenol oxidase, as well as the contents of total phenolics, flavonoid, lignin, and anthocyanin, to strengthen the cell wall of blueberries (Ge et al., 2019). He et al. (2025) used methyl jasmonate to regulate phenylpropanoid metabolism by increasing the activities of PAL, cinnamate-4-monooxygenase (C4H), and 4-coumarate-CoA ligase (4CL) enzymes, as well as by up-regulating the expression of related genes, to promote phenolic and flavonoid enrichment and delay peel browning in litchi during cold storage. Similarly, acetylsalicylic acid and salicylic acid treatments can increase the activities of PAL, 4CL, and C4H in phenylpropanoid metabolism, promote the accumulation of phenolic and flavonoid compounds, and slow the degreening and senescence of Chinese flowering cabbage leaves (Zhang et al., 2022). It has been confirmed that melatonin can delay the leaf senescence of postharvest flowering Chinese cabbage by promoting flavonoid accumulation (Yue et al., 2023).

In this work, postharvest dandelions (*Taraxacum antungense* Kitag.) were treated with 0.5% (w/v) $CaCl_2$ and 0.9 g/L ε-PL. This study examined changes in the transcript levels and enzyme activities of PAL, C4H, and 4CL in the phenylpropanoid metabolism pathway, as well as the contents of Chl, lignin, total flavonoid, total phenolics, and chlorogenic acid, following the combined treatment of $CaCl_2$ and ε-PL during cold storage at 4±0.5 ºC. The research aims at exploring the effects of combined treatment of $CaCl_2$ and ε-PL on the postharvest storage quality of dandelions and elucidating the underlying mechanisms.

2. Materials and Methods

2.1. Plant materials, treatments, and sample collection

Dandelions (*Taraxacum antungense* Kitag.) (root removed) were harvested from a commercial planting base in Shenyang, Liaoning Province, China (41.48°N, 123.25°E) on August 10, 2024. After harvest, dandelions were quickly placed in a cool and sheltered place to dissipate field heat and pre-cooled at 4±0.5 ºC for 2 h. Subsequently, dandelions without rot and mechanical damage were selected and randomly divided into four groups. The control group was soaked with distilled water. The other three groups were soaked with 0.5% (w/v) $CaCl_2$ solution, 0.9 g/L ε-PL solution, and 0.5% (w/v) $CaCl_2$ and 0.9 g/L ε-PL composite solution, respectively. Based on the results of the pre-experiment with different concentrations of $CaCl_2$ and ε-PL soaking (Figures S1–S2), 0.5% (w/v) $CaCl_2$ and 0.9 g/L ε-PL were selected for dandelion soaking. After soaking for 8 min, the samples were dried naturally at room temperature (20±1 ºC). The dandelions were sealed in 0.035-mm thick polyethylene bags (100 g each) and stored at 4±0.5 ºC (80%–85% relative humidity). Each treatment group had three biological replicates, and samples were collected every 2 d for sampling and determination. The leaves, after removing the main veins, were frozen with liquid nitrogen and stored at –80 °C for further use.

2.2. Measurement of leaf color change

The leaf color change was determined using a CR-400 colorimeter (Konica Minolta, Tokyo, Japan). Nine dandelion leaves were randomly selected from each parallel of each group. To avoid the main vein, each leaf had three measurement locations: one above it and two symmetrical spots on the left and right sides of the main vein. The color parameters L^* (lightness), a^* (red-green phase), and b^* (yellow-blue phase) of the dandelion leaves were determined, and the average value was taken.

2.3. Measurement of Chl a, Chl b, and total Chl

The method of Wang et al. (2022) with some modifications was used. A total of 2.0 g of dandelion leaf tissue was homogenized with 80% (v/v) cold acetone at 4 °C and extracted by filtration in the dark. The resulting extract was centrifuged at 10,000×*g* at 4 °C for 10 min. The supernatant was analyzed for absorbance at 645 nm and 663 nm using a spectrophotometer (TU-1810, Puxi General Instrument Co., Ltd., Beijing, China).

2.4. Evaluation of leaf browning index

The browning index was rated based on dandelion leaf browning area: grade 0, no browning; grade 1, proportion of browned area≤5%; grade 2, 5%<proportion of browned area≤10%; grade 3,

10%<proportion of browned area≤30%; grade 4, 30%<proportion of browned area≤60%; and grade 5, proportion of browned area>60%. The browning index was assessed using the following formula:

$$\text{Browning index (\%)}=\frac{\Sigma(N_0\times L)}{N_T\times H}\times 100\%$$

Where N_0 was the number of leaves at each grade, L was the browning grade, N_T was the total number of leaves and H was the highest browning grade.

2.5. Determination of total phenolic and total flavonoid contents

The content of total phenolics was determined as described by Sun et al. (2021), with slight modifications. A 2.0 g sample was ground in an ice bath with 5 mL of methanol, left at low temperature for 12 h, and then centrifuged at 12,000×*g* for 20 min at 4 °C. The reaction system consisted of 20 μL of supernatant, 180 μL of H_2O, 1 mL of 10% (v/v) Folin-Ciocalteu reagent, and 0.5 mL of 7.5% (w/v) Na_2CO_3. The above solution was mixed and incubated at 30 °C for 10 min, after which the absorbance at 760 nm was measured. Gallic acid was used as the standard to establish a standard curve, and the results were expressed as mg/g.

The total flavonoid content was determined using the method of Pérez-Ambrocio et al. (2018), with some modifications. A total of 2.0 g of sample was ground into a homogenate with 5 mL of methanol and centrifuged at 12,000×*g* at 4 °C for 20 min. The reaction system consisted of 1 mL of supernatant, 1 mL of 3% (w/v) $AlCl_3$, and 0.5 mL of 30% ethanol, which was mixed well and then reacted at 25 °C for 10 min, after which the absorbance at 490 nm was measured. A standard curve was established using rutin as the standard, and the results were expressed as mg/g.

2.6. Determination of lignin content

The lignin content was determined according to the kit manufacturer's instructions (G0708W48; Suzhou Grace Biotechnology Co., Ltd., Suzhou, China). The absorbance of the reaction system was measured at 280 nm. The lignin content was calculated from absorbance values and the standard curve. The results were expressed as mg/g.

2.7. Determination of chlorogenic acid content

Chlorogenic acid was extracted according to the kit manufacturer's instructions (BC4474; Solarbio, Beijing, China). The chlorogenic acid content was detected by a liquid chromatograph (LC-2030 plus, Shimadzu, Tokyo, Japan) with a C18 liquid chromatography column. The injection volume was 10 μL, the column temperature was at room temperature (27 ℃), the flow rate was 1 mL/min, and the wavelength was 327 nm. The mobile phase was acetonitrile (B):0.4% phosphoric acid aqueous solution (A)=13:87, and the travelling time was 15 min. The content of chlorogenic acid was calculated based on the peak area and the standard curve, and the results were expressed as μg/g.

2.8. Analysis of enzyme activities

The enzyme activities of PAL, C4H, and 4CL in the phenylpropanoid metabolism pathway were determined using enzyme activity kits (G0114W48, G1001W48, and G1003W48; Suzhou Grace

Biotechnology Co., Ltd., Suzhou, China). The absorbance values were measured at 290, 340, and 333 nm according to the manufacturer's instructions. The activities of PAL, C4H, and 4CL were calculated from the absorbance values. The results of PAL activity were expressed as $\Delta OD_{290}/(g \cdot h)$ fresh weight (FW). The activities of C4H and 4CL are expressed as U/g FW.

2.9. RNA isolation, cDNA synthesis, and gene expression analysis

The extraction of total RNA from dandelion leaves was performed via an OminiPlant RNA kit (CWBiotech, Taizhou, China), and total RNA was reverse-transcribed to cDNA as a template for subsequent real-time quantitative polymerase chain reaction (RT-qPCR) analyses using the HiFiScript cDNA synthesis kit (CWBiotech, Taizhou, China) and stored at –20 ℃. RT-qPCR amplification was performed using the Real Master Mix (SYBR-Green) kit (CWBiotech, Taizhou, China). The internal reference gene (*Ta18s*) and primers are shown in Table 1. The gene-specific primers were referenced from the known sequences (Zhang, 2023b; Liu, 2019b; Liu et al., 2021; Liu et al., 2024b) and synthesized by the Genewiz Biotechnology Synthesis Laboratory (Suzhou, China). To calculate $2^{-\Delta\Delta Ct}$, 0 d was considered as the control.

Table 1. Primers for RT-qPCR analysis

Gene	Forward Primer (5′-3′)	Reverse Primer (5′-3′)
Ta18s	ATTCTGAGCGTGTCCTCCTTT	GCTCCCAATCACCACGACTA
TaPAL	GGCGAGAAGGAGAAAGAC	TCAAATACCCTGTTCCCAAT
Ta4CL	TGGCGCTACCGTACTCCTC	CAAATCAACACATCCTCC
TaC4H	GCGACGGAAGGTATTGTGAT	CTTCTCAAAAACGGCCTCAG

2.10. Statistical analysis

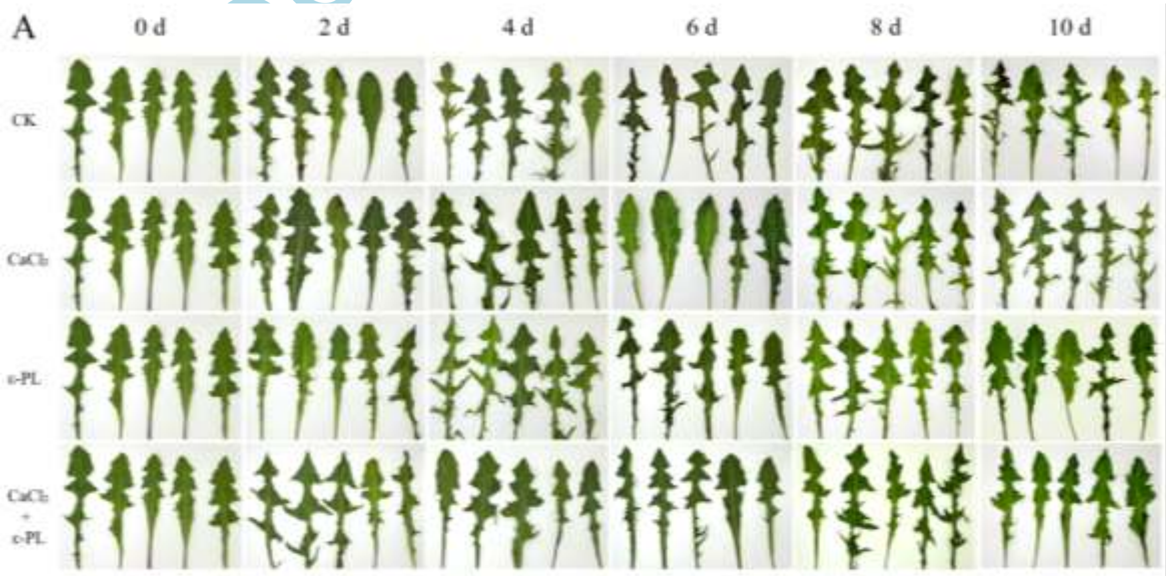
Each group was designed with three biological replicates at each time point. Statistical analyses were performed using SPSS 27.0 software (IBM Corp, Armonk, NY, USA) for analysis of variance and comparison of differences between groups, with $P<0.05$ indicating significant differences. Origin 2024 software (MicroCal Software Inc., Northampton, MA, USA) was used to generate correlation plots for all the figures. SIMCA® software was used to perform principal component analysis (PCA).

3. Results

3.1. Changes in the color of dandelion leaves and the contents of Chl a, Chl b and total Chl

As shown in Figure 1A, with the extension of storage time, the apparent changes in the dandelion leaves in the four groups were different. On the 10th day at the end of storage, the dandelion leaves in the control group turned significantly yellow and the degree of leaf browning was greater, while the above symptoms of the leaves treated with $CaCl_2$ and ε-PL ($CaCl_2$+ε-PL) were milder. The color parameters L^*, a^*, and b^* can reflect the color change of dandelion leaves during cold storage at 4±0.5 ºC. The higher the L^* value is, the brighter the color. When the b^* value is positive, the higher the b^* value is, the more yellow the color tends to be. As shown in Figures 1B and 1D, the b^* values of the four groups of dandelion leaves were all positive during cold storage, and the L^* and b^* values of the four groups showed a stable upward trend. This indicates that the color of all four groups of dandelion leaves gradually turned yellow during storage. During the storage of 2–10 d, the L^* and b^* values of the dandelion leaves in the control group were significantly higher than those in the $CaCl_2$ treatment group, the ε-PL treatment group, and the $CaCl_2$+ε-PL treatment group (P<0.05), and the L* and b* values of the leaves in the $CaCl_2$+ε-PL treatment group were the lowest (P<0.05). As shown in Figure 1C, during cold storage, the a* values of the four groups of dandelion leaves were all negative and showed a fluctuating upward trend. When the a* value is negative, the smaller the absolute value is, the more the color deviates from green. Therefore, the color of the dandelion leaves in all four groups gradually deviated from green in the middle and late stages of storage, and the control group had the highest degree of deviation.

As shown in Figures 1E–1G, the Chl a, Chl b, and total Chl contents in all four groups of dandelion leaves decreased gradually with increasing storage time. During cold storage, the contents of Chl a and total Chl in the leaves of the control group were consistently significantly lower than those in the leaves of the $CaCl_2$, ε-PL, and $CaCl_2$+ε-PL treatment groups (P<0.05), and the contents of Chl a and total Chl in the $CaCl_2$+ε-PL treatment group were the highest (P<0.05). During the storage of 4–10 d, the Chl b content in the control group was significantly lower than that in the $CaCl_2$+ε-PL treatment group (P<0.05). During the storage of 4–8 d, there was no significant difference in the Chl b content among the control group and the $CaCl_2$ and ε-PL treatment groups. On day 10, the Chl b content in the control group was significantly lower (P<0.05).



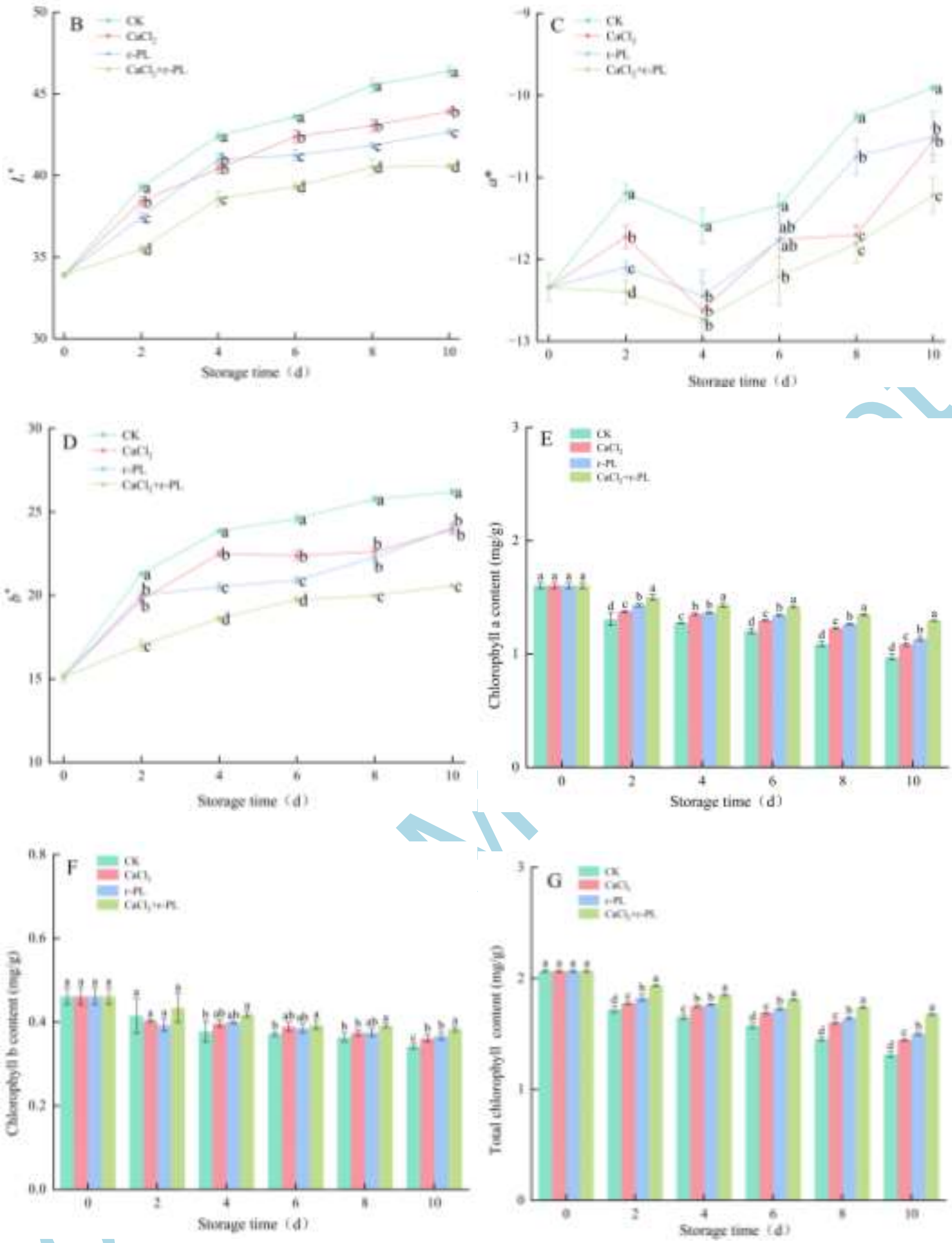


Figure 1. Changes in the color of dandelion leaves and the contents of Chl a, Chl b, and total Chl. Visual map of dandelions in different groups during cold storage (A). Changes in *L** (B), *a** (C), and *b** (D) values and the contents of Chl a (E), Chl b (F), and total Chl (G) of dandelion leaves under different treatments during cold storage. Means±standard errors (SEs) of three biological replicate experiments are shown. Different lowercase letters at each time point represent significant differences among groups. CK: control.

3.2. Changes in the browning index of dandelion leaves

As shown in Figure 2, starting from day 2, all four groups of dandelions had browned leaves, but the number and area of browned leaves varied among the groups. During cold storage, the browning index values of the four groups of dandelion leaves gradually increased. During 2–8 d of storage, the browning index values of the $CaCl_2$+ε-PL treatment group were significantly lower than those of the other three groups (P<0.05). Starting from day 6, the browning index values of the control group rose rapidly and were significantly higher than those of the other three groups (P<0.05).

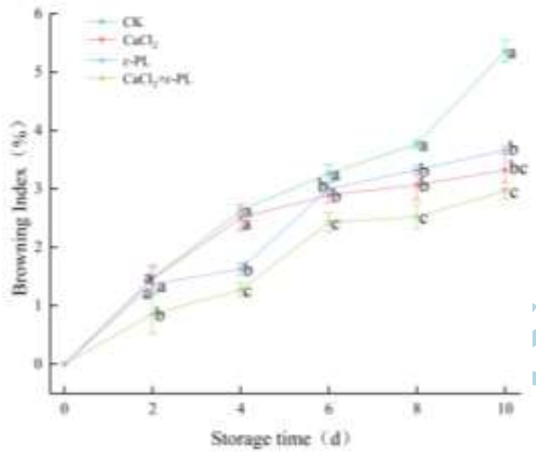


Figure 2. Changes in the browning index of dandelion leaves under different treatments during cold storage. Means±SEs of three biological replicate experiments are shown. Different lowercase letters at each time point represent significant differences among groups.

3.3. Changes in the contents of total phenolics, total flavonoid, lignin, and chlorogenic acid

The contents of total phenolics and total flavonoid in the dandelions treated with $CaCl_2$+ε-PL reached their peak values on day 6 and then gradually decreased (Figures 3A–3B). The total phenolic content in the $CaCl_2$+ε-PL treatment group was significantly higher than those of the other three groups from 6–10 d, whereas the content in the control group was the lowest (P<0.05). The peak total phenolic content in both the ε-PL treatment and $CaCl_2$ treatment groups occurred on the 6th day of storage. At this time point, the total phenolic content in the ε-PL treatment group was higher than that in the $CaCl_2$ treatment group (P<0.05). The total flavonoid contents of the four groups varied significantly at each time point throughout the 2–10 d of cold storage. The total flavonoid contents decreased in the order of the $CaCl_2$+ε-PL treatment group, ε-PL treatment group, $CaCl_2$ treatment group, and control group (Figure 3B).

During the storage of 2–10 d, the lignin contents of dandelions treated with $CaCl_2$+ε-PL and $CaCl_2$ were higher than those of the other two groups (P<0.05), with those in the $CaCl_2$+ε-PL treatment group being the highest (P<0.05) (Figure 3C). During storage of 2–8 d, the lignin contents of the control group were significantly lower than those of the other three treatment groups (P<0.05).

On the 4th day of cold storage, the maximum chlorogenic acid contents were detected in both the $CaCl_2$ treatment and control groups, which was two days earlier than those in the other two groups (Figure 3D). The contents of chlorogenic acid in dandelions treated with $CaCl_2$+ε-PL and ε-PL were significantly higher than those in the $CaCl_2$ treatment group and the control group (P<0.05). The chlorogenic acid content in the $CaCl_2$ + ε-PL treatment group was substantially higher than those of the other three groups from 2–10 d (P<0.05). Except for day 4, the chlorogenic acid contents of the dandelions in the control group were the lowest (P<0.05).

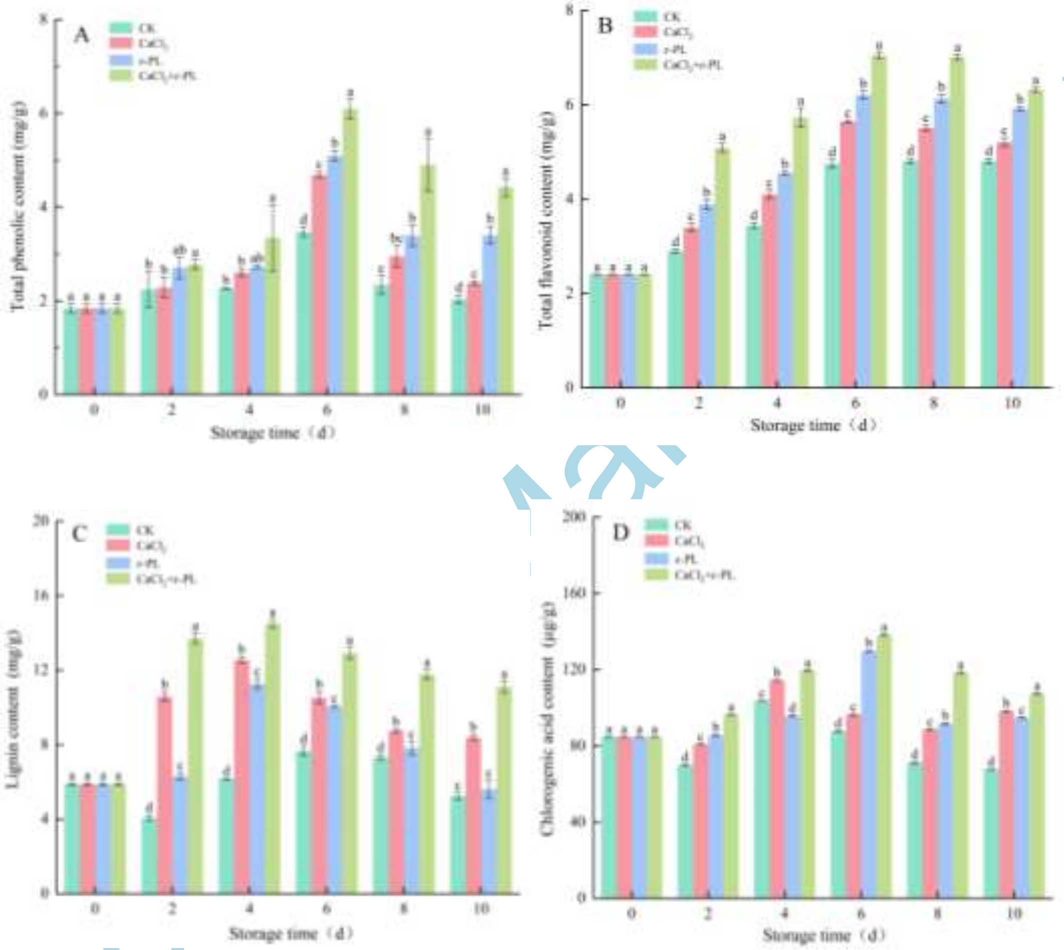


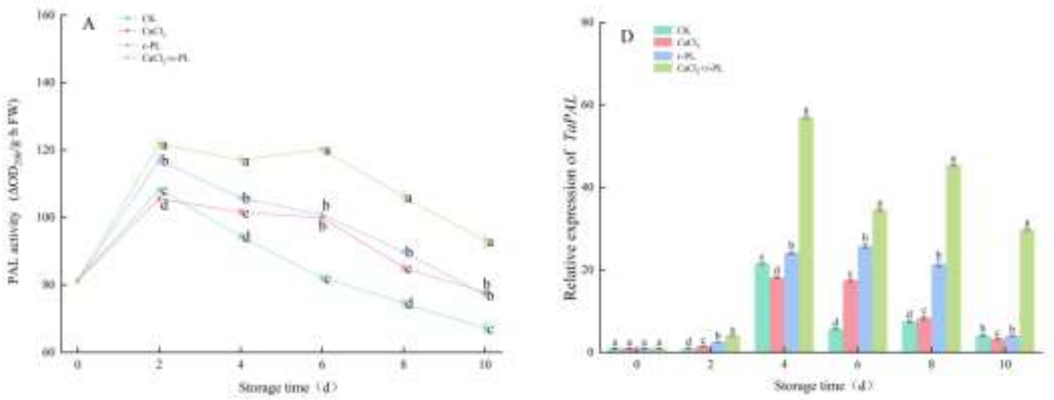
Figure 3. Changes in the contents of total phenolics (A), total flavonoid (B), lignin (C), and chlorogenic acid (D) of dandelion leaves under different treatments during cold storage. Means±SEs of three biological replicate experiments are shown. Different lowercase letters at each time point represent significant differences among groups.

3.4. Changes in the enzyme activities and gene expression levels of PAL, C4H, and 4CL

PAL, C4H, and 4CL are three key enzymes in phenylpropanoid metabolism and play important roles in the production of secondary metabolized compounds. During cold storage, the PAL activity in all four groups of dandelions increased on day 2, followed by an overall decreasing trend (Figure 4A). The PAL activity in the ε-PL treatment group was significantly higher than that in the $CaCl_2$ treatment group at 2, 4, and 8 d of storage (P<0.05). At 2–10 d of storage, the PAL activity in the $CaCl_2$+ε-PL treatment group was significantly higher (P<0.05) than that in the other three groups. During the storage of 4–10 d, the PAL activity in the control group was the lowest (P<0.05). As shown in Figure 4D, the *TaPAL* expression levels of all four groups of dandelions increased substantially on the 4th day of storage, followed by the fastest decrease in *TaPAL* expression in the control group. At 6–8 d, *TaPAL* expression levels were significantly lower in the control group (P<0.05). During storage for 4–10 d, the *TaPAL* expression levels were the highest (P<0.05) in the $CaCl_2$+ε-PL treatment group, followed by the ε-PL treatment group.

As shown in Figure 4B, C4H activity decreased in the control dandelions on day 2 of storage, whereas its activity increased in the other three treatment groups. During the storage of 2–10 d, the C4H activity in the $CaCl_2$+ε-PL treatment group was significantly higher than those in the other three groups (P<0.05). Except on the 4th day, the C4H activities of both the $CaCl_2$ treatment and ε-PL treatment groups were significantly higher than that of the control group (P<0.05). The *TaC4H* expression levels of all four groups of dandelions peaked on day 4 (Figure 4E). During the storage of 2–10 d, the expression level of *TaC4H* in the $CaCl_2$+ε-PL treatment group was consistently the highest (P<0.05). *TaC4H* expression level was also higher in the ε-PL treatment group from 4–10 d of storage, which was higher than the 2 times of the expression in the $CaCl_2$ treatment group, whereas the levels were the lowest in the control group (P<0.05).

As shown in Figure 4C, similar to the changes in PAL activity, there was an overall decreasing trend in 4CL activity in the four groups of dandelions at 2–10 d of cold storage. During the storage of 4–6 d, the 4CL activities in the $CaCl_2$ treatment group and the ε-PL treatment group were significantly higher than those in the control group (P<0.05). At 2–10 d, the 4CL activity in the $CaCl_2$+ε-PL treatment group was consistently the highest (P<0.05). *Ta4CL* gene expression levels peaked on day 4 in all four groups of dandelions (Figure 4F). The expression level of *Ta4CL* was the highest in the $CaCl_2$+ε-PL treatment group, followed by the ε-PL treatment group, whereas the expression was the lowest in the control group (P<0.05) at 2–10 d of cold storage.



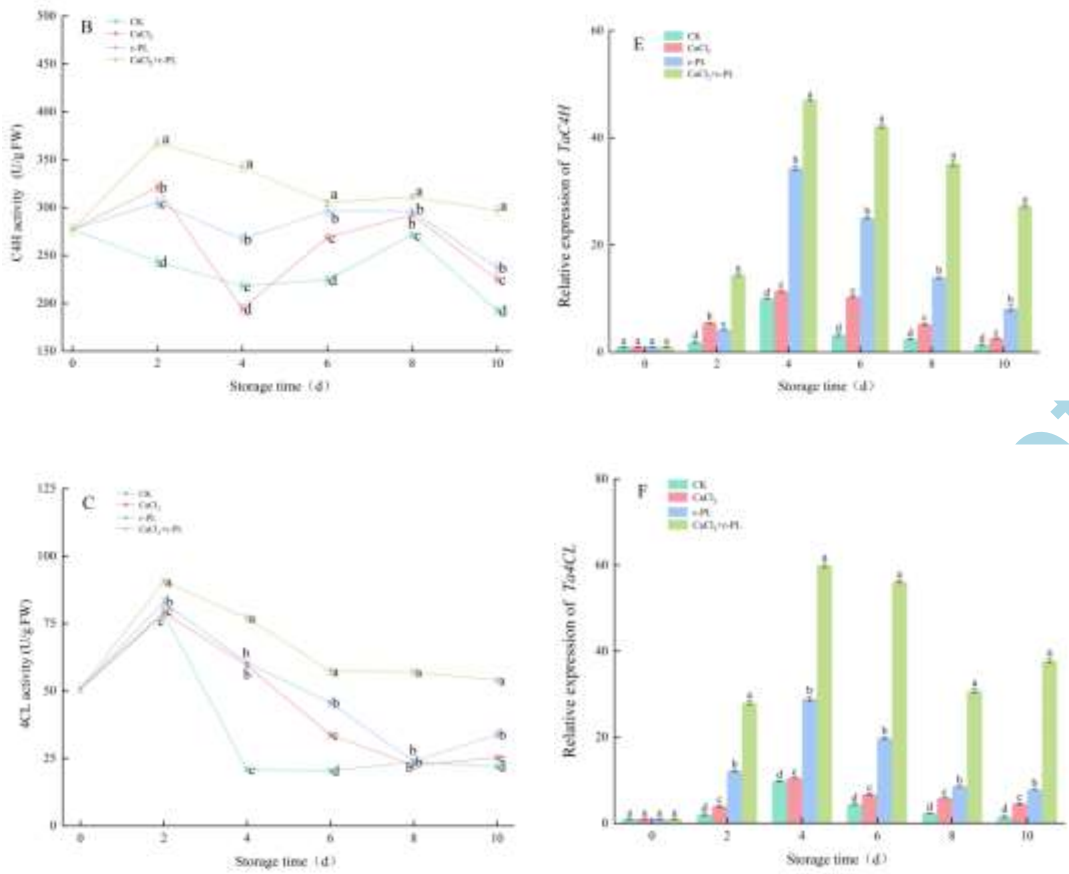


Figure 4. Changes in the enzyme activities and gene expression levels of PAL (A, D), C4H (B, E), and 4CL (C, F) under different treatments during cold storage. Means±SEs of three biological replicate experiments are shown. Different lowercase letters at each time point represent significant differences among groups.

3.5. Correlation analysis

The present study further analyzed the correlation of parameters of the $CaCl_2$+ε-PL treatment of dandelions during cold storage (Figure 5). Total phenolic content, total flavonoid content, and chlorogenic acid content showed positive correlation with browning index and L^* and b^* values and negative correlation with the contents of Chl a, Chl b, and total Chl. Lignin content showed a positive correlation with total flavonoid content and chlorogenic acid content, as well as PAL, C4H, and 4CL enzyme activities, while showing a negative correlation with Chl a and total Chl contents. There was a positive correlation between total flavonoid content and chlorogenic acid content, and chlorogenic acid content showed a positive correlation with the contents of the other three secondary metabolites. In addition, PAL activity showed a positive correlation with total flavonoid and chlorogenic acid contents. The expression levels of the three enzyme genes showed a positive correlation with the contents of the four secondary metabolites and a negative correlation with the Chl content. These data indicate that the quality changes in dandelion leaves treated with $CaCl_2$+ε-PL during cold storage are related to the transcription levels and activities of the three key enzymes in phenylpropanoid metabolism, as well as the contents of secondary metabolites.

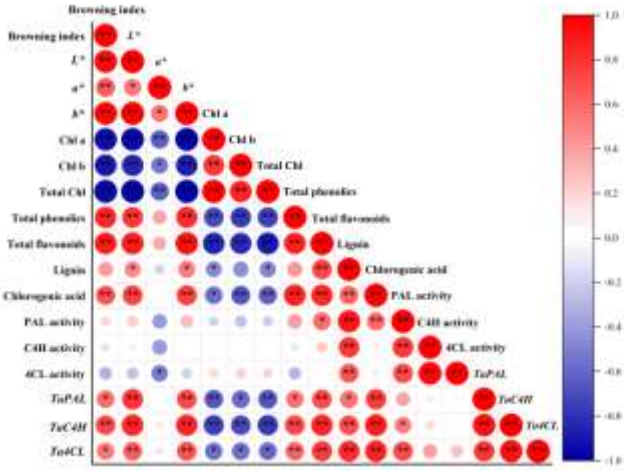


Figure 5. Pearson correlation coefficients of parameters during cold storage of dandelions after $CaCl_2$+ε-PL treatment. *P<0.05 and **P<0.01.

3.6. Principal component analysis (PCA) of storage quality of dandelions

3.6.1. Determination of the number of principal components

As shown in Figure 6, dandelion leaves treated in different ways can be easily distinguished in separate spaces. The distributions of the $CaCl_2$ and ε-PL single treatments were close to each other, indicating no significant difference between the two groups. In contrast, the $CaCl_2$+ε-PL treatment and control groups were distributed in the upper left quadrant and upper right quadrant, respectively, and were not in the same quadrant as the other two groups. This indicated that the $CaCl_2$+ε-PL treatment group was significantly different from the other three groups. Table 2 shows that the cumulative variance contribution of PC1 (88.293%) and PC2 (6.079%) was 94.372%, and the eigenvalues of both PC1 and PC2 were greater than 1. Therefore, it indicated that the two extracted principal components can better reflect the freshness preservation effect of dandelions during cold storage.

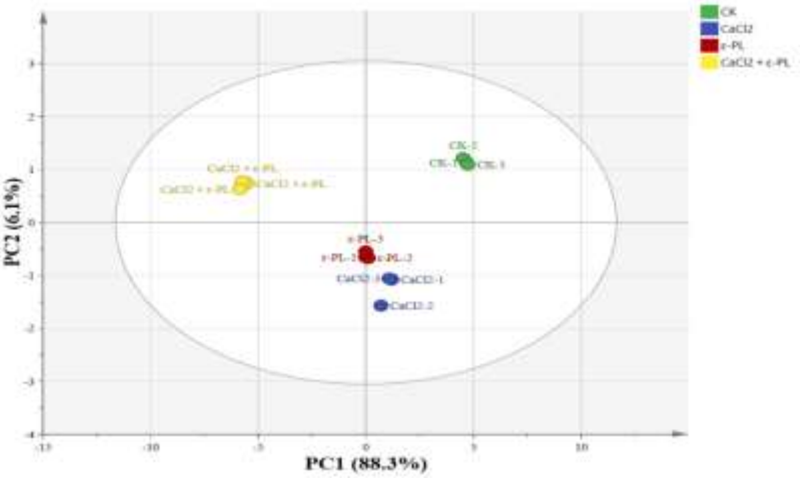


Figure 6. PCA diagram of each treatment during cold storage of dandelions.

Table 2. Eigenvalues and variance contributions of each principal component

ID	Characteristic root			Principal component extraction		
	Characteristic root	Variance explanation rate (%)	Accumulate rate (%)	Characteristic root	Variance explanation rate (%)	Accumulate rate (%)
1	15.010	88.293	88.293	15.010	88.293	88.293
2	1.033	6.079	94.372	1.033	6.079	94.372
3	0.621	3.651	98.023	-	-	-

ID	Characteristic root			Principal component extraction		
	Characteristic root	Variance explanation rate (%)	Accumulate rate (%)	Characteristic root	Variance explanation rate (%)	Accumulate rate (%)
4	0.174	1.022	99.046	-	-	-
5	0.093	0.546	99.592	-	-	-
6	0.028	0.167	99.759	-	-	-
7	0.016	0.093	99.852	-	-	-
8	0.012	0.072	99.924	-	-	-
9	0.007	0.042	99.966	-	-	-
10	0.004	0.022	99.989	-	-	-
11	0.002	0.011	100.000	-	-	-
12	0.000	0.000	100.000	-	-	-
13	0.000	0.000	100.000	-	-	-
14	-0.000	-0.000	100.000	-	-	-
15	-0.000	-0.000	100.000	-	-	-
16	-0.000	-0.000	100.000	-	-	-
17	-0.000	-0.000	100.000	-	-	-

"-" means the characteristic root less than 1, so it is not included in the core analysis.

3.6.2. Composite score of PCA

A comprehensive evaluation system for the storage quality of dandelions was constructed based on PCA. The results showed that the composite quality score (F-value) was obtained by extracting the two principal components with variance contributions of PC1 (88.293%) and PC2 (6.079%) and calculating them using a weighted linear combination method as follows. A higher F value represents better storage quality of dandelions.

F_1=–0.251×Z_1–0.240×Z_2–0.255×Z_3+0.255×Z_4+0.235×Z_5+0.256×Z_6–0.215×Z_7+0.244×Z_8+0.240×Z_9+0.221×Z_{10}+0.229×Z_{11}+0.255×Z_{12}+0.257×Z_{13}+0.249×Z_{14}+0.228×Z_{15}+0.245×Z_{16}+0.243×Z_{17} (Z_i data need to be standardized)

F_2=0.144×Z_1+0.126×Z_2+0.008×Z_3–0.016×Z_4–0.179×Z_5–0.036×Z_6+0.521×Z_7+0.119×Z_8–0.050×Z_9+0.010×Z_{10}–0.443×Z_{11}–0.020×Z_{12}+0.047×Z_{13}+0.235×Z_{14}+0.435×Z_{15}+0.311×Z_{16}+0.319×Z_{17} (Z_i data need to be standardized)

F=(88.293×F_1 + 6.079×F_2)/94.372%

F_1 and F_2 are the first and second principal component scores, respectively.

As shown in Table 3, the F-values of the four groups of dandelions during cold storage were sorted as follows: $CaCl_2$+Ɛ-PL>Ɛ-PL>$CaCl_2$>control. This indicates that the $CaCl_2$+Ɛ-PL treatment had the best preservation effect on dandelions.

Table 3. Principal component score and comprehensive score of dandelions treated in different ways during cold storage

Treatment group	F_1	F_2	F
Control	0.083	0.041	0.080
$CaCl_2$	0.472	0.192	0.454
Ɛ-PL	0.809	0.348	0.780
$CaCl_2$+Ɛ-PL	2.150	1.468	2.107

4. Discussion

Leaf senescence is a major postharvest problem in leafy vegetables, mainly characterised by leaf yellowing, decay, and browning, and the retention of green color is critical in postharvest quality assessment of leafy vegetables (Able et al., 2005). Dandelion leaves are prone to yellowing and regional browning during storage. In the present study, the changes in the L^*, a^*, and b^* values showed that all four groups of dandelion leaves gradually turned yellow during cold storage. Leaf yellowing is a typical feature of plant senescence and is usually caused by the breakdown of Chl (AI Ubeed et al., 2018; Xylia et al., 2021). Similarly, a decrease in the contents of Chl a, Chl b, and total Chl of dandelions was found during cold storage in this study. Meanwhile, it was found that the combination treatment of $CaCl_2$ and ε-PL on postharvest dandelion leaves delayed the color change and Chl loss (Figure 1), and also alleviated the increase in the browning index (Figure 2). Li et al. (2023) treated postharvest Chinese flowering cabbage with melatonin, which inhibited Chl degradation and delayed leaf senescence. Song et al. (2023) found that treatment with melatonin was able to inhibit Chl degradation, thereby delaying the yellowing of pak choi, which is consistent with the results of this study.

PAL, 4CL, and C4H are three key enzymes of phenylpropanoid metabolism, which start from phenylalanine and gradually convert to 4-coumarate-coenzyme A, with dimensionally different branching subclass metabolism to provide precursors (Toscano et al., 2019). Liu et al. (2023) found that postharvest methyl jasmonate treatment significantly activated the gene expression levels and enzyme activities of PAL, C4H, and 4CL, involved in phenylpropanoid metabolism, which in turn facilitated the accumulation of secondary metabolites (total phenolic content and total flavonoid content) in lily scales, thereby increasing their nutritional value. The results of this study also showed that $CaCl_2$+ε-PL treatment can alleviate the decrease in the enzyme activities of PAL, C4H, and 4CL (Figure 4A–4C), up-regulate the gene expression levels of *TaPAL*, *Ta4CL*, and *TaC4H*, and maintain higher contents of total phenolics, total flavonoid, lignin, and chlorogenic acid (Figures 3A–3D). Phenylpropanoid metabolism is a unique secondary metabolic pathway in plants that plays an important role in antioxidant and disease resistance (Dong et al., 2024). Phenolics and flavonoids have strong non-enzymatic antioxidant activity and may help maintain the normal function of the reactive oxygen species (ROS) scavenging system (Morrissey, 2009). Phenolics can alleviate oxidative stress damage in plants by providing protonated hydrogen, scavenging ROS or breaking down peroxides (Rivero et al., 2001). Similarly, flavonoids in plants play an important role in the defense system with their strong free radical scavenging ability (Silva et al., 2002). The contents of phenolics and flavonoids directly affect the ROS scavenging capacity, and a decrease in phenolic and flavonoid contents may be associated with a decrease in the activities of shikimate dehydrogenase (SKDH), PAL, and 4CL, as well as a downregulation in the expression of *PuPAL* and *Pu4CL* (Sun et al., 2022). Ozone treatment at appropriate concentrations enhances the antioxidant capacity of strawberry fruit by increasing the total phenolic content and total flavonoid content through the promotion of key proteins associated with phenylpropanoid metabolism (Chen et al., 2019). Para-coumaric acid and cinnamic acid treatments can induce the activities of PAL, C4H, and 4CL and the contents of major metabolites (phenolics, flavonoids, and lignin), enhance antioxidant-related enzyme activities, and attenuate brown blotch disease in *Agaricus bisporus* mushrooms (Shi et al., 2025).

In the present study, the results of correlation analysis revealed that PAL activity showed a positive correlation with *TaC4H* and *Ta4CL* gene expression, and a positive correlation was shown between total phenolic content and total flavonoid content, both of which were positively correlated with *TaC4H* and *Ta4CL* gene expression. Similar results were obtained in a study on cantaloupe (Ren et al., 2024). In addition, there was a negative correlation between secondary metabolites and Chl content. This may be due to the fact that Chl a, Chl b, and total Chl contents in the four groups of dandelion leaves showed a gradual decreasing trend during the storage period, whereas the contents of secondary metabolites first increased but then decreased. This significant upward process may be responsible for their negative correlation. Similar variations were found in other leafy vegetables. The Chl a and Chl b contents of postharvest Chinese flowering cabbage gradually decreased during 1–4 d of storage, while the contents of total phenolics and total flavonoid increased (Chen et al., 2023). With the increase in the yellowing index of pak choi, the values of L^*, a^*, and b^* gradually increased, while the Chl content showed a decreasing trend, the total phenolic content first increased but then decreased; and the total flavonoid content fluctuated, but there was also a process of elevation. 2-

Ethylhexanol treatment significantly inhibited the yellowing of pak choi, and the content of chlorogenic acid in the treated leaves was significantly elevated on the 5 d of storage, which was higher than that of the control ($P<0.01$) (Wang et al., 2025). It was speculated that postharvest dandelion leaves may trigger defense responses and activate phenylpropanoid metabolism due to cutting damage at harvest and exposure to stresses such as new environments (changes in temperature, humidity, etc.) (Liu et al., 2025b). In this study, the $CaCl_2$, ε-PL, and $CaCl_2$+ε-PL treatments better promoted the accumulation of secondary metabolites. At the later stage of storage, the contents of secondary metabolites may gradually decrease due to factors such as a low level of synthesis and depletion of antioxidant defense.

The yellowing and senescence of postharvest Chinese flowering cabbage are attributed to higher respiration levels, ethylene synthesis, and ROS accumulation, and the combined effects of ROS metabolism and the phenylpropanoid pathway delay the senescence of acetylsalicylic acid- and salicylic acid-treated leaves (Zhang et al., 2022). Melatonin has been shown to up-regulate the expression of flavonoid biosynthesis-related genes (*BrPAL3*, *BrC4H*, *Br4CL*, *BrFLS1*, *BrFLS2*, *BrFLS3.1*, *BrFLS3.2*, and *BrFLS4*), especially *BrFLS1* and *BrFLS3.2*, during postharvest senescence and to promote the accumulation of flavonoid, thereby delaying leaf senescence in postharvest flowering Chinese cabbage (Yue et al., 2023). It has also been shown that phenolic compounds act as non-enzymatic antioxidants with the ability to delay fruit senescence and maintain postharvest fruit quality (Guo et al., 2023). Marine-derived *Bacillus velezensis* fermentation broth treatment could prolong the shelf life of strawberry, and enhance PAL, C4H, and 4CL activities and the accumulation of phenolic compounds (Yang et al., 2024). It is therefore inferred that phenylpropanoid metabolism and accumulation of secondary metabolites also play an important role in delaying senescence in leafy vegetables. Similarly, in fruits, phenylpropanoid metabolism plays an important role in cantaloupe ripening and senescence, and ozone treatment helps maintain postharvest firmness of cantaloupe and promotes the production and accumulation of secondary metabolites in cantaloupe, such as total phenolics, flavonoid, and lignans (Ren et al., 2024).

5. Conclusions

In summary, the $CaCl_2$ and ε-PL single treatments and combination treatment had different effects on the postharvest quality of dandelions, with the $CaCl_2$+ε-PL composite treatment of dandelions achieving the greatest results. $CaCl_2$+ε-PL treatment effectively delayed leaf yellowing and Chl degradation and reduced the browning index of the leaves to some extent. $CaCl_2$+ε-PL treatment could promote the synthesis and accumulation of secondary metabolites (total phenolics, total flavonoid, lignin, and chlorogenic acid) by enhancing the activities of the key enzymes of the phenylpropanoid metabolic pathway, such as PAL, 4CL, and C4H, and by up-regulating the expression levels of *TaPAL*, *Ta4CL*, and *TaC4H*, which could then improve the postharvest storage quality of dandelions. This suggests that the $CaCl_2$+ε-PL treatment provides an effective method for maintaining the storage quality of postharvest dandelions (Figure 7).

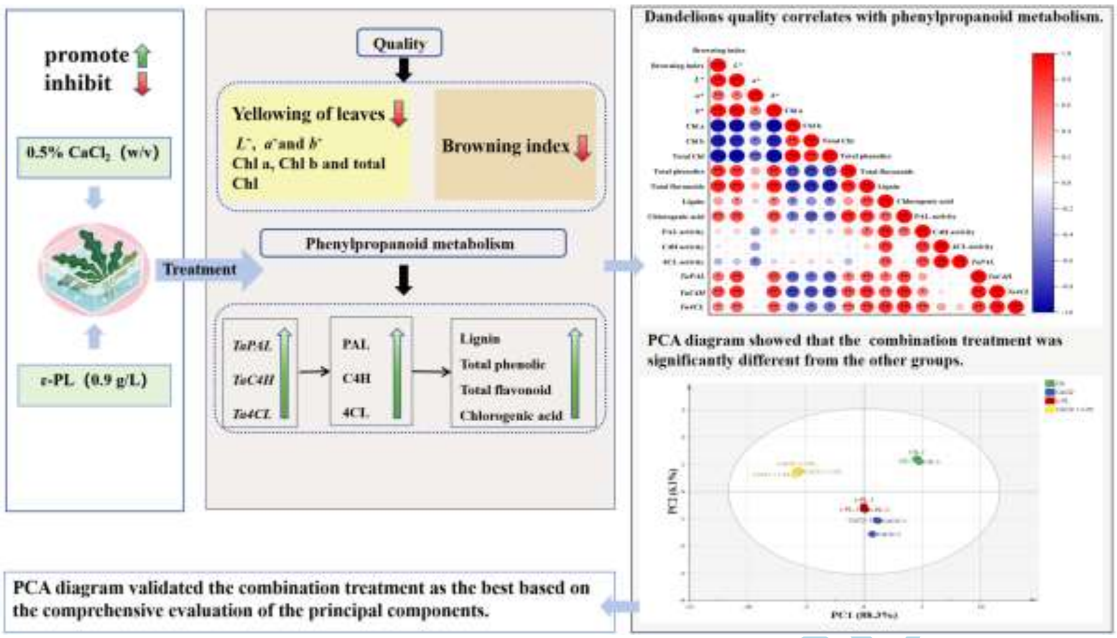


Figure 7. Model for the role of $CaCl_2$+ε-PL treatment in maintaining postharvest quality of dandelions during cold storage at 4±0.5 °C.

CRediT authorship contribution statement

Xin Zhou: Writing original Draft, data Curation, review and editing, and conceptualization. Xinyuan Shi: Writing original draft, data Curation, and review and editing. Mingyue Wang: Conceptualization and visualization. Yulu Jiang: Methodology and visualization. Hanfei Wang: Software. Siyao Wang: Resources. Qian Zhou: Project administration and review and editing. Jie Wu: Funding acquisition, project administration, and resources.

Declaration of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

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Graphical

abstract

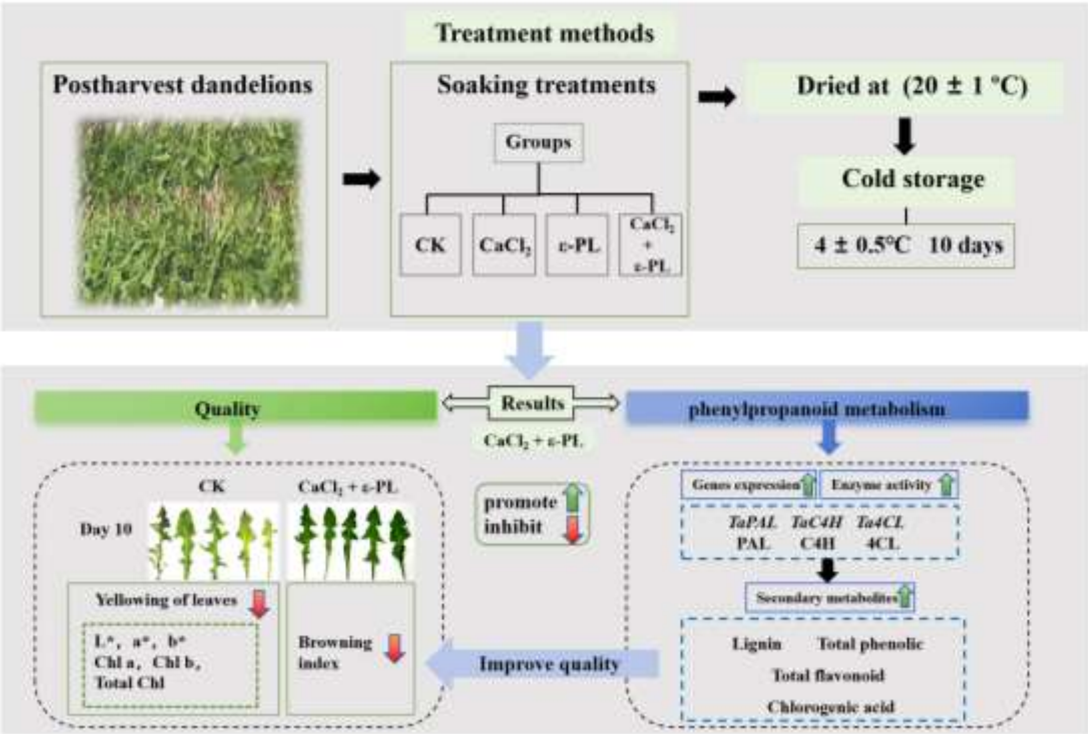

Treatment methods
Postharvest dandelions
Soaking treatments
Groups
CK
$CaCl_2$
ε-PL
$CaCl_2$ + ε-PL
Dried at (20 ± 1 °C)
Cold storage
4 ± 0.5°C 10 days
Quality
Results
$CaCl_2$ + ε-PL
phenylpropanoid metabolism
CK
$CaCl_2$ + ε-PL
Day 10
Yellowing of leaves
L*, a*, b*
Chl a, Chl b,
Total Chl
Browning index
promote
inhibit
Improve quality
Genes expression
Enzyme activity
TaPAL TaC4H Ta4CL
PAL C4H 4CL
Secondary metabolites
Lignin Total phenolic
Total flavonoid
Chlorogenic acid

Figure_1A

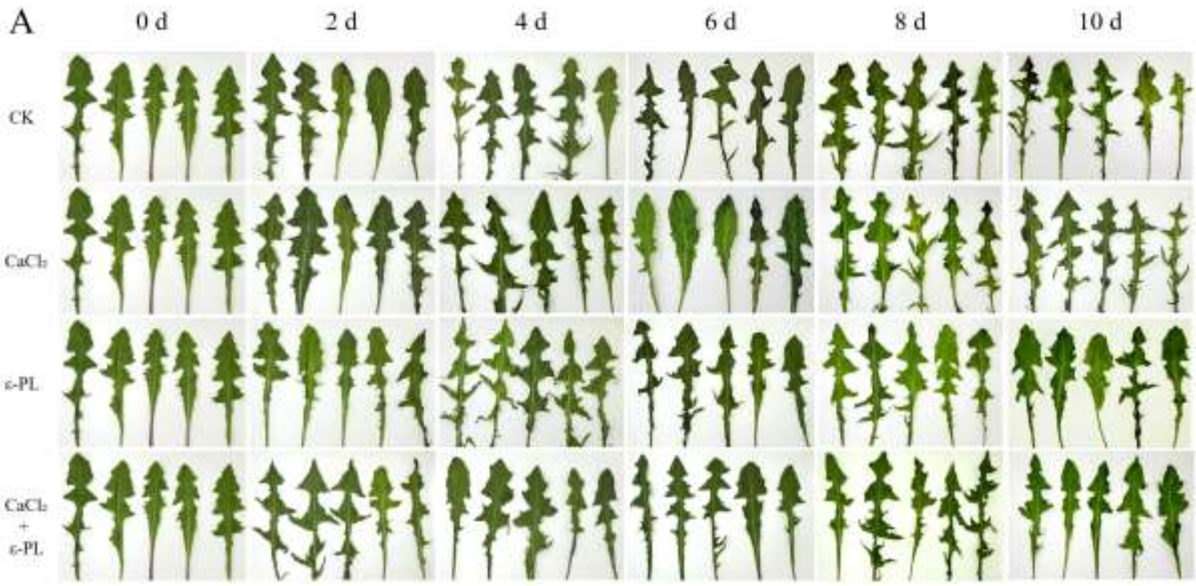


Figure_1B

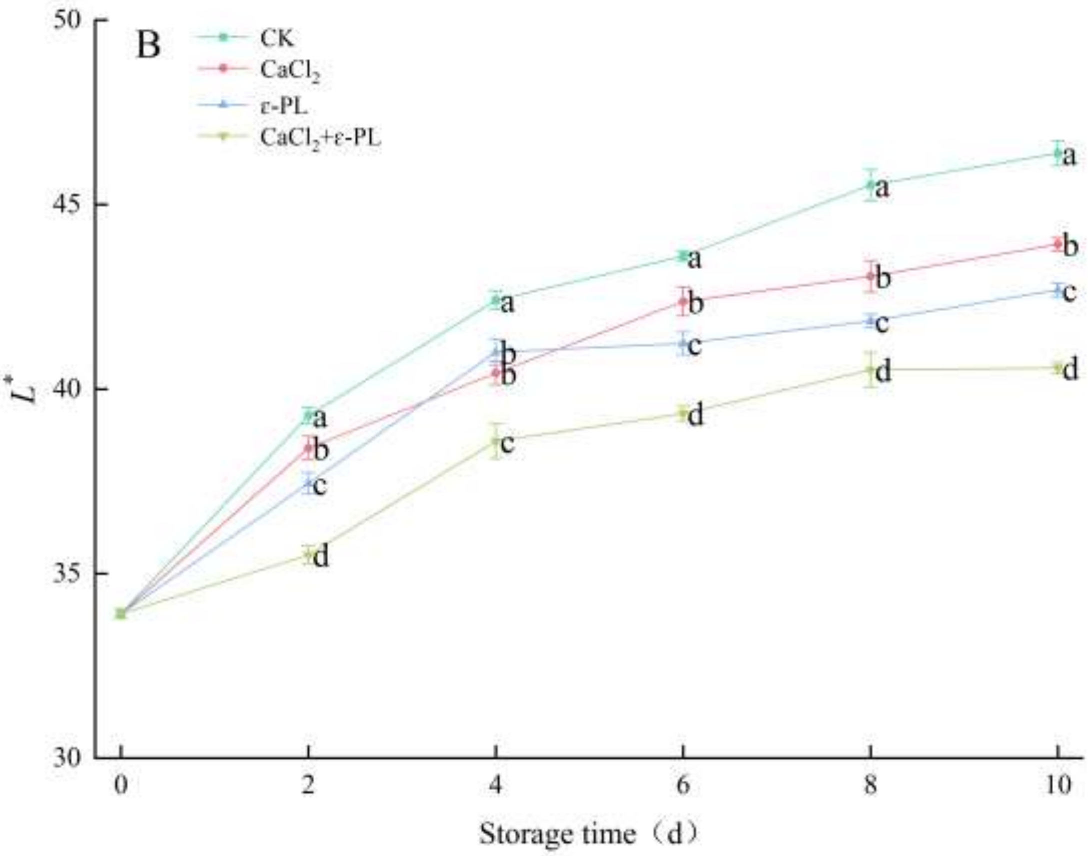

B
CK
$CaCl_2$
ε-PL
$CaCl_2$+ε-PL
L^*
50
45
40
35
30
0
2
4
6
8
10
Storage time（d）
a
b
c
d

Figure_1C

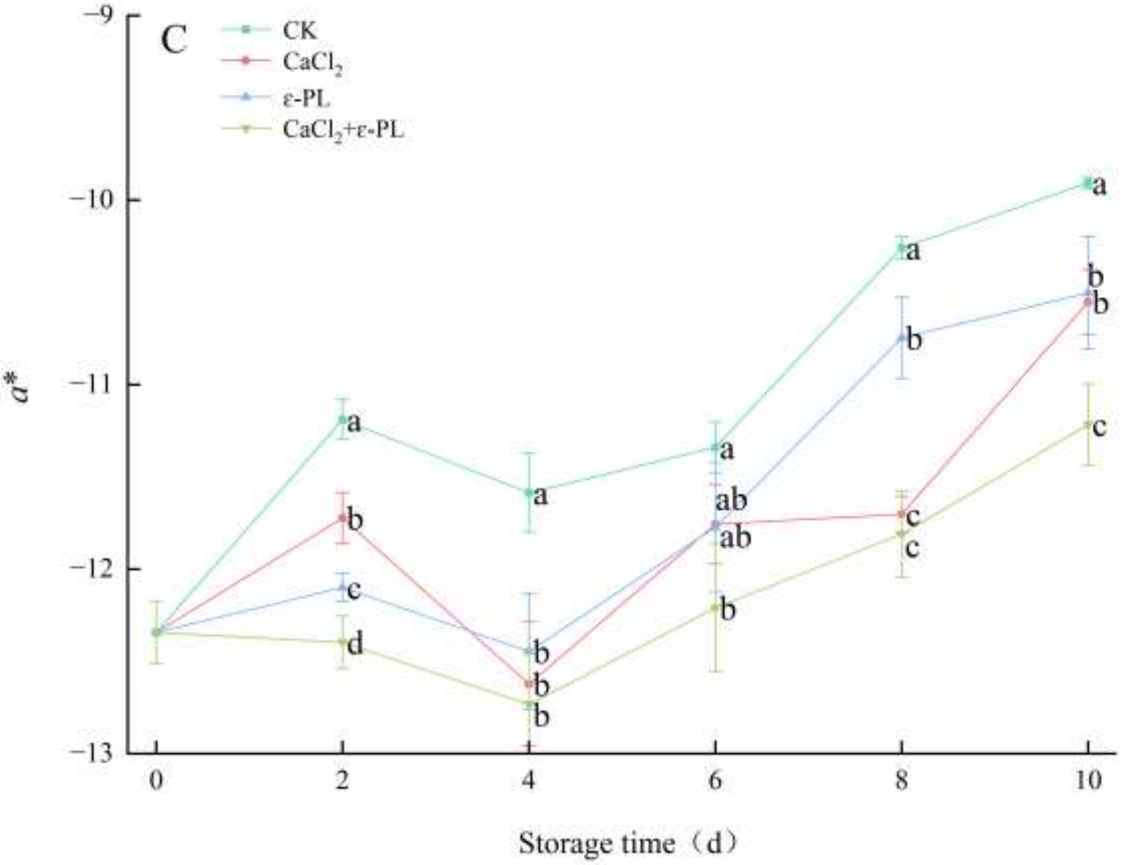

C
CK
CaCl2
ε-PL
CaCl2+ε-PL
a*
−9
−10
−11
−12
−13
0
2
4
6
8
10
Storage time（d）
a
b
c
d
ab

Figure_1D

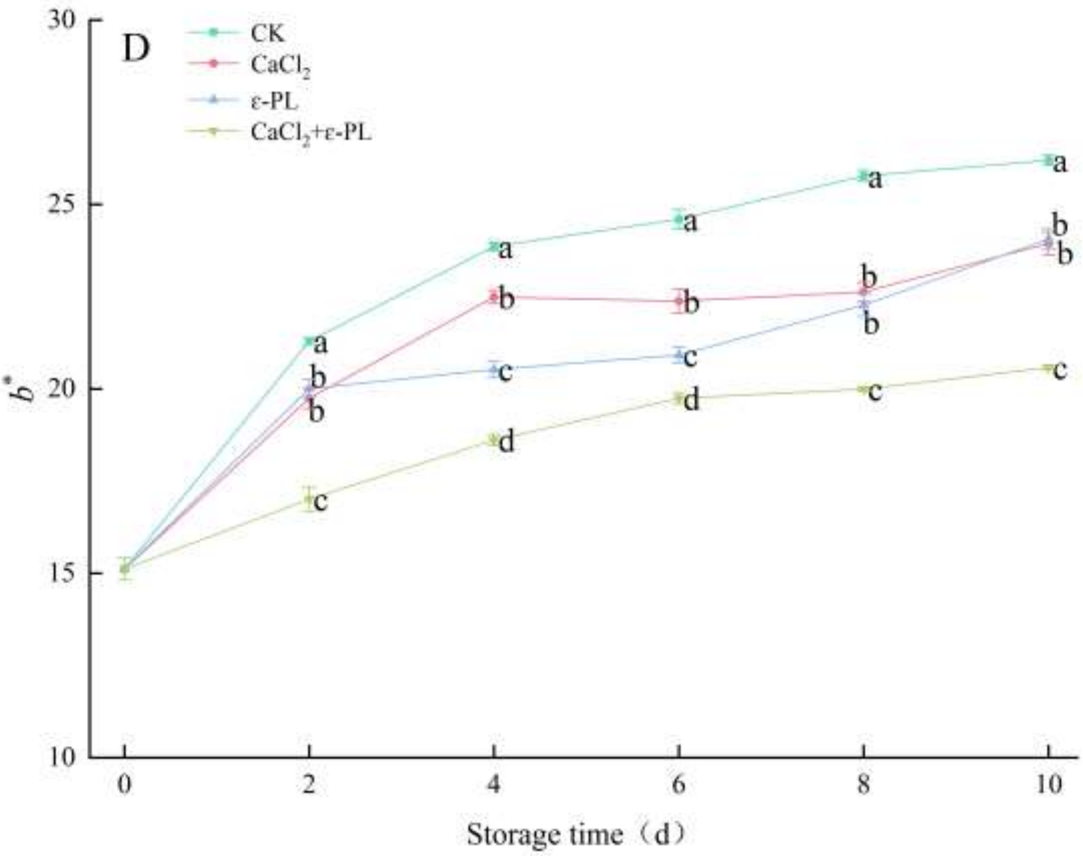

D
CK
$CaCl_2$
ε-PL
$CaCl_2$+ε-PL
b^*
Storage time（d）
30
25
20
15
10
0
2
4
6
8
10
a
b
c
d

Figure_1E

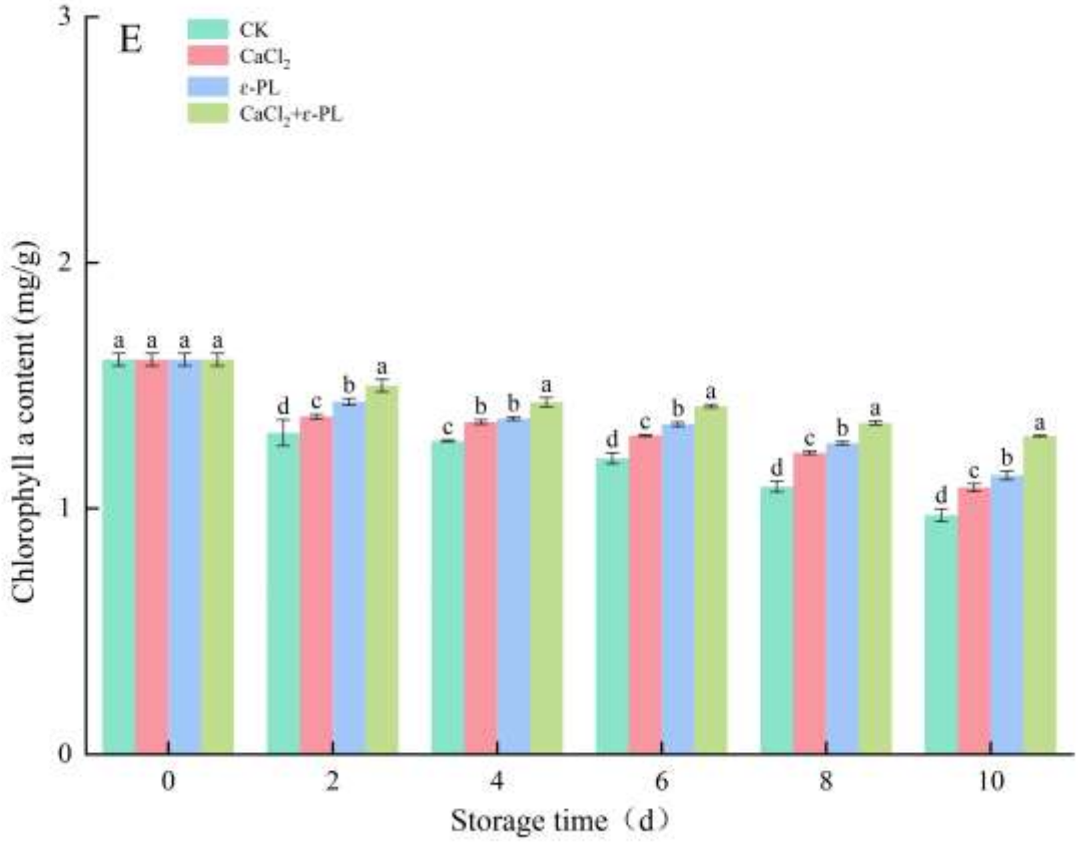
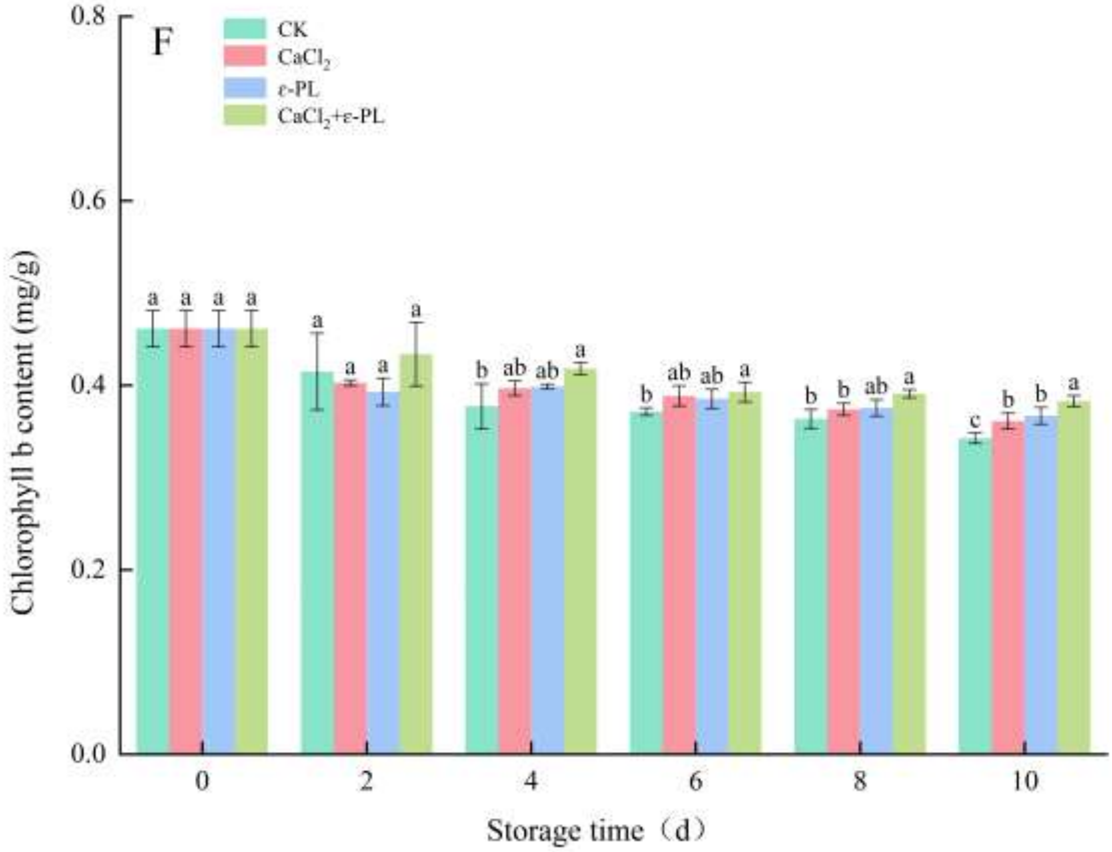
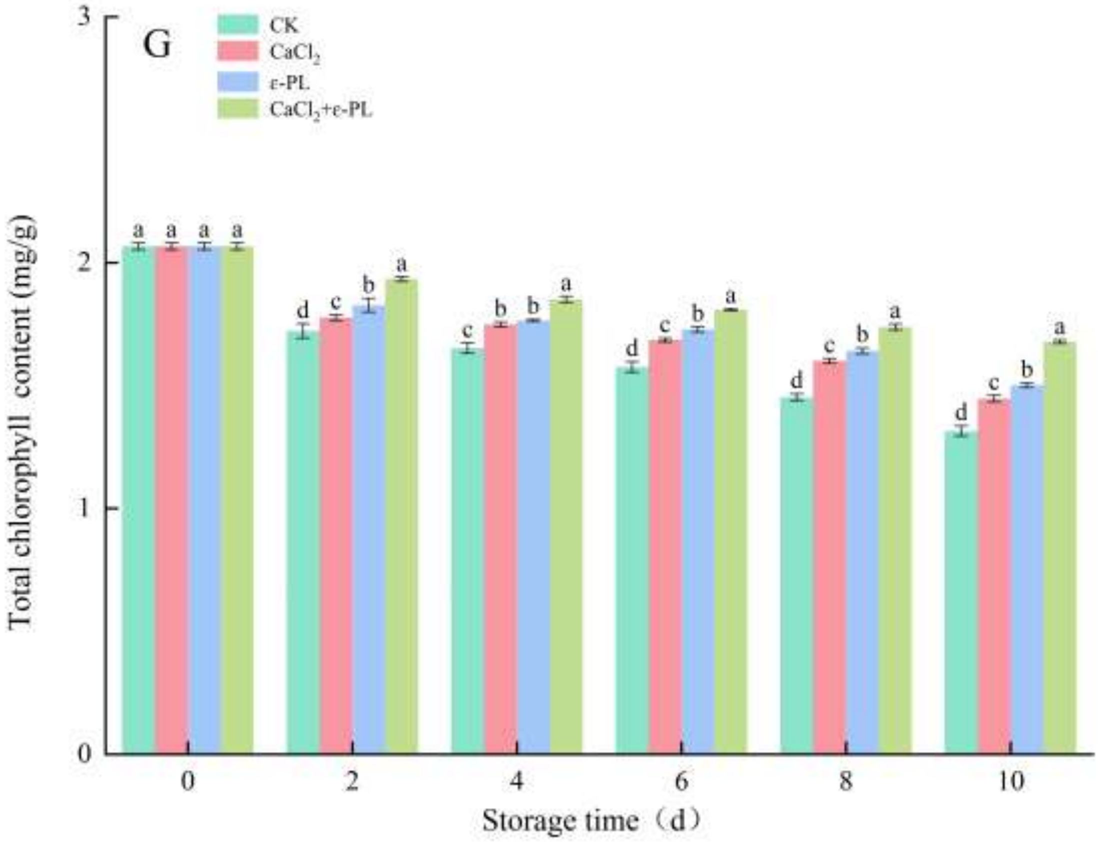

E
CK
CaCl2
ε-PL
CaCl2+ε-PL
Chlorophyll a content (mg/g)
Storage time（d）
0
1
2
3
0
2
4
6
8
10
a a a a
d c b a
c b b a
d c b a
d c b a
d c b a

Figure_1F



F
CK
CaCl2
ε-PL
CaCl2+ε-PL
Chlorophyll b content (mg/g)
0.0
0.2
0.4
0.6
0.8
0
2
4
6
8
10
Storage time（d）

Figure_1G



G
CK
$CaCl_2$
ε-PL
$CaCl_2$+ε-PL
Total chlorophyll content (mg/g)
Storage time（d）
0
1
2
3
0
2
4
6
8
10
a a a a
d c b a
c b b a
d c b a
d c b a
d c b a

Figure_2

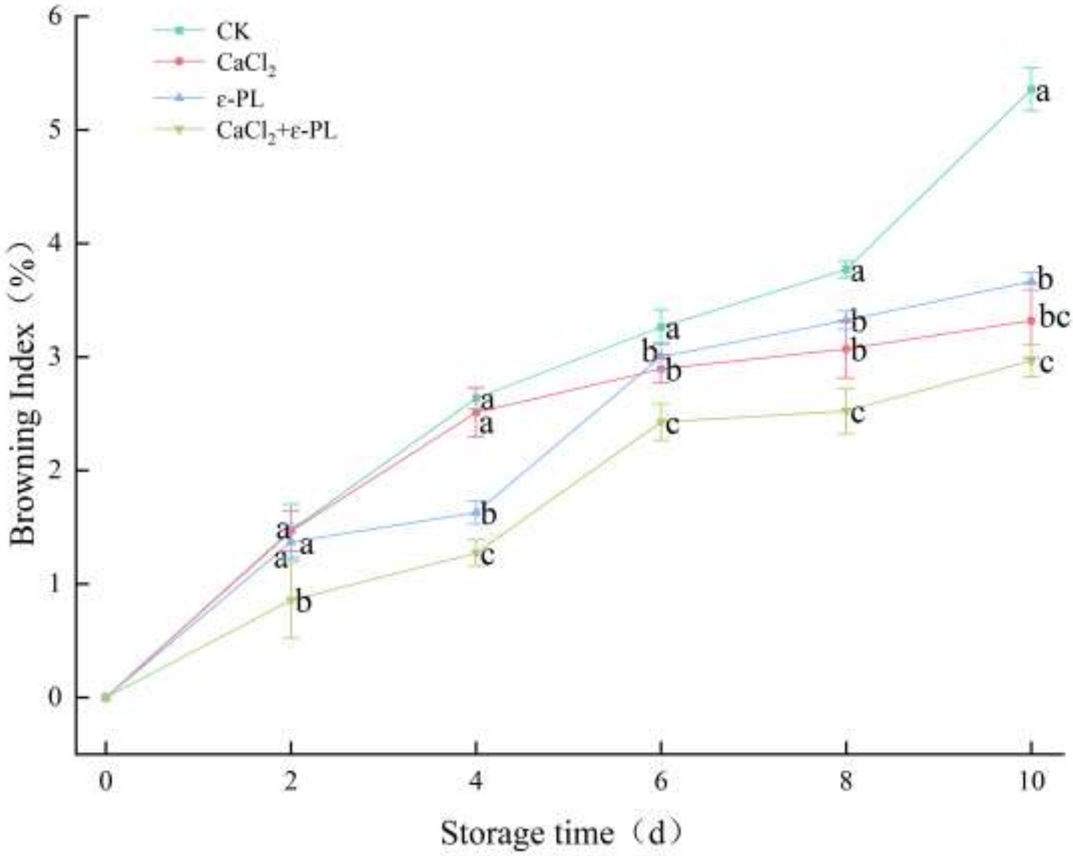
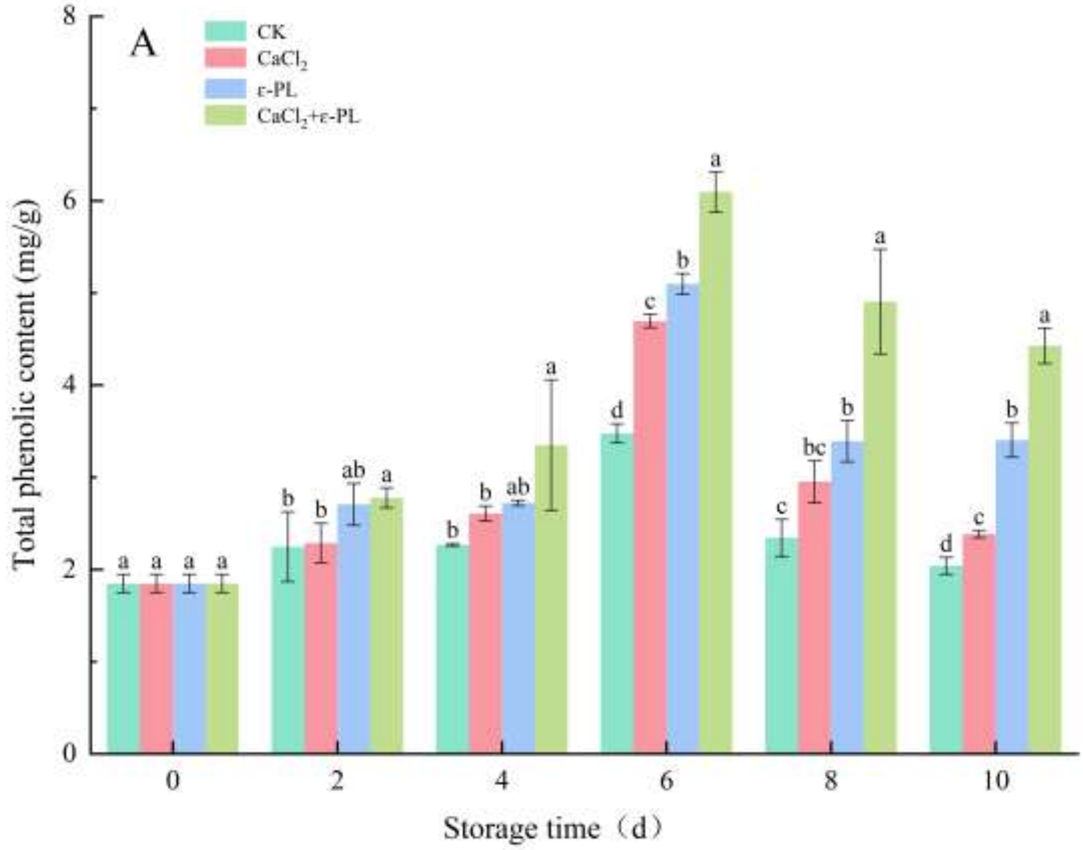

CK
CaCl2
ε-PL
CaCl2+ε-PL
Browning Index（%）
Storage time（d）
0
1
2
3
4
5
6
0
2
4
6
8
10
a
b
bc
c

Figure_3A



A
CK
$CaCl_2$
ε-PL
$CaCl_2$+ε-PL
Total phenolic content (mg/g)
Storage time（d）

Figure_3B

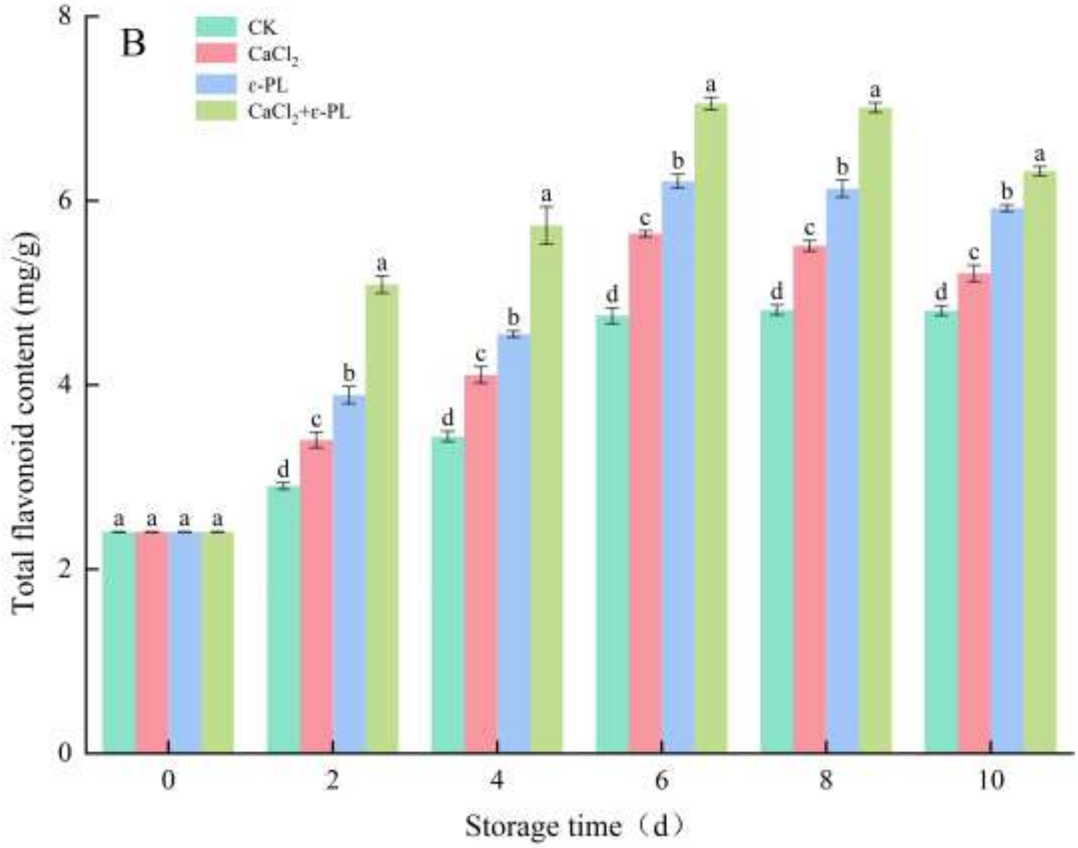

B
CK
$CaCl_2$
ε-PL
$CaCl_2$+ε-PL
Total flavonoid content (mg/g)
Storage time（d）
0
2
4
6
8
10
a a a a
d c b a
d c b a
d c b a
d c b a
d c b a

Figure_3C

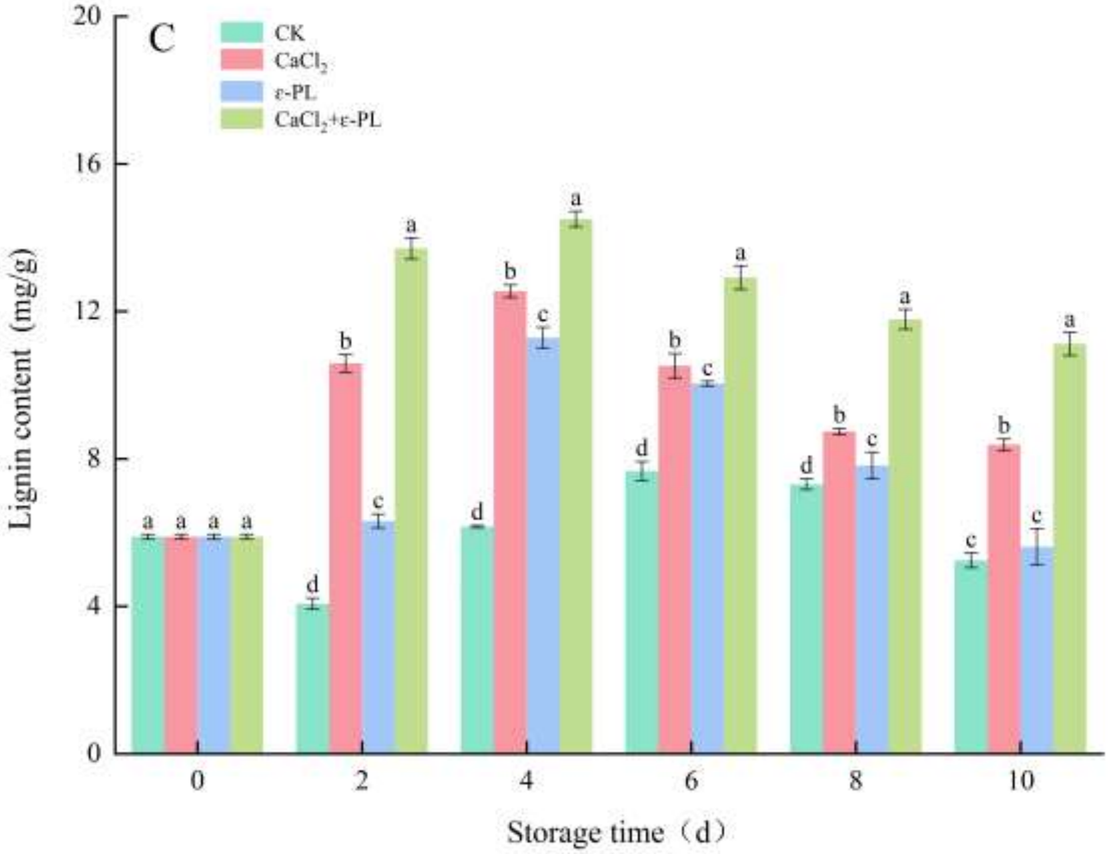
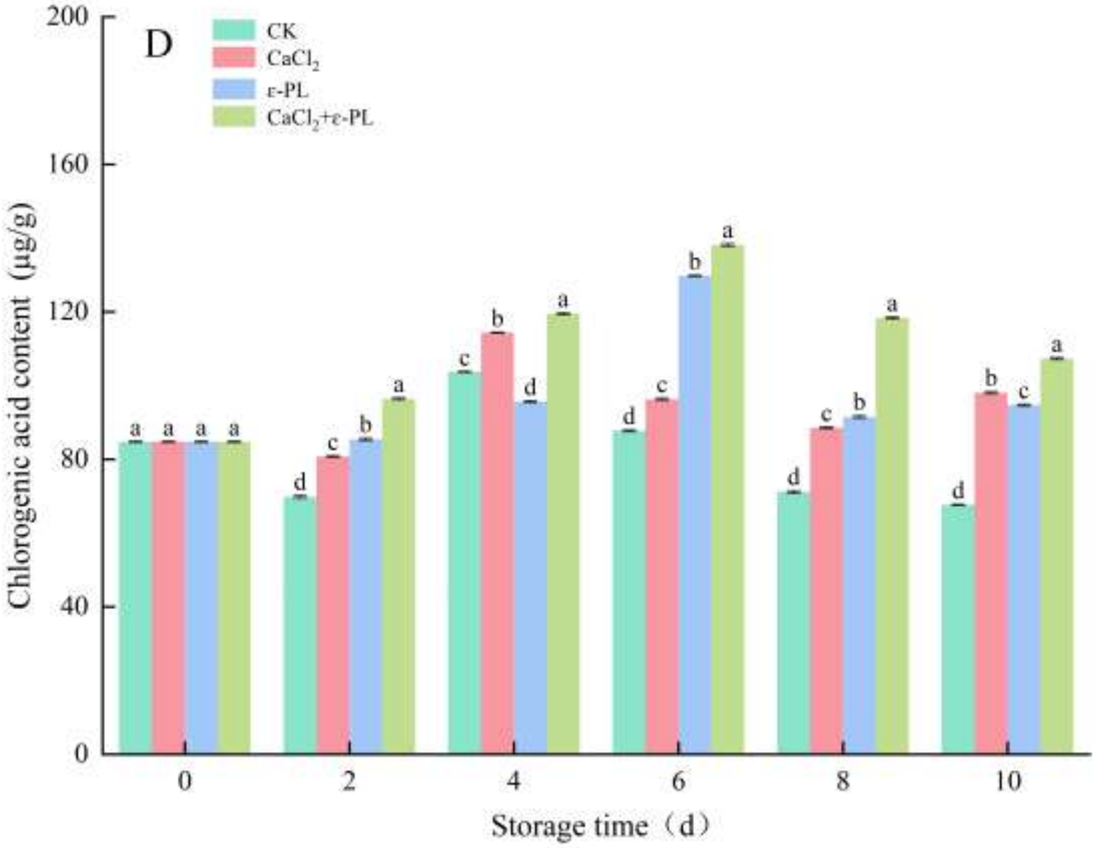
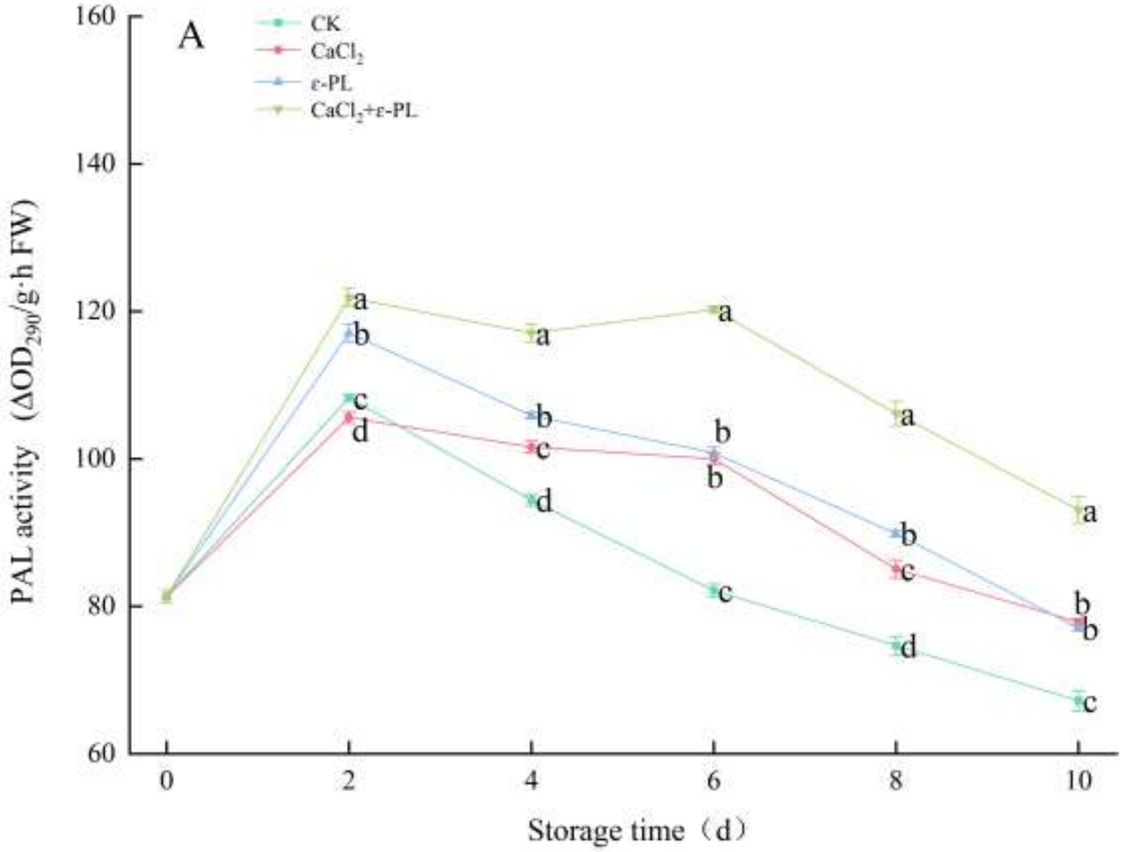

C
CK
$CaCl_2$
ε-PL
$CaCl_2$+ε-PL
Lignin content (mg/g)
Storage time（d）
0
4
8
12
16
20
0
2
4
6
8
10

Figure_3D



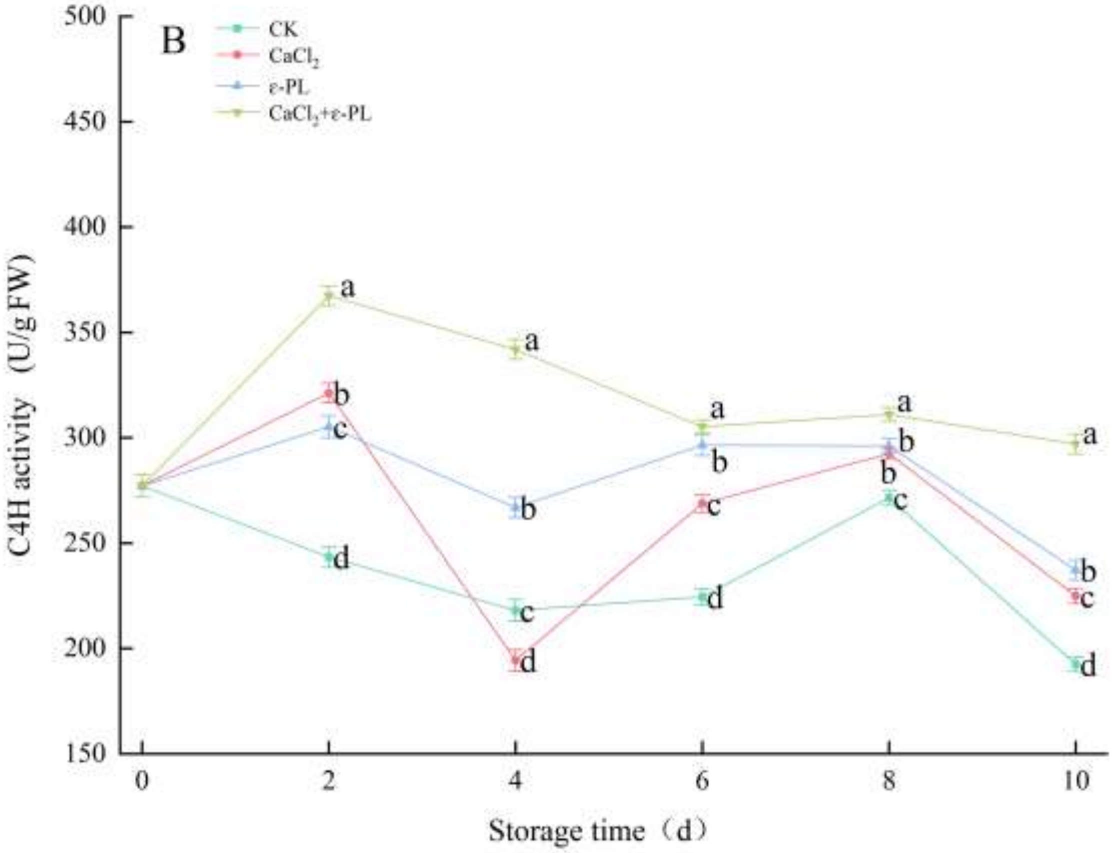
D
CK
CaCl2
ε-PL
CaCl2+ε-PL
Chlorogenic acid content (μg/g)
200
160
120
80
40
0
a
a
a
a
d
c
b
a
c
b
d
a
d
c
b
a
d
c
b
a
d
b
c
a
0
2
4
6
8
10
Storage time (d)

Figure_4A



A
CK
$CaCl_2$
ε-PL
$CaCl_2$+ε-PL
PAL activity (ΔOD_{290}/g·h FW)
Storage time（d）

Figure_4B



B
CK
CaCl2
ε-PL
CaCl2+ε-PL
C4H activity (U/g FW)
Storage time（d）
500
450
400
350
300
250
200
150
0
2
4
6
8
10
a
b
c
d

Figure_4C

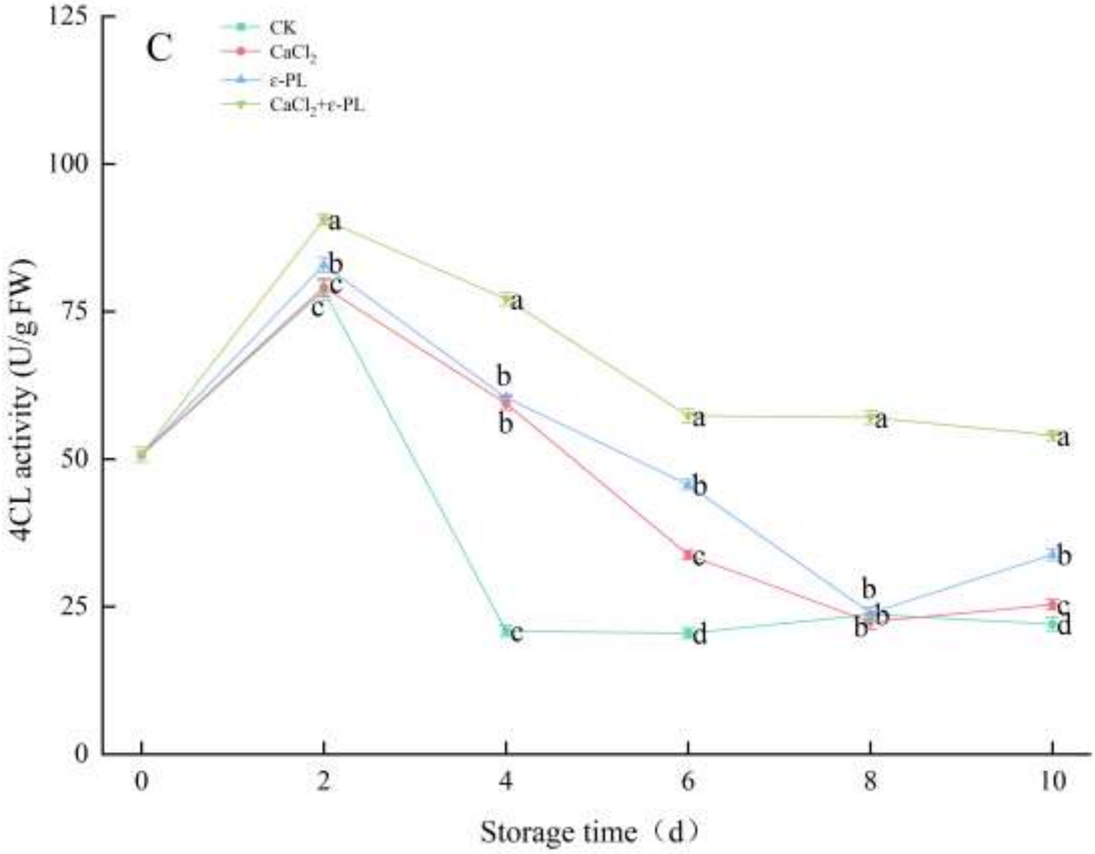
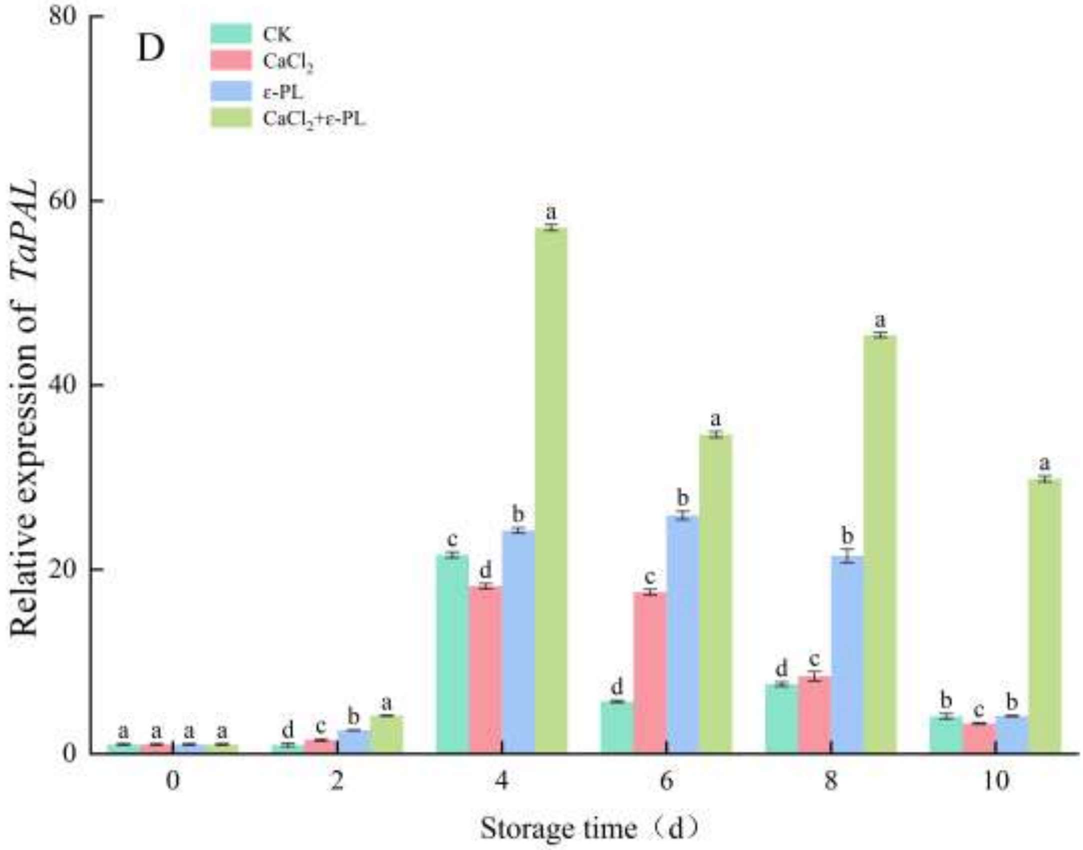


Figure_4D



D
CK
$CaCl_2$
ε-PL
$CaCl_2$+ε-PL
Relative expression of *TaPAL*
Storage time（d）
80
60
40
20
0
0
2
4
6
8
10

Figure_4E

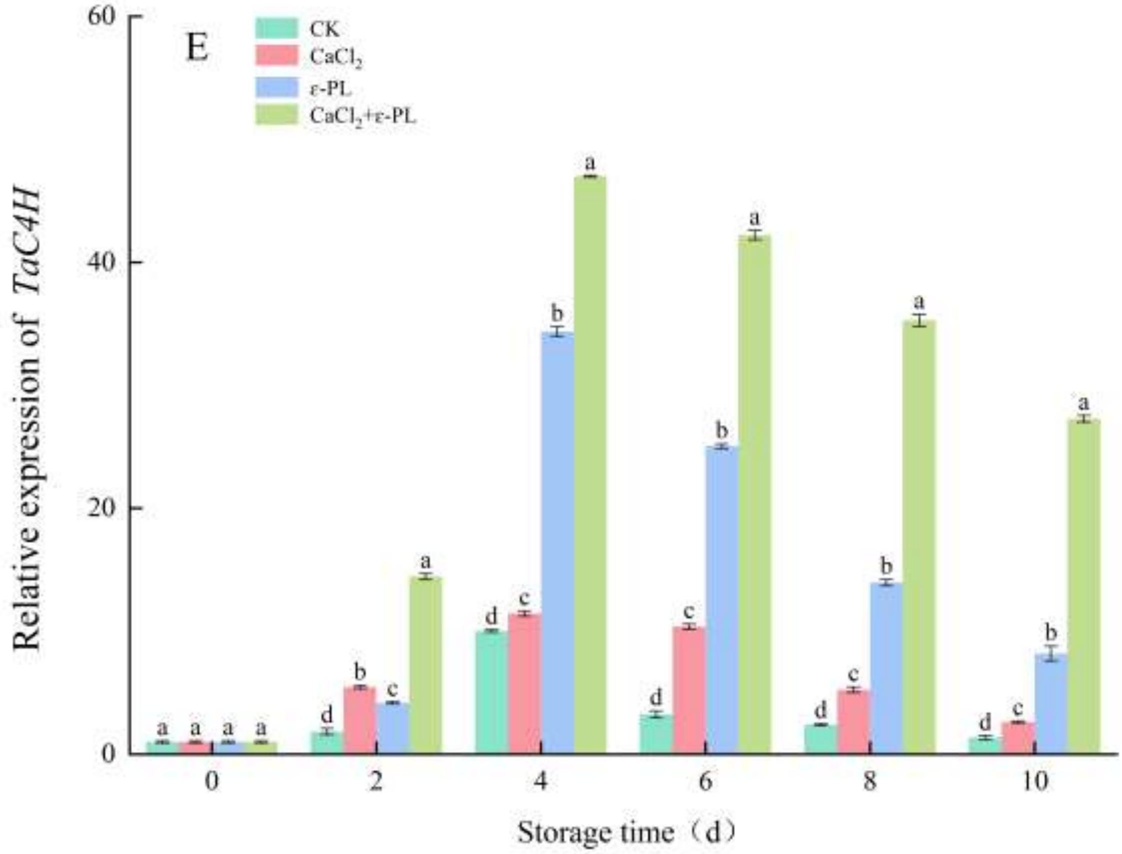

E
CK
CaCl2
ε-PL
CaCl2+ε-PL
Relative expression of TaC4H
Storage time（d）
0
20
40
60
0
2
4
6
8
10

Figure_4F

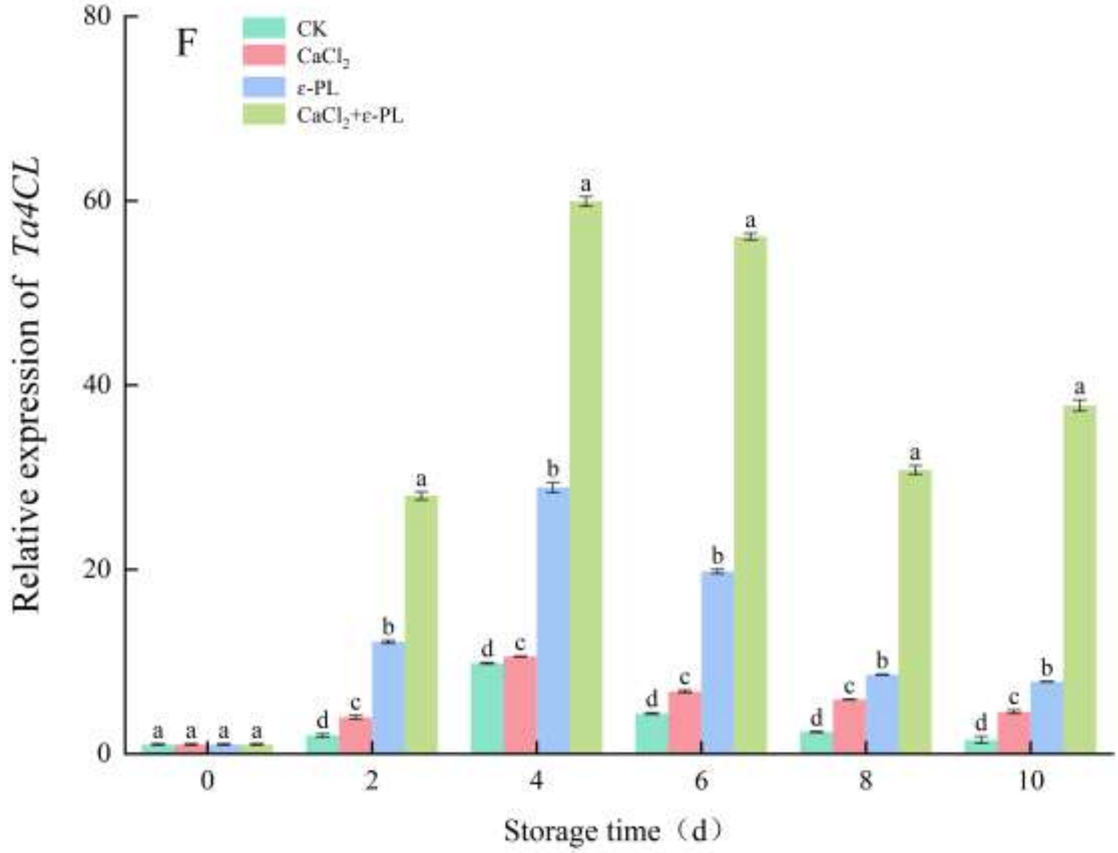

F
CK
CaCl2
ε-PL
CaCl2+ε-PL
Relative expression of Ta4CL
Storage time（d）
80
60
40
20
0
0
2
4
6
8
10

Figure_5

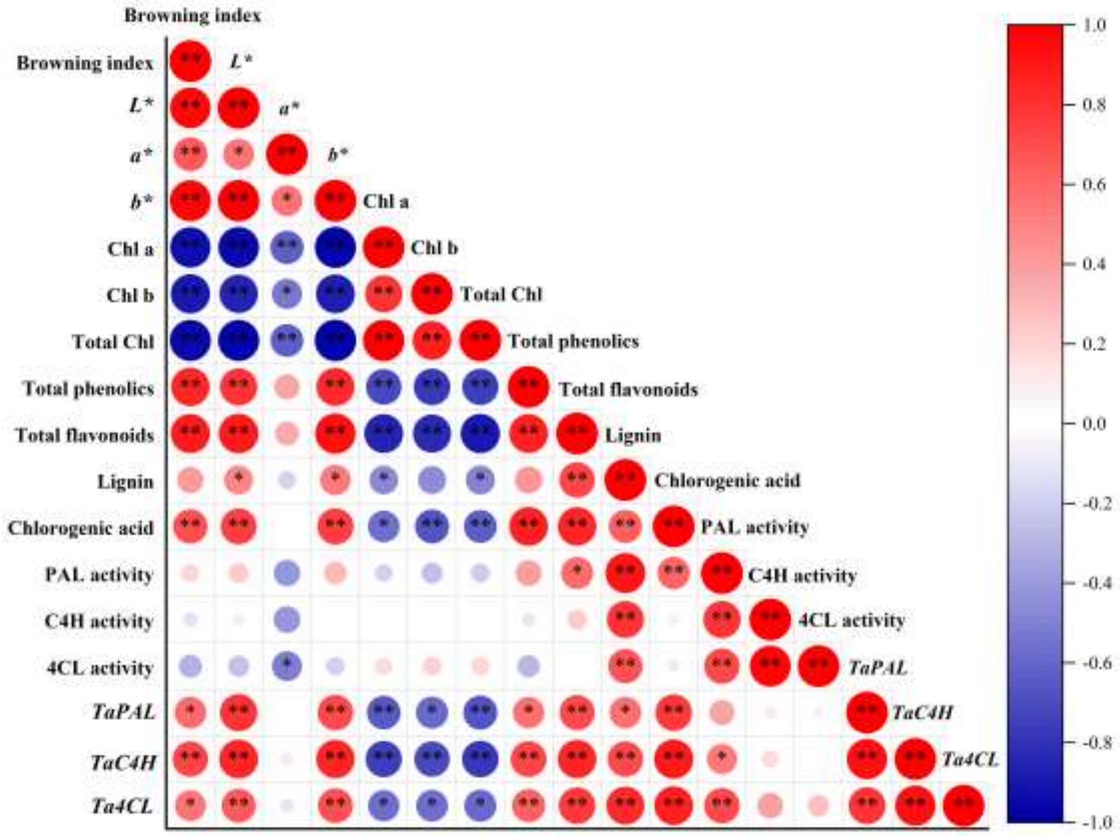
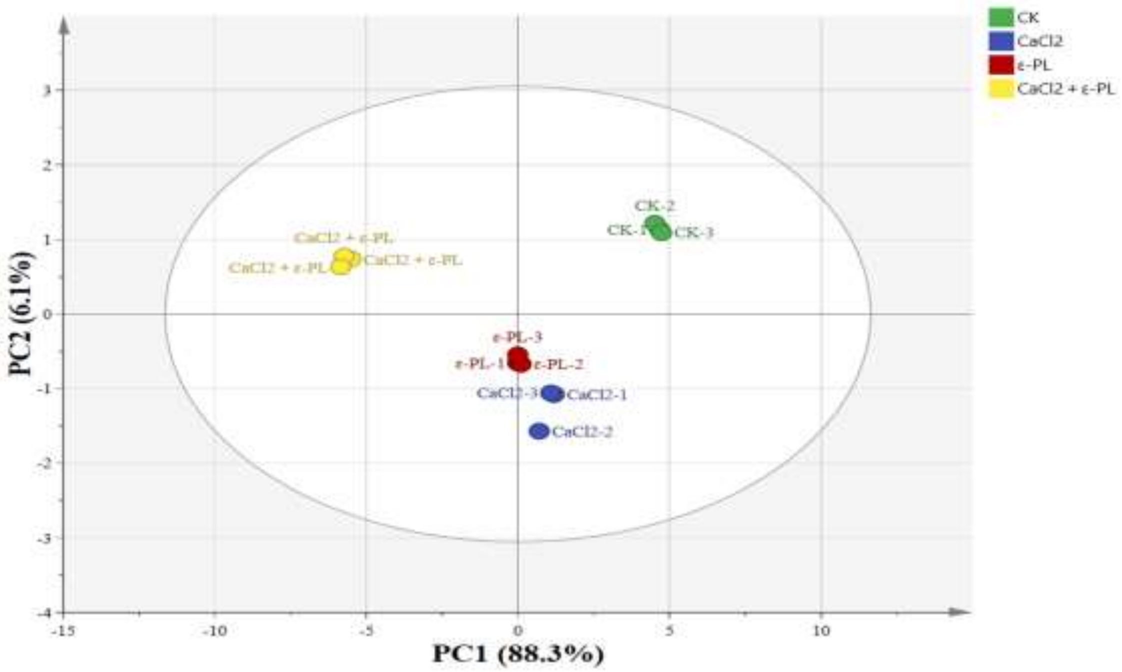
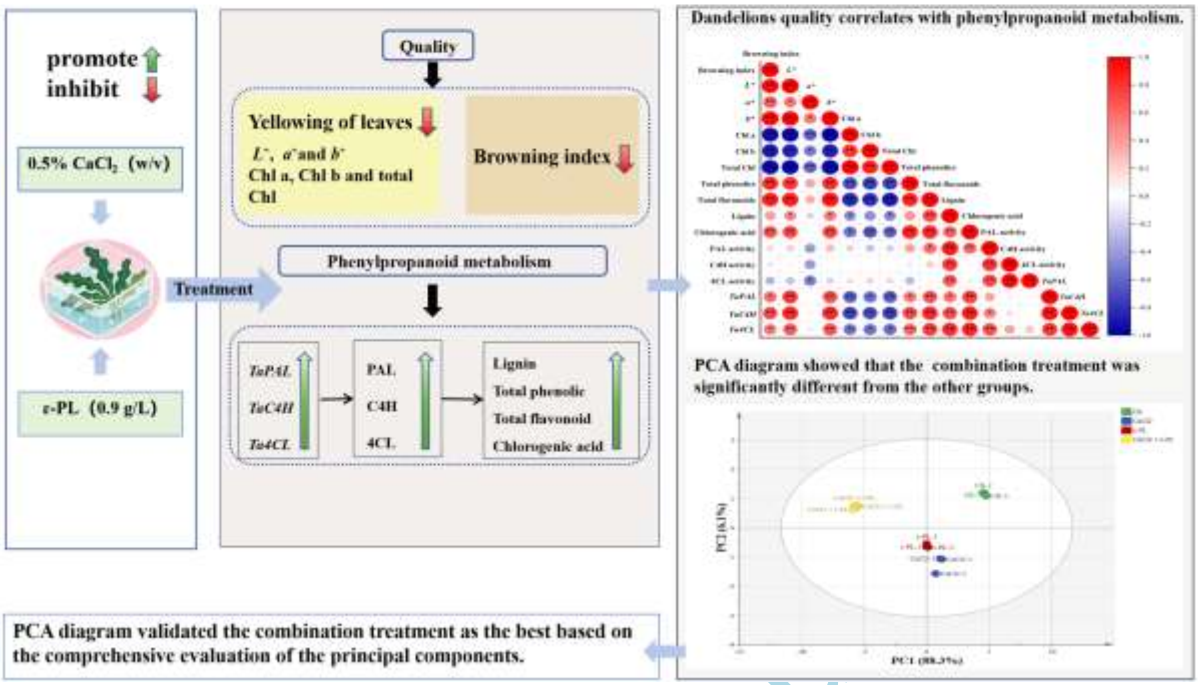

Browning index
L*
a*
b*
Chl a
Chl b
Total Chl
Total phenolics
Total flavonoids
Lignin
Chlorogenic acid
PAL activity
C4H activity
4CL activity
TaPAL
TaC4H
Ta4CL
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0

Figure_6



CK
CaCl2
ε-PL
CaCl2 + ε-PL
PC2 (6.1%)
PC1 (88.3%)
CK-2
CK-1
CK-3
CaCl2 + ε-PL
CaCl2 + ε-PL
CaCl2 + ε-PL
ε-PL-3
ε-PL-1
ε-PL-2
CaCl2-3
CaCl2-1
CaCl2-2

Figure_7



promote
inhibit
0.5% CaCl₂ (w/v)
ε-PL (0.9 g/L)
Treatment
Quality
Yellowing of leaves
L*, a* and b*
Chl a, Chl b and total Chl
Browning index
Phenylpropanoid metabolism
TaPAL
TaC4H
Ta4CL
PAL
C4H
4CL
Lignin
Total phenolic
Total flavonoid
Chlorogenic acid
Dandelions quality correlates with phenylpropanoid metabolism.
PCA diagram showed that the combination treatment was significantly different from the other groups.
PCA diagram validated the combination treatment as the best based on the comprehensive evaluation of the principal components.