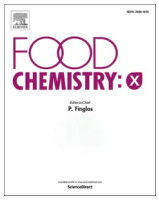
Food Chemistry: X 24 (2024) 102006

Contents lists available at ScienceDirect

Food Chemistry: X

journal homepage: www.sciencedirect.com/journal/food-chemistry-x



Modified atmosphere packaging maintains stem quality of Chinese flowering cabbage by restraining postharvest lignification and ROS accumulation

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ARTICLE INFO

Keywords:
Antioxidant capacity
Modified atmosphere packaging
Quality deterioration
Reactive oxygen species
Stem senescence
Vegetables

ABSTRACT

In this study, the impact of modified atmosphere packaging (MAP) on quality, lignin biosynthesis, reactive oxygen species (ROS) metabolism, and microstructures of stem in Chinese flowering cabbages was investigated. Compared with control, MAP treatment retained higher content of protein, total soluble solid, and vitamin C, while lower weight loss rate, carbon dioxide (CO_2) production rate, electrolyte leakage, firmness and hollowing of stems. Lignin content in MAP-treated stems was 1.23-fold higher than that of control stems on the twelfth day. Moreover, MAP treatment inhibited the increasing in cell wall thickness by inhibiting activities of lignin biosynthesis-related enzymes. In addition, MAP suppressed ROS contents, while enhanced levels of ascorbic acid and reduced glutathione through promoting activities of antioxidant enzymes. The above results suggest that maintaining stems quality of Chinese flowering cabbages through MAP treatment is related to prevent lignin accumulation around the vascular tissue and enhance antioxidant capacity.

1. Introduction

Chinese flowering cabbage, a leaf vegetable classified under the cruciferous brassica, is highly favored by consumers in South China owing to its delicious taste and rich nutritional value (Mou, Wang, Wei, et al., 2023). However, it is prone to leaf yellowing, wilting and decay, severely limiting its supply period in the market and consumers' preference. Although the shelf life of Chinese flowering cabbages can be prolonged under low temperature storage, its stems still deteriorate, showing hollowing and lignification with the progress of cold storage (Wang et al., 2020). Stem lignification in Chinese flowering cabbages leads to enhanced firmness (texture toughing), diminished taste, and reduced nutritional content, thereby significantly diminishing its commercial appeal (Ban et al., 2025). Hence, the management of lignification is crucial for preserving the quality of Chinese flowering cabbages under cold storage (Wang et al., 2023). In the previous study, it was found that modified atmosphere packaging (MAP) was an effective treatment to delay the leaf senescence of Chinese flowering cabbages (Mou, Wang, Wei, et al., 2023). However, the impact of MAP on the stem lignification of Chinese flowering cabbages remains unexplored.

Lignification refers to the metabolic process in which lignin accumulates in the plant cell walls. Lignin biosynthesis generally involves two steps: the synthesis of monolignols and the subsequent polymerization reaction between these monolignols (Alejandro et al., 2012). There is a broad consensus that monolignols originates from phenylalanine through a sequence of enzymatic reactions. Key catalytic enzymes involved in this process include those found in the phenylpropanoid pathway upstream of phenylalanine, such as phenylalanine ammonia-lyase (PAL), 4-coumarate coenzyme A ligase (4CL), and cinnamate 4-hydroxylase (C4H), as well as enzymes in specific monolignols pathway

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https://doi.org/10.1016/j.fochx.2024.102006
Received 10 September 2024; Received in revised form 3 November 2024; Accepted 13 November 2024
Available online 15 November 2024
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like cinnamyl alcohol dehydrogenase (CAD), p-hydroxycinnamoyl-CoA: quinate/shikimate hydroxycinnamoyl transferase cinnamoyl-CoA reductase, etc. (Zhao, 2016). Subsequently, monolignols are transfered into the cell wall and polymerized by laccase (LAC) and peroxidase (POD) to form lignin macromolecules (Wang et al., 2013). In general, changes in enzymes and corresponding gene expression in the lignin biosynthesis pathway can affect lignin content. For example, observations on postharvest loquat fruit indicated a progressive rise in the activity of lignin-related enzymes, showing a positive correlation with lignin content throughout the storage period (Li et al., 2017). Conversely, inhibiting the activity of PAL, C4H, and 4CL contributed to a delay in lignin accumulation in horticultural products like asparagus spears (Toscano et al., 2018), bamboos shoots (Li et al., 2019), kiwifruit (Jin et al., 2021), and mushrooms (Wang, Li, et al., 2022). From the results of available studies, these enzymes mentioned above may also be the potential targets in regulation of stem lignification of Chinese flowering cabbage.

As signaling molecules, reactive oxygen species (ROS) function in the modulation of plant senescence and respond to various stresses (Mittler et al., 2011). Numerous postharvest treatments have proven that delay the senescence of fruits and vegetables and maintain the storage quality by modulating ROS production. For instance, microporous modified atmosphere packaging (MMAP) improved the activity of antioxidant enzymes, reduced the excessive accumulation of ROS, delayed postharvest senescence and rot of winter jujube, and maintained a high sensory quality (Zuo et al., 2024). Lei et al. (2022) demonstrated that MMAP could stimulate heightened antioxidant enzyme activity, thus preserving a superior antioxidant capacity and maintaining quality of strawberries. Moreover, a positive relevance between the level of ROS and lignin accumulation had been reported previously, implying that ROS might mediate lignin synthesis (Denness et al., 2011). For instance, Huang et al. (2016) found that cell lignification process is accompanied by the burst of ROS, and a large accumulation of both lignin and hydrogen peroxide (H_2O_2) could be observed during infection of root-knot nematode in rice. The lignification observed in postharvest mushrooms could be linked to the increased ROS concentration (Wang et al., 2019). Iron deficiency stress would increase ROS content and cause root lignification in pear (Donnini et al., 2011). ROS could expedite the lignification in postharvest bamboo shoots by enhancing the activities of phenylpropanoid pathway-related enzymes (Li et al., 2019). Moreover, the synthesis of lignin involves the polymerization of various lignin monomers catalyzed by peroxidase and laccase to form lignin. In this process, POD mainly used H_2O_2 as an electron acceptor to react (Renard et al., 2020). Nonetheless, the connection between postharvest ROS metabolism and stem lignification in Chinese flowering cabbages remains uncertain and requires further investigation.

The primary goal of this study is to evaluate the influence of MAP on stem lignification and ROS homeostasis during senescence. The parameters examined include quality attribute, epidermal microstructure, lignin content and lignin synthesis-related enzymes, ROS production and ROS-scavenging system in Chinese flowering cabbage. Findings from this work aim to reveal the possible mechanism by which MAP influences the stem senescence and quality deterioration through phenylpropanoid pathway and ROS metabolism during storage, and provide new insights into the deterioration of stem quality induced by lignification.

2. Materials and methods

2.1. Plant materials and treatments

The Chinese flowering cabbages used in this work were sourced from a vegetable farmland situated in proximity to Guangzhou. The selection criteria for the cabbages include uniform stem lengths and thickness, as well as the absence of pests, diseases, damage, and flower buds.

Treatments: the chosen cabbages were sealed with modified polyethylene film (supplied by Sericultural and Agri-Food Research Institute, Guangdong Academy of Agricultural Sciences; thickness, 30 μm; water vapor transmission rate: 17.812 $g/m^2/day$; O_2 transmission rate: 5625 $cm^3/m^2/day/atm$; CO_2 transmission rate: 8437.5 $cm^3/m^2/day/atm$), which was designed as MAP treatment. Moreover, the samples were packed with conventional commercial polyethylene film packaging (thickness, 30 μm), which was designed as Control group. The concentration of O_2 and CO_2 both in the modified polyethylene film and conventional commercial polyethylene film bags was 20.3 % and 0.03 %, respectively. Each packaging contains four Chinese flowering cabbages. Following packaging, the cabbages were stored at 8 ± 1 °C. During storage, the stem tissues between the second and fourth leaves (counting from base to top) were periodically sampled at designated intervals (0 d, 3 d, 6 d, 9 d and 12 d), and promptly frozen at −80 °C for subsequent experimental analysis.

2.2. Determination of quality attributes

Total soluble solid (TSS) level of stem was assayed by a refractometer (PAL-2, Atago, Japan). Contents of protein and ascorbic acid (AsA) were measured with biochemical kits according to the procedure outlined by Mou, Wang, Wei, et al. (2023); Mou, Wang, Zeng, et al. (2023), and the results were expressed as mg g^{-1} and μg g^{-1}, respectively.

Stem firmness was measured using a durometer (GY-4, Tuopu, China), fitted with a cylinder probe (2 mm diameter). The measurement of firmness was taken at the midpoint of the stem (approximately 2–3 cm above the base) and expressed as the N.

Six packages of cabbages were selected from the two groups (three packages per group) and their initial weights were accurately recorded post-selection. Subsequently, at different time courses (3 d, 6 d, 9 d, and 12 d), six packages of cabbages were weighted, respectively, regard as current weight. The weight loss rate was computed with the formula:

$$\text{Weight loss rate}\ (\%) = \frac{(\text{origin weight} - \text{current weight})}{\text{origin weight}} \times 100 \qquad (1)$$

2.3. Measurement of respiration rate and electrolyte leakage

The respiration rate was conducted based on the description of Tan et al. (2021). Briefly, four cabbages were put into a container and sealed at storage temperature for 3 h. Subsequently, a milliliter of the headspace gas collected from the container was gathered and injected into gas chromatograph fitted with thermal conductivity detector. Data were represented as mg kg^{-1} h^{-1}.

The electrolyte leakage rate was assayed referring to the previous method (Li, Huang, et al., 2021). Fifteen discs (1 cm in diameter) obtained from stems of fifteen Chinese flowering cabbages were put into test tubes, 20 mL of deionized water was added for a shock treatment of 1 h. Then, the initial conductivity was determined using a conductometer, and the test tube was kept into boiling water at 100 °C for 20 min, cooling to room temperature. The conductivity was measured again by the conductometer. The relative conductivity was expressed by the ratio of the first and last electrical conductivity.

2.4. Measurement of lignin content

Lignin content was measured following the method outlined by Wang et al. (2020). Stem samples were subjected to freeze-drying for a duration of 12 h, and the resultant dried samples were further processed by grinding into a fine powder and filtered by a 40-mesh sieve. Two mg of sieved powder were then precisely measured and utilized for determining the lignin content. This analysis was conducted following the detailed instructions provided with the detection kit (MZS-1-G, Suzhou Keming Biotechnology Co., Ltd., China). Lignin content was expressed as mg g^{-1}.

2.5. Histochemical staining

The degree of lignification in stem tissues was determined by staining cross section slices with Weisner reagent (phloroglucinol-HCl) (Blanco-Portales et al., 2002). The stem tissues (about 2–3 cm above the bottom) of Chinese flowering cabbages were cut into discs with a thickness of 2 mm. Collected discs were immersed into 1 % phloroglucinol (Beijing Solarbio Science & Technology Co., Ltd., China, analytical reagent) for 5 min. Subsequently, 1 mL of concentrated hydrochloric acid was added to the cross-section of the soaked cabbage discs to induce the Wiesner reaction. After 5 min, the color of cross-section of stem discs was observed, and the presence of red coloration indicated lignin deposition.

2.6. Microstructure observation by scanning electron microscope (SEM)

The alterations of stem tissue microstructures were observed utilizing SEM, adhering to the methodology detailed by Wang et al. (2023). Briefly, transverse sections (measuring 3 × 3 mm from the external layer to the inner pith) were sliced and subsequently immersed in 3 % glutaraldehyde (0.1 M phosphate buffered saline (PBS), pH 6.8, Beijing Solarbio Science & Technology Co., Ltd., China, analytical reagent). Following this, the tissue sections were washed in a PBS buffer before being systematically dehydrated. Dehydration was carried out using ethanol solutions of 30 %, 50 %, 70 %, 80 %, 90 %, and 100 % (v/v) (analytical reagent from Shanghai Acmec Biochemical Technology Co., Ltd., China), with each concentration for 10 min. Dehydrated samples were dried in a freeze-dryer (EP CPD300, Leica, Germany) and sputter coated with gold in ion sputter coater (EM ACE600, Leica, Germany). Finally, the observation was performed using a SEM (EVO MA 15, ZEISS, Germany) at 30 kV accelerating voltage.

2.7. Assay of activity of lignin biosynthetic enzymes

The enzymatic activities of PAL, C4H, 4CL and CAD was evaluated according to the method as described by Shen et al. (2024), using commercial assay kits produced from Suzhou Keming Biotechnology Co., Ltd., China. PAL activity was represented as U g^{-1}, whereas C4H, 4CL and CAD activities was represented as nmol min^{-1} g^{-1}.

2.8. Measurement of ROS metabolism-related parameters

2.8.1. Determination of superoxide anion ($O_2^{\bullet-}$) production rate, H_2O_2 and malondialdehyde (MDA) content

The quantities of H_2O_2, MDA content and the generation rate of $O_2^{\bullet-}$ production rate in the cabbage stem tissue were measured adherence to the detailed procedures outlined by Mou, Wang, Wei, et al. (2023). The result of $O_2^{\bullet-}$ production rate, H_2O_2 and MDA content was expressed as nmol g^{-1} min^{-1}, μmol g^{-1} min^{-1} and nmol g^{-1} on a fresh weight basis, respectively.

2.8.2. Determination of antioxidant enzyme activity

Activity of superoxidase (SOD), catalase (CAT), POD, monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), ascorbate peroxidase (APX), and glutathione reductase (GR) were analyzed following the methodology outlined by Tan et al. (2020).

2.8.3. Determination of antioxidant content in ascorbic acid (AsA)-glutathione (GSH) cycle

The concentrations of dehydroascorbic acid (DHA), reduced GSH, and oxidized glutathione (GSSG) in the stems of Chinese flowering cabbages was measured, following the protocol outlined by Mou, Wang, Wei, et al. (2023). GSSG content was represented as nmol g^{-1}, while DHA and GSH content was represented as μmol g^{-1}.

2.9. Statistical analysis

The data are depicted as mean values ± standard errors based on three biological replicates. Statistical analysis to determine significant differences at the 0.05 or 0.01 level between mean values was conducted using Student's *t*-test in GraphPad Prism.

3. Results

3.1. Senescence and quality changes in stem of Chinese flowering cabbages under MAP treatment

After harvest, the stems of fresh Chinese flowering cabbage typically exhibit a green color, firm texture, and high water content. Stems senescence developed gradually during storage, as manifested by hollows in the middle of the stems on the third day of storage. The stems hollowing aggravated severely after 6 d of storage, while MAP obviously alleviated this process (Fig. 1A). Meanwhile, content of nutrient components in stems, including protein, total soluble solid, and vitamin C, declined as the hollowing of stems advanced; however, the utilization of MAP effectively slowed down these reductions (Fig. 1B-D). On day 7, protein and vitamin C levels in the MAP-treated stems was 10.93 % and 37.85 % higher than those in control stems, respectively. In contrast to the nutrient components, the weight loss rate of Chinese flowering cabbages constantly rose during storage (Fig. 1E). At the peak of stem hollowing on the twelfth day, the weight loss rate was reached to 1.51 % in control stems. In addition, the CO_2 production rate (Fig. 1F) and electrolyte leakage rate (Fig. 1G) increased from 0 d to 6 d, after which they were declined in control stems. However, MAP treatment inhibited the increase of weight loss rate, respiration rate and electrolyte leakage rate throughout the storage period. These data show that MAP is an effective strategy to delay stem senescence of Chinese flowering cabbages.

3.2. Changes in firmness, lignin accumulation, and microstructure in stem of Chinese flowering cabbages under MAP treatment

During the initial six days, stem firmness saw a progressive rise, followed by a mild decrease over the remainder of the storage duration (Fig. 2A). Notably, the application of MAP exerted a significant ($P < 0.05$) dampening effect on the increase of firmness. By the end of storage period, stem treated with MAP displayed a 13.64 % reduction in stem firmness compared to that in the control group. In parallel, the lignin content in control stems exhibited a sustained upward trend (Fig. 2B), rose from 1.37 mg g^{-1} to 2.01 mg g^{-1} over the storage period. However, MAP treatment markedly suppressed the buildup of lignin, resulting in an 18.89 % reduction compared to the control group.

As depicted in Fig. 2C, the vascular bundle cells in the peeled tissues and parenchyma cells in pith tissues were regularly arranged at the harvest day (Fig. 2C1—C2). The cell wall of vascular bundle was thin, and the surrounding pith cells were closely arranged. Following stems senescence, noticeable changes were observed in the control group where the cell wall of the vascular bundle thickened, and the demarcation between the vascular bundle cells and pith cells became more distinct (Fig. 2C5—C6, C9C10). On day 12, an obvious increase in cell wall thickness of vascular bundle in the control group was appeared compared with day 0 (Fig. 2C9—C10), while MAP treatment inhibited the cell wall thickening of vascular bundle and maintained stems structure (Fig. 2C11—C12). Consequently, the enhancement of cell wall thickness and the lignification of vascular cells facilitated the stem hardening.

The cross-sections of the stems were further analyzed by phloroglucinol-hydrochloric acid staining to identify the location of lignin deposition, indicating by the red part. The staining results displayed that the lignin deposition was mainly in the vascular bundle tissues of stems, with a minor presence in the pith tissues following

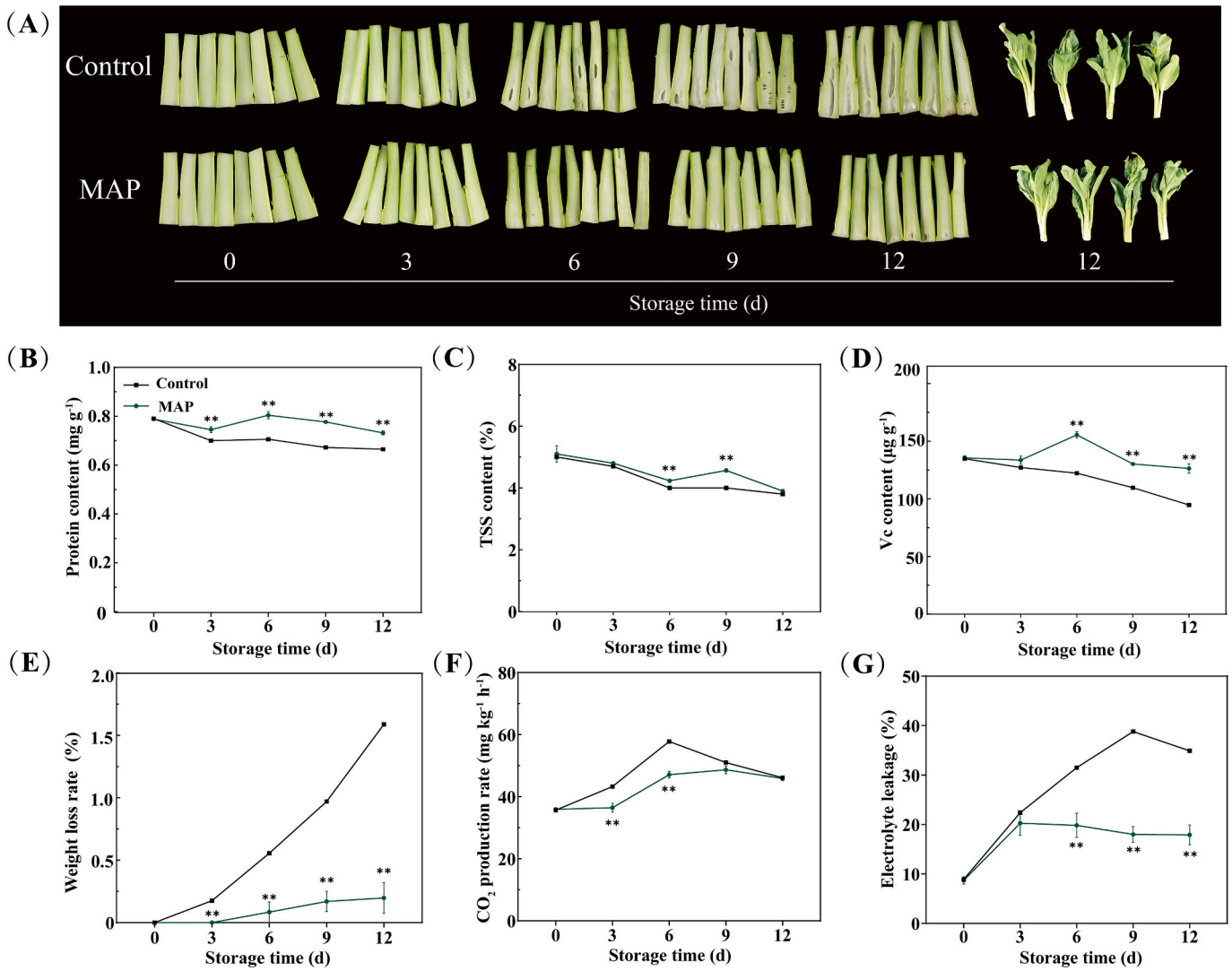

Fig. 1. The visual and quality parameters changes of the Chinese flowering cabbage stem under modified atmosphere packaging (MAP) treatment. (A) The visual observation of stem hollowing development. (B) protein content, (C) total soluble solid (TSS) content, (D) Vc content, (E) weight loss rate, (F) carbon dioxide (CO_2) production rate, (G) electrolyte leakage. Statistical significance between different groups at the same time point is denoted by asterisks (*$P < 0.05$ and **$P < 0.01$).

hollowing (Fig. 2D). At harvest day, the vascular bundle tissues were slightly stained. However, as the storage period progressed, the color of the vascular bundle tissues was gradually deepened, and even the central pith cavity acquired a faint pink tint over time. As storage period progressed, the red spots of the vascular bundle tissues with MAP were relatively light, while the pith tissues began to be pink at 12 d. In contrast to the MAP, the vascular bundle of the control section showed obvious pink spots at 6 d, and the pith cavity began to turn pink. On day 12, the vascular bundle tissue was totally red. These results further indicate that MAP alleviates lignin accumulation in stems during storage.

3.3. Changes in activity of PAL, C4H, 4CL, and CAD in stems of Chinese flowering cabbages upon MAP treatment

Changes of PAL activity (Fig. 3A) was similar in both control and MAP-treated stems, showing a decrease in the first 3 d, followed by an increase over the subsequent 6 d, and a subsequent decline in the final 3 d. Generally, PAL activity in MAP-treated stems kept at relative low level during the whole storage. On the 6 d of storage, PAL activity in MAP-treated stem tissues was 14.47 % lower than that in the control group. In the stems of Chinese flowering cabbages, C4H activity exhibited an increase after MAP treatment, reaching 60.01 nmol min^{-1} g^{-1} at 6 d, then gradually decreased until 12 d (Fig. 3B). Without MAP treatment, C4H activity showed a fluctuating upward trend. Obviously, MAP application led to a reduction in C4H activity in the stems compared to the control group throughout the entire storage duration. On day 6, the C4H activity of control stems was 23.91 % higher than that of MAP-treated stems ($P<0.01$). Regarding the 4CL activity in stems of Chinese flowering cabbages (Fig. 3C), there was a consistent decline over the entire storage period. However, MAP treatment promoted this decline when contrasted with the untreated control samples. On day 12, 4CL activity was 3.48 % lower in the MAP treatment group than in the control group. During storage, the activity of CAD in stems of Chinese flowering cabbages increased slightly within the initial 6 d, followed by a rapid decrease (Fig. 3D). Specifically, on the 3 d and 6 d of storage, the activity of CAD in the control stems were 1.15- and 1.25- times higher that of MAP-treated stems, respectively. These findings demonstrate that MAP inhibits the activity of enzymes related to lignin biosynthesis.

3.4. Changes in $O_2^{\cdot-}$ production rate, H_2O_2, and MDA content in stems of Chinese flowering cabbages under MAP treatment

$O_2^{\cdot-}$ production rate and H_2O_2 content in stems of Chinese flowering

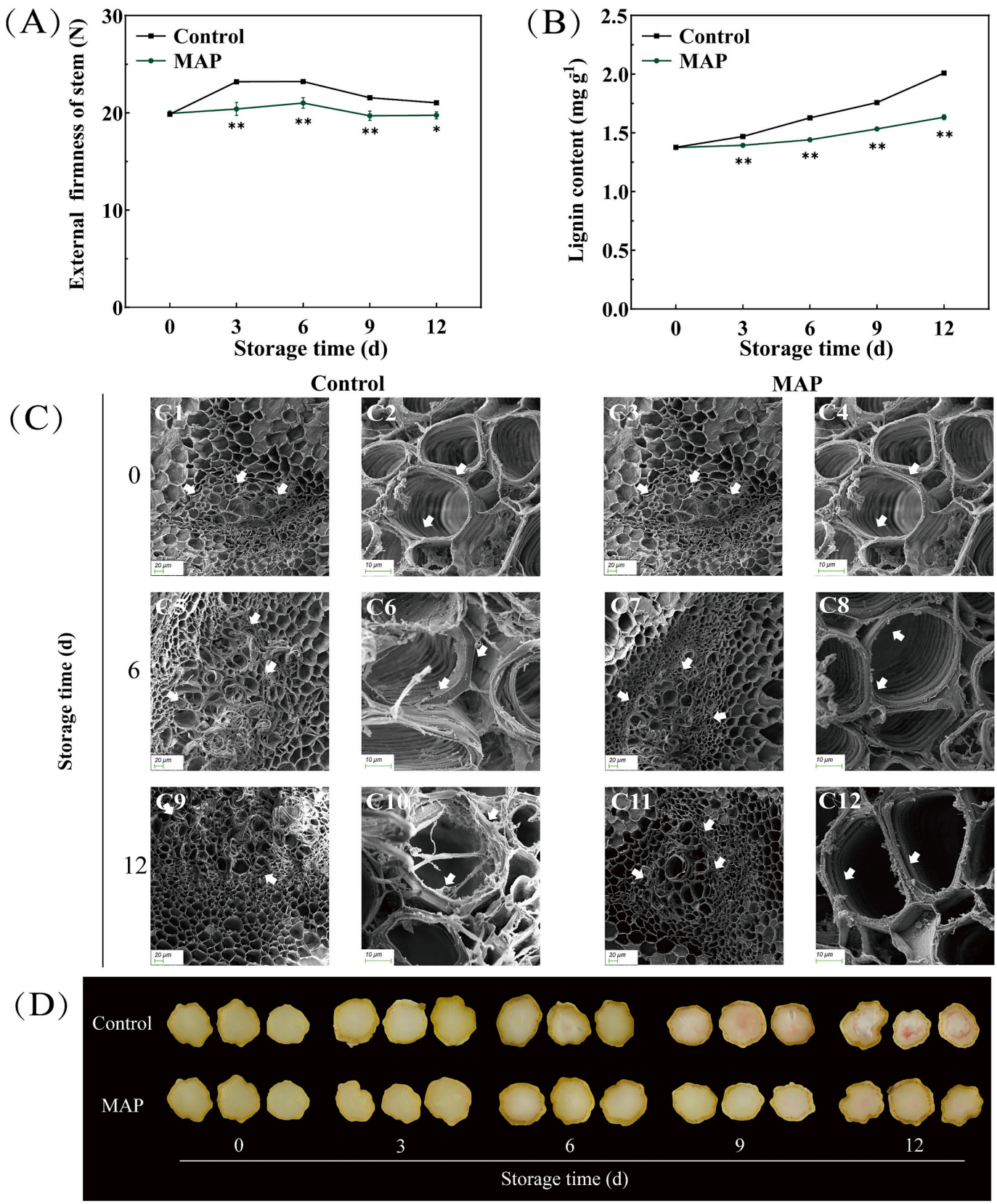

Fig. 2. The firmness, lignin content, morphological changes and histochemical stain in stem of Chinese flowering cabbage under MAP treatment. (A) stem firmness, (B) lignin content, (C) morphological changes, (D) histochemical stain. In A-B, statistical significance between different groups at the same time point is denoted by asterisks (*$P < 0.05$ and ** $P < 0.01$).

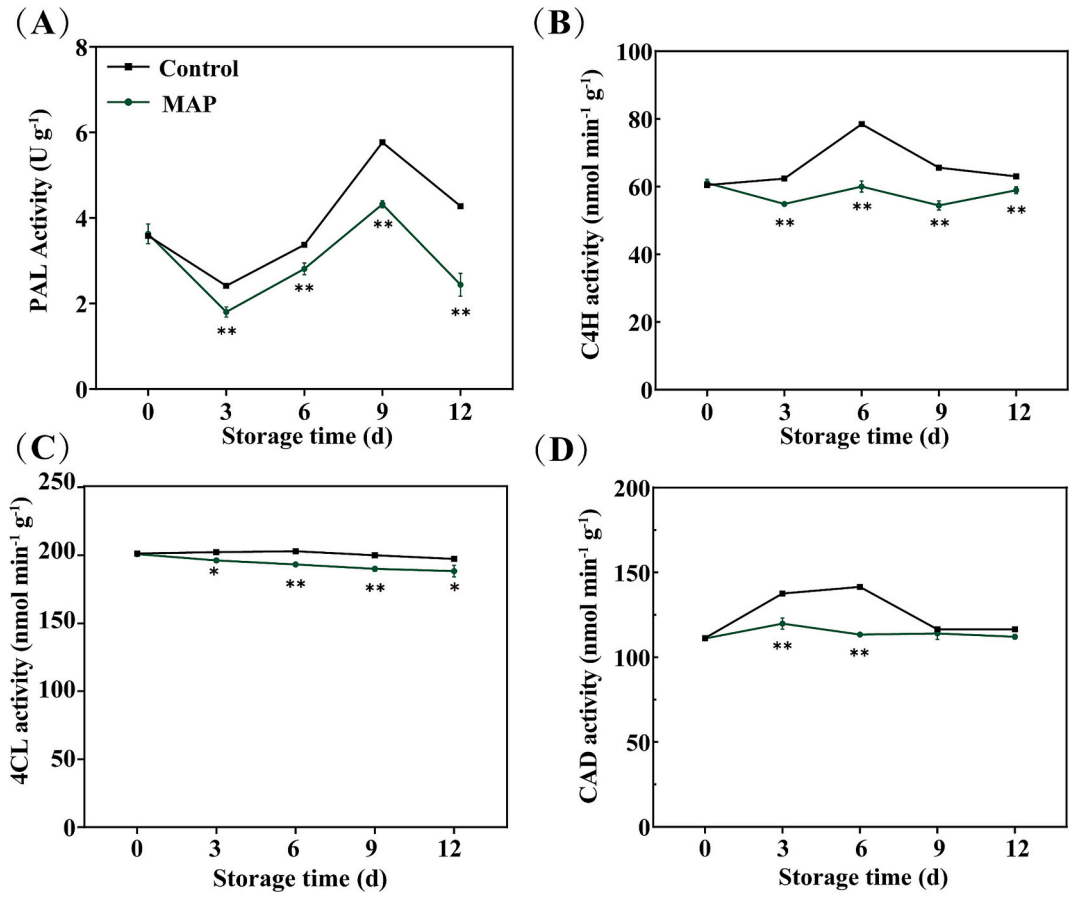

Fig. 3. Changes in activity of lignin biosynthetic enzyme including phenylalanine ammonia-lyase (PAL) (A), cinnamate 4-hydroxylase (C4H) (B), 4-coumarate coenzyme A ligase (4CL) (C), and cinnamyl alcohol dehydrogenase (CAD) (D) in stem of Chinese flowering cabbage under MAP treatment. Statistical significance between different groups at the same time point is denoted by asterisks (*$P < 0.05$ and ** $P < 0.01$).

cabbages exhibited a rapid increase followed by a decline, reaching peak levels at 6 d (Fig. 4A and B). The levels of $O_2^{\cdot-}$ and H_2O_2 in control stems were 34.82 % and 10.00 % higher, respectively, in comparison with stems of MAP-treated cabbages. The MDA content in the stems of the control group increased from 1.24 to 1.50 nmolg^{-1} (Fig. 4C). In contrast, the MAP treatment effectively suppressed the increase in MDA content of stems in Chinese flowering cabbages throughout the storage period ($P < 0.05$). On day 12, the content of MDA in the stems of the control group was 1.24 times higher that of the MAP group.

3.5. Changes in activity of SOD, POD, and CAT in stems of Chinese flowering cabbages under MAP treatment

The activities of SOD (Fig. 5A) and CAT (Fig. 5C) in stems of Chinese flowering cabbages gradually increased and peaked at day 12 during storage. On the other hand, activities of SOD and CAT in MAP treatment were significantly enhanced by 50.82 % and 23.55 %, respectively, at 7 d compared to the control ($P < 0.05$). For POD activity (Fig. 5B), there was slightly enhanced during the first 3 d of storage, followed by a continuous rise. There was higher POD activity in MAP-treated stems of Chinese flowering cabbages than in the control stems.

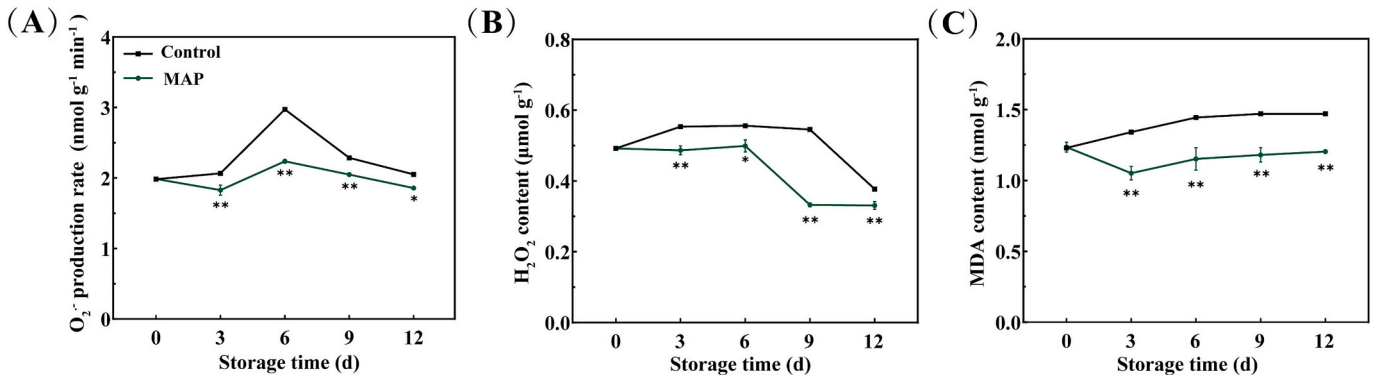

Fig. 4. Changes in superoxide anion ($O_2^{\bullet-}$) production rate (A), hydrogen peroxide (H_2O_2) (B) and malondialdehyde (MDA) content (C) in stem of Chinese flowering cabbage under MAP treatment. Statistical significance between different groups at the same time point is denoted by asterisks (*$P < 0.05$ and ** $P < 0.01$).

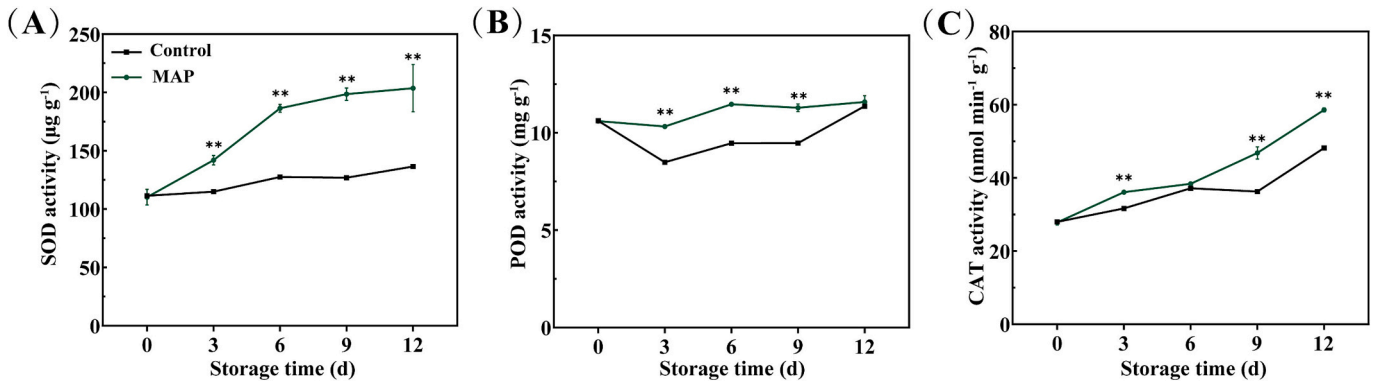

Fig. 5. Changes in activity of superoxide dismutase (SOD) (A), peroxidase (POD) (B), and catalase (CAT) (C) in stem of Chinese flowering cabbage under MAP treatment. Statistical significance between different groups at the same time point is denoted by asterisks (*$P < 0.05$ and **$P < 0.01$).

3.6. Changes in components of AsA-GSH cycle in stems of Chinese flowering cabbages under MAP treatment

The levels of AsA and GSH (as depicted in Fig. 6A and B, respectively) along with the AsA/DHA and GSH/GSSG (as shown in Fig. 6E and F) exhibited a progressive decline over the extended storage duration across all treatments. Notably, MAP treatment effectively mitigated this decline, maintaining notably higher concentrations of AsA and GSH, and keeping a higher ratio of AsA/DHA and GSH/GSSG, in comparison to the untreated control group throughout the storage period. At day 6, the MAP-treated stems exhibited increases of 27.27 % in AsA content, 26.67 % in GSH content, 128.21 % in the AsA/DHA ratio, and 37.75 % in the GSH/GSSG ratio, compared to the respective values in the control cabbages, with statistical significance at $P < 0.01$. Moreover, DHA and

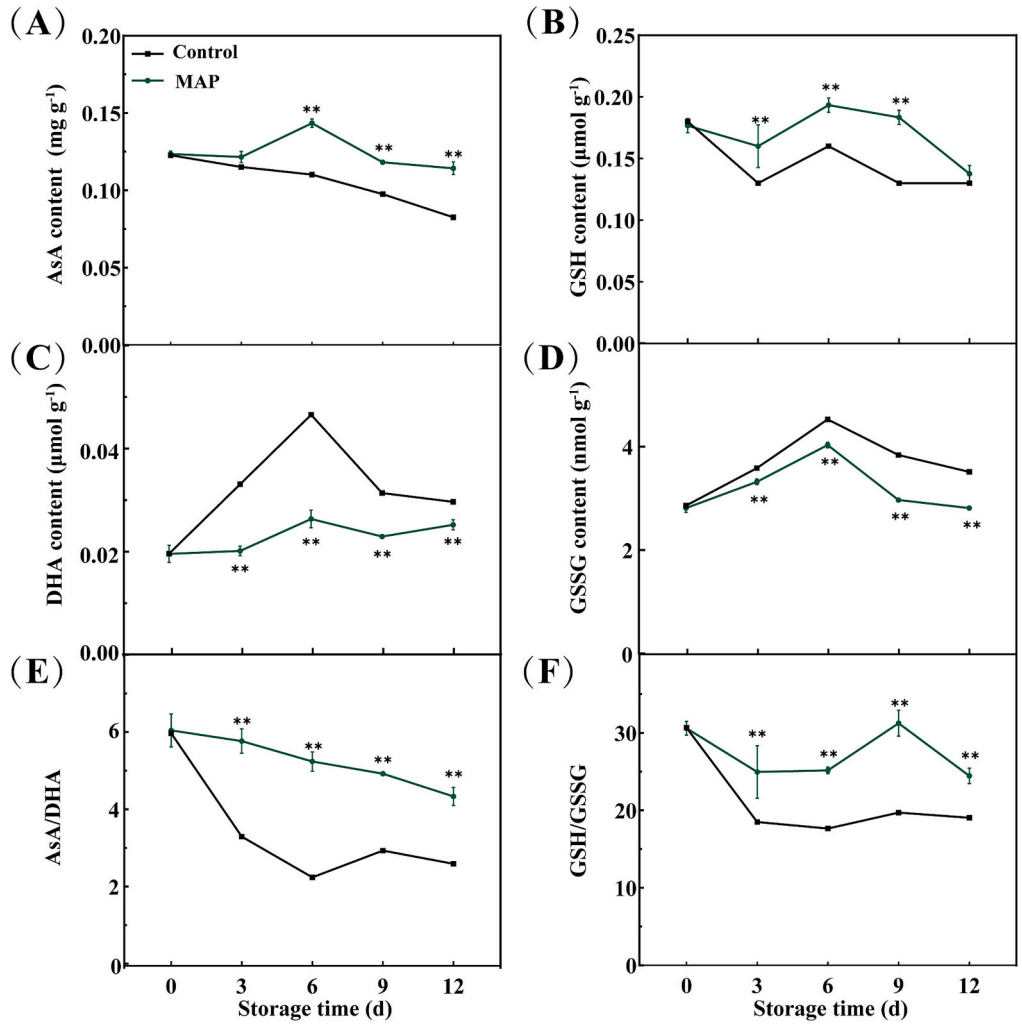

Fig. 6. Changes in ascorbic acid (AsA)-glutathione (GSH) cycle components in stem of Chinese flowering cabbage under MAP treatment. (A) AsA content, (B) GSH content, (C) dehydroascorbic acid (DHA) content, (D) oxidized glutathione (GSSG) content, (E) the ratio of AsA/DHA, (F) the ratio of GSH/GSSG. Statistical significance between different groups at the same time point is denoted by asterisks (*$P < 0.05$ and **$P < 0.01$).

GSSG contents increased steadily during the 6 days and then gradually decreased in both treatment groups. The DHA and GSSG contents (Fig. 6C-D) in MAP stems was lower in comparison with those of control. The DHA and GSSG contents of stems in control stems were 66.67 % and 10.67 % higher ($P < 0.01$) than those of stems in MAP-treated stems at 6 d, respectively.

3.7. Changes in enzymes of AsA-GSH cycle in stems of Chinese flowering cabbages under MAP treatment

The activities of APX (Fig. 7A), GR (Fig. 7B), DHAR (Fig. 7C), and MDHAR (Fig. 7D) in MAP-treated stems increased and reached the peak value at 9 and 6 d, respectively, before declining. Throughout the storage period, these enzyme activities in MAP-treated stems consistently maintained higher levels compared to control stems. Specifically, at 6 d, the APX, GR, DHAR and MDHAR activities in MAP-treated stems increased by 31.34 %, 32.01 %, 21.13 % and 23.53 %, respectively, when contrasted with control stems.

4. Discussion

Chinese flowering cabbage after harvest undergoes both leaf senescence and stem senescence, resulting in quality deterioration and loss of edible value (Wang et al., 2023). Within storage period, both stem hollowing and leaf yellowing in Chinese flowering cabbages occurred nearly simultaneously (Fig. 1A). Concurrent with the visible stem hollowing, there was an increase in weight loss (Fig. 1E), while the levels of protein, TSS, and Vc exhibited a continuous decline (Fig. 1B-D), implying the irreversible loss of water and nutrients. The reservation of water and nutrients for horticultural products were strongly linked to respiration rate and changes in membrane permeability. In comparison to control, MAP treatment inhibited the increase of CO_2 production rate (Fig. 1F) and electrolyte leakage (Fig. 1G) in stems of Chinese flowering cabbages. These results mean that MAP is effective in delaying stem senescence and quality deterioration. Similar boosted effect on quality maintenance by MAP treatment had also been demonstrated in Chinese kale during storage (Wang, Wu, et al., 2021).

Texture also is one of the important contributors for edible quality of vegetables, with changes during storage largely attributed to modifications in cellular structure (Wang et al., 2023). The external peeled tissues of Chinese flowering cabbages stem have proven to include epidermal cells, cortex tissues, and vascular bundle cells (Wang et al., 2023). Adjacent to these, the inner pith tissues are primarily composed of loosely arranged parenchyma cells. The vascular bundle, which acts as a critical bridge, connecting the external peeled tissues seamlessly with the inner pith tissues. In previous work, collapse of parenchyma cells and thickened cell walls around vascular cells induced the pith cavity and stem hardening of Chinese flowering cabbages, respectively, indicating that different cell types with distinct cell structures play a role in regulating stem senescence. Likewise, thickened cell walls of the vascular bundle were noted in the control group, and the demarcation between vascular bundle cells and pith tissue became more distinct (Fig. 2C). A previous study demonstrated a close relationship between the thickening of cell walls and the rise in lignin content near the vascular bundle (Barros et al., 2015). Histochemical observations in this work confirmed that the stained parts of the stem are mainly concentrated in the vascular bundle tissue, with minimal staining observed in the inner pith tissues. With extension of storage time, the red spots

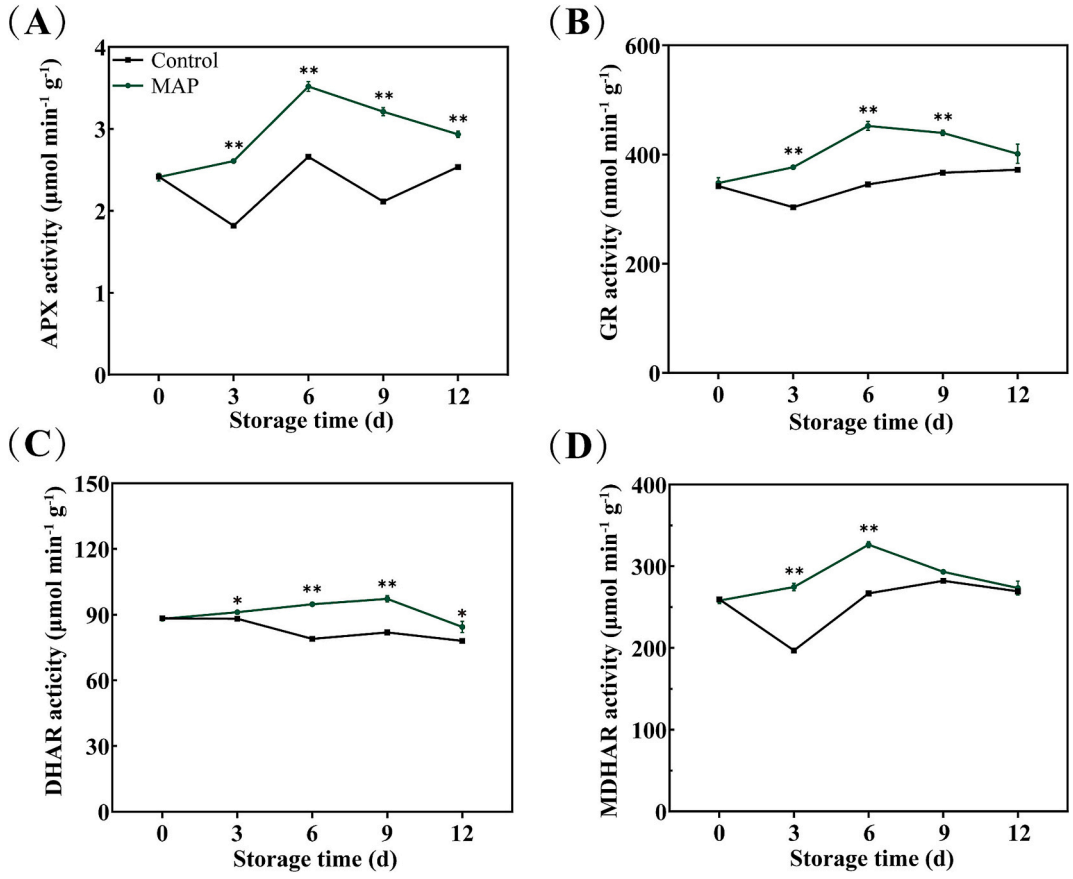

Fig. 7. Changes in activity of enzymes involved in AsA-GSH cycle in stem of Chinese flowering cabbage under MAP treatment. (A) ascorbate peroxidase (APX) activity, (B) glutathione reductase (GR) activity, (C) dehydroascorbate reductase (DHAR) activity, (D) monodehydroascorbate reductase (MDHAR) activity. Statistical significance between different groups at the same time point is denoted by asterisks (*$P < 0.05$ and **$P < 0.01$).

around the vascular bundle tissue changed from pink to dark red, and the hollow area in the inner pith tissues were gradually stained as pink. These changes suggest an increase in stem lignification, aligning well corresponding with higher firmness and lignin content (Fig. 2A-B). This result could improve the mechanical strength but result in stem hardening of Chinese flowering cabbage. However, MAP treatment could effectively delay the occurrence of stem lignification of Chinese flowering cabbage (Fig. 2D). During senescence of carrot (Li, Li, et al., 2021) and asparagus (Pu et al., 2020), accumulation of lignin content also could be inhibited by MAP treatment.

Lignin, a sophisticated phenylpropanoid polymer, significantly contributes to the buildup of dietary fiber and provides essential mechanical reinforcement for cell walls in plant (Liu et al., 2018). The excessive build-up of lignin accelerates the senescence process and diminishes the commercial value and edible value of crops, such as pear (Wang, Gong, et al., 2022), water-bamboo shoots (Zhang et al., 2021), and carrot (Sun et al., 2024). Li et al. (2016) found that lignin accumulation occurred as a consequence of the activation of lignin biosynthesis-related enzymes, including PAL, C4H, 4CL and CAD. In this work, enzymatic activities of PAL, C4H and 4CL in this study exhibited a rapid increase during the initial phases of storage. Subsequently, these activities declined progressively during the latter storage stages. However, this decline was notably attenuated by the MAP treatment (Fig. 4), potentially reducing the extent of lignification within the vascular bundle tissue. Likewise, in post-harvest *Flammulina velutipes*, similar outcomes were observed, showing that nanocomposite packaging diminished lignin deposition via restraining the PAL, C4H, and 4CL activities (Zuo et al., 2021). Furthermore, the application of melatonin was effective in decreasing lignification and maintaining the nutritional quality of loquat fruit during cold storage by modulating the activities of key enzymes involved in lignin biosynthesis (PAL, 4CL, CAD, and POD) (Wang, Chen, et al., 2021). Wang, Li, et al. (2022) documented that the synergistic application of 1-methylcyclopropene alongside polypropylene crispers exerted a notable suppression on the enzymatic activities of PAL and CAD, retarding the lignification process in postharvest golden needle mushroom during storage. Collaborating with these results, it is proposed that MAP may reduce stem lignification of Chinese flowering cabbage by inhibiting enzymes that are involved in lignin metabolism, thereby preserving its edible quality.

It has been established that the over-accumulation of ROS plays a key role in lignification via oxidative polymerization of monolignols to lignin in fruit (Wang, Liu, et al., 2021). Previous studies have also verified the occurrence of stem lignification in Chinese flowering cabbage concurrent with bursts of ROS (Wang et al., 2020). These findings were consistent with the increment observed in firmness and lignin content in the current work, in parallel with an elevation in the $O_2^{\bullet-}$ production rate and H_2O_2, leading to higher MDA accumulation (Fig. 4C). To combat this situation, fruits and vegetables can induce their own stress response system to adapt and to protect from oxidative stress (Meitha et al., 2020). SOD, CAT, and POD as vital ROS-scavenging enzymes, are important targets for regulating oxidative stress during senescence. For example, the enhanced activity of antioxidant enzymes and their synergistic effects have been implicated in the prevention of oxidative damage and senescence in mushroom (Wang et al., 2019), pear (Li et al., 2020) and freshly cut water chestnuts (Wu et al., 2024). In previous work, different postharvest treatment strategies, including the application of melatonin (Tan et al., 2021) and cytokinin ((Wang et al., 2022)), have proven effective in stimulating ROS-scavenging enzyme activity. This enhancement contributes to slowing down leaf senescence in Chinese flowering cabbage, thereby extending its postharvest shelf life. Similarly, in the current study, MAP enhanced activities of SOD, CAT, and POD in stem of Chinese flowering cabbage, which help explain the reduced ROS accumulation and a lower MDA content (Fig. 4C), postponing the occurrence of stem hollowing (Fig. 1A). On the other hand, H_2O_2 may coordinate with PAL and POD to control lignin synthesis, or trigger xylem differentiation (Barceló, 2005). Thus, the restricted H_2O_2 by MAP treatment in this work also contributed to preventing the stem lignin deposition. Additionally, Zuo et al. (2021) reported that nanocomposite packaging treatment could delay the lignification process of *Flammulina velutipes* by the regulation of ROS in mitochondria. Collectively, these findings indicate that MAP has an inhibitory role in ROS-scavenging enzymes, resulting in reduced ROS levels and subsequently helping to restrain the stem senescence and lignification.

The ASA-GSH cycle, consisting of APX, GR, DHAR, and MDHAR, is vital for scavenging ROS (Hasanuzzaman et al., 2019). This cycle also comprises the important antioxidants GSH and AsA, which are produced by following reactions. As an electron donor, AsA participates in the process of converting intracellular H_2O_2 into water in the cell via APX, while AsA is oxidized to the MDHA (Hasanuzzaman et al., 2019). MDHA is recycled into AsA through the action of MDHAR and it also spontaneously transforms into DHA. DHA is reduced back to AsA via GSH, which is then oxidized by DHAR to form GSSG. The regeneration of GSH from GSSG is facilitated by GR (Li, Huang, et al., 2021). In current research, the endogenous AsA and GSH content in cabbage stem paralleled with DHAR activity declined in the control during senescence. Hence, the reduction in enzyme activity and antioxidant content increased ROS production and the risk of oxidative stress. The correlation between GSH and AsA levels and oxidative stress-induced senescence previously has been documented on jujube (Li et al., 2023; Ban et al., 2024), *Rosa roxburghii* fruit (Dong et al., 2021), and apple (Wei et al., 2019). Additionally, degradation and regeneration of AsA and GSH are intimately linked to the activities of GR, APX, DHAR, and MDHAR, thus their concentrations are directly tied to the enzymatic activities within the AsA-GSH cycle. Increasing the activities of DHAR, MDHAR, APX and GR as well as their corresponding gene expression can improve the antioxidant capacity of Chinese flowering cabbage leaves (Mou, Wang, Wei, et al., 2023; Tan et al., 2021). In this study, MAP application significantly promoted the APX, GR, and MDHAR activity, leading to increased endogenous AsA and GSH content, retained higher GSH/GSSG, lowered GSSG and DHA content in stem of Chinese flowering cabbage. These results align with studies on gaseous ozone-treated pitaya (Li et al., 2023), acibenzolar-*S*-methyl-treated pears (Huang et al., 2022), and cinnamaldehyde-treated water chestnuts (Wu et al., 2024).

5. Conclusion

In summary, during postharvest storage, the decline in stem quality of Chinese flowering cabbage resulted from the increased in respiration consumption, weight loss and firmness, but that was inhibited by MAP treatment. Anatomical observations and histochemical staining confirmed that the elevation of lignin content and deposition associated with stem hardening was attenuated by MAP treatment through suppressing activity of lignin biosynthesis related enzymes. Moreover, the inhibition of stem senescence and lignification under MAP treatment might be related to the enhanced ability to diminish ROS accumulation through the activation of antioxidant mechanisms. However, the current experiment has only verified at the physiological level, and the in-depth mechanism needs to be explored by further molecular biological means, such as transcription factor-mediated transcriptional regulation, and functional verification of key genes. Our findings provide the basis for the application of MAP treatment in vegetable preservation and new insights for revealing the regulation mechanism of stem senescence of Chinese flowering cabbage.

CRediT authorship contribution statement

Xue-mei Chen: Writing – original draft, Investigation, Data curation. **Zhen-liang Mou:** Investigation. **Ya-ting Zhao:** Writing – review & editing. **Xin-guo Su:** Data curation. **Yan-chao Han:** Data curation. **Hang-jun Chen:** Data curation. **Wei Wei:** Conceptualization. **Wei Shan:** Data curation. **Jian-fei Kuang:** Data curation. **Wang-jin Lu:** Writing –

review & editing. **Jian-ye Chen:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgments

This research was supported by the National Key Research and Development Program of China (grant No. 2022YFD2100101), Guangdong Basic and Applied Basic Research Foundation (grant No. 2022A1515012491) and Key Project of Universities in Guangdong Province (grant No. 2023ZDZX4108).

Data availability

Data will be made available on request.

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