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Anti-browning effects of citronellal on fresh-cut taro (*Colocasia esculenta*) slices under cold storage condition

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The browning on the cut surface is a big problem reducing the quality of fresh-cut taro (FCT), which causes severe postharvest losses and may raise environmental impacts. Citronellal (CA) is a natural compound in several aromatic plants. This study investigated the effects of CA treatments in different concentrations (0.2, 0.5, and 1 mL/L) on the browning of FCT under cold storage at 5°C. The results indicated that low-dose (0.2 mL/L) CA treatment showed best anti-browning effects, reflecting at the maintained L^* values but the reduced a^*, b^* and browning index values by CA treatment during cold storage. A repeated experiment using 0.2 mL/L CA confirmed fine anti-browning effects again. Furthermore, CA (0.2 mL/L) treatment markedly reduced the contents of total phenolic compounds and soluble quinones, restrained the activities of phenylalanine ammonia lyase, peroxidase and polyphenol oxidase, down-regulated the gene expression of 18 browning-related enzymes in FCT. These results together strongly demonstrate the validity of CA on FCT browning prevention. Given that CA is a natural compound existing in plants, low concentration of CA possesses strong anti-browning effects on FCT and also inhibitory effects on pathogens, implying that its application has potentiality to preserve high quality of fresh-cut produce for processing and storage. Moreover, CA treatment significantly decreased malondialdehyde contents and lipoxygenase activity. Correlation analysis indicated that the lipid peroxidation of cell membrane was mostly correlated with FCT browning. The results suggest that membrane lipid peroxidation was a possible reason for FCT browning and CA treatment reduced browning, in part, through alleviating the lipid peroxidation of cell membrane. Overall, our results demonstrate that CA is a novel browning mitigator for FCT under cold storage condition.

KEYWORDS

fresh-cut taro, enzymatic browning, browning mitigator, natural extract, citronellal

Introduction

The food industry shows increased interests in the innovation of products bringing health and convenience benefits (Rodríguez-Arzuaga et al., 2021). Fresh-cut foods (known as minimally processed products) are ready-to-eat healthy foods with a lot of advantages such as high nutrition, fresh appearance, great convenience, low waste and free pollution (María et al., 2020). Therefore, the economic importance of fresh-cut food market is becoming more remarkable (Alves et al., 2017; Zhang et al., 2020b). Nevertheless, the cut surface browning is still a big problem restricting the shelf life of many fresh-cut products including taro (*Colocasia esculenta*) during postharvest storage and consumption (Xiao et al., 2021), even though the products are stored under low temperature conditions (Mendoza-Enano et al., 2019). Taro is a staple food and/or root vegetable in many developing countries in the South Pacific, the Caribbeans, Asia, Central Africa, and South/Central America, due to the existence of abundant starch and other nutrients in root tissues (Bellinger et al., 2020). In China, fresh taro corms are used to manufacture delicious snacks, soups, or dishes after peeling (Xiao et al., 2022).

It is well-established that the main causes resulted in color degradation of fresh-cut products are enzymatic activity (Capotorto et al., 2017; Giannakourou and Tsironi, 2021). Mechanical operations such as handling and cut processing cause physical damages on cell tissues of fresh-cut foods, and enable the immediate interactions between substrates and enzymes under the existence of oxygen molecules (Giannakourou and Tsironi, 2021). The key enzymes involved in the reaction of enzymatic browning in fresh-cut foods include polyphenol oxidase (PPO), peroxidase (POD), phenylalanine ammonia lyase (PAL) and lipoxygenase (LOX; Qiao et al., 2021; Xiao et al., 2022). PPO and POD are two major pro-oxidative enzymes in plant, they involved in fresh product browning through contributing to phenolic oxidation to form dark-colored compounds (Rouet-Mayer et al., 1990; Ma et al., 2015; Sikora and Swieca, 2018; Zhu et al., 2022). Apart from PPO and POD, PAL activity positively correlates with the browning of fresh-cut products, as the enhanced activity can accelerate the process of phenolic biosynthesis (Banerjee et al., 2015). Unsaturated fatty acids are the major constituents of cell membrane (Kalappurakkal et al., 2020), and the oxidation of unsaturated fatty acids caused by LOX might be an important mechanism resulting in the browning of fresh-cut foods (Gao et al., 2017; Kan et al., 2019; Qiao et al., 2021). Therefore, the inhibition of the activities of those browning-related enzymes *via* the application of some chemicals may be a feasible strategy for the browning inhibition of fresh-cut products.

Dipping the cut products into solutions of anti-browning chemicals is the widest method of browning control in the fresh-cut industry (Rojas-Graü et al., 2007). Several compounds have been proposed to control fresh-cut product browning. For example, hydrogen sulfide is effective in reducing the surface browning of fresh-cut Chinese water chestnuts (Dou et al., 2021), lotus (Sun et al., 2015), apple (Chen et al., 2017), pears (Hu et al., 2014), and fresh litchi fruit (Siddiqui et al., 2021). Chlorine-containing solutions are widely used, and the efficacy of such solutions on browning inhibition of fresh-cut foods was evaluated in several food species including asparagus lettuce (Chen et al., 2010), apple (Fu et al., 2007), lotus (Du et al., 2009), and longan fruit (Intarasit et al., 2018). Electrolyzed water and ozone are also suggested to have potential anti-browning effects on fresh-cut foods (Ali et al., 2018). However, as the above-mentioned, the most commonly used compounds are chemicals which might pose potential risks to human health considering the food safety (Fan and Wang, 2022). Therefore, it is an important priority to develop more effective and safe browning inhibitors for fresh-cut products.

Several studies have been reported that some plant essential oils possess preventive effects on fresh-cut food browning. For example, clove essential oil was showed to prevent the browning of fresh-cut lettuce and table grapes (Talab and Gholami, 2012; Chen et al., 2017) by inhibiting browning-related enzyme activities. Tragacanth gum coating thyme essential oil delayed button mushroom browning (Nasiri et al., 2017). The application of essential oil extracted from pine leaves to fresh-cut lettuce significantly prevented the browning (Kim et al., 2014). These studies suggest that plant essential oils could be a resource of browning inhibitors controlling enzymatic browning of fresh-cut foods. Citronellal (CA) is one of the major components of citronella aromatic oil (Sharma et al., 2019). CA does not present a concern for genetic, developmental and reproductive toxicities based on the current existing data and usage levels (Api et al., 2021). It has been fully confirmed in many studies that CA displays strong antifungal activities against various pathogens in food system (Wu et al., 2016; Sharma et al., 2019; OuYang et al., 2021; Zhang et al., 2022). However, few studies were conducted to determine whether CA application could prevent fresh-cut food browning.

The purpose of this study was to assess CA effects on the browning inhibition of fresh-cut taro (FCT) under cold condition. In addition, CA-treatment-induced changes in browning indicators such as activities of PAL, PPO, LOX and POD, and contents of malondialdehyde (MDA), total phenolic compound (TPC) and soluble quinone (SQ) were investigated in FCT. The results from this study would lay a foundation for probable applications of CA in the fresh-cut industry.

Materials and methods

Material selection, processing, storage condition, and sampling

Taro (*Colocasia esculenta* cv Binglang) were harvested at a commercially ripe stage in a vegetable garden in Shaoguan city,

Guangdong Province, China, in November and December 2020. In this stage, the corm expansion comes to a complete stop, nutrients are fully accumulated, and the aboveground leaves begin to turn yellow and even some wither seriously. Trial taros were selected based on the standard of uniform sizes, free physical damages and disease symptoms. Before treatment, taros were washed with running water and peeled using a peeler. Then the peeled corms were cut into equal slice with 1 cm thickness.

For treatments, the FCT pieces were dipped into distilled water (DW) and different concentrations of CA solutions (0.2, 0.5, or 1 mL/L) for 30 min, respectively, and dried at room temperature (25°C) for 20 min. Three replications were applied for each treatment, and each replication contained 30 slices. After treatment, DW- and CA-treated FCTs were hermetically wrapped with plastic bags (0.02 mm thickness), and then were stored at 5°C and 90–95% relative humidity for 12 days for progressive assessments. Each bag contained 10 thin pieces. The whole FCT slices were used to sampling, and samples were collected every 3 days during storage. The collected samples from the same treatment were pooled and ground to a powder in liquid nitrogen and stored at −80°C for subsequent measurements.

Color assessment on the surface of FCT

Color (CIELAB values) on the surface of FCT was quantitatively measured using a CR-400 Chroma meter (KONICA MINOLTA, Japan) calibrated by the standard white tile (Y = 84.4, x = 0.3205, and y = 0.3377; Xiao et al., 2022). Measurements were made at central area of the cut faces of each taro slice. Values of L^*, a^*, and b^* were recorded in the Chroma meter, and the browning index (BI) was also evaluated according a formula previously established (Xiao et al., 2020).

Determination of total phenolic compound (TPC) and soluble quinone (SQ) and malondialdehyde (MDA) contents

TPC contents were measured basing on the Folin-Ciocalteu method (Xiao et al., 2022). Briefly, 1.0 g of taro samples were homogenized with a 5 mL of 1 % (v/v) HCl-methanol reagent and extracted at ambient temperature (25°C) for 3 h. Then, the extracts were centrifuged at 4°C (12,000 × *g*) for 10 min. The supernatant was collected as crush extracts for the determination of TPC content in taro samples. For determination, 0.5 mL of the supernatants, 1.5 mL of 1 M sodium carbonate, and 1.0 mL of Folin-Ciocalteu reagent were orderly added in a new tube and then were well-mixed. Then reaction mixture was reacted at 25°C for 30 min in the darkened environment. The absorbance of reaction solution was recorded at 765 nm with an UV-visible spectrophotometer (MAPADA UV-1800, China). A standard curve of gallic acid (GA) was established to quantify TPC contents as milligram GA equation per kilogram of fresh weight (mg kg^{-1} FW).

For the measurement of SQ concentrations, quinone extracts were prepared with 5.0 g of taro samples in a 10 mL of methanol at 25°C for 2 h. Then, the extract solutions were centrifuged at 12,000 × *g* for 10 min, and the collected supernatants were used to determine SQ contents. The absorbance of each supernatant at 437 nm was recorded using the above mentioned UV-visible spectrophotometer. The SQ concentrations of each sample were expressed as OD437 per gram of fresh weight (OD437 g^{-1} FW; Ali et al., 2021).

MDA contents in FCT were estimated with a commercial kit (D799761, Sangong Biotech, China) based on the manufacturer's specifications. The 0.3 g of taro powders from three different slices were added in 5 mL of trichloroacetic acid (5%) solution and then were fully mixed in ice bath. The mixtures were centrifuged (8,000 × *g*) at 4°C for 10 min and the supernatants were carefully collected before measurement. 0.2 mL of supernatant was mixed with 0.8 mL of thiobarbituric acid (1%) solution and boiled in a water bath for 60 min. Thereafter, boiled reactions were cooled to ambient temperature (25°C) and centrifuged at 10,000 × *g*. The absorbance of supernatant was noted at 600, 532, and 450 nm. The MDA content of taro samples was calculated using the following equation.

MDA content = [6.45 × (A532–A600) – 0.56 × A450] × Vt/(Vs × m) (Ali et al., 2021). Vs represents the extract volume required for measurement, while Vt represents the total volume of sample extract. The result of MDA concentration was expressed as μmol per kilogram of fresh weight (μmol kg^{-1} FW).

The activities of browning-related enzymes

Phenylalanine ammonia lyase (PAL) activity was determined according to a previous publication (Wang et al., 2022). Taro grinding liquid was composed of precooled borate buffer (pH 7.8, 0.2 M) and 2% (w/v) polyvinylpyrrolidone (PVP). The homogenates were centrifuged at 4°C (12,000 × *g*) for 10 min to collect the supernatants. For PAL activity measurement, 0.5 mL of the supernatants were admixed with 1.5 mL of 0.1 mM sodium borate (pH 8.8), 0.5 mL of 5 mM dithiothreitol and 0.5 mL of 0.02 M L-phenylalanine, and kept at 25°C for 2 h. The generation of trans-cinnamate was monitored at a wavelength of 290 nm using the above mentioned UV-visible spectrophotometer.

The crushed extracts of POD, PPO, and LOX were prepared before measurement with the method of Xiao et al. (2020). First, 1.0 g of taro samples were homogenized into a 5 mL of precooled sodium phosphate buffer (pH 7.0, 0.05 M) containing 0.1 g of PVP and centrifuged at 4°C (12,000 × *g*) for 15 min. After centrifugation, the supernatants were collected into a new centrifugal tube and used to determine enzyme activities.

For the POD activity assessment, a 3 mL of reaction mixture was composed of 0.1 mL of the supernatants, 2.7 mL of 0.1 M phosphate buffer (pH 7.0), 0.1 mL of 1% (v/v) guaiacol and 0.1 mL of 0.5% H_2O_2 (Xiao et al., 2022). The absorbance of mixture at 470 nm was continuously recorded every 1 min during the monitored 3 min.

For the PPO activity measurement, 0.2 mL of the supernatants and 0.1% (w/v) pyrocatechol were added in order and mixed well in a centrifugal tube. The absorbance of each mixture at 398 nm was recorded every 1 min and continuously detected for 3 min (Wang et al., 2022).

For LOX activity determination, 0.1 mL of the supernatants, 2.7 mL of 0.5 M borax-borate buffer (pH 7.0) and 0.2 mL of 5 mM linoleic acid solution were orderly added in a tube and mixed well. Taro LOX activity was measured by monitoring the formation of conjugated diene at 234 nm (Xiao et al., 2021).

The results of all enzyme activities were shown as units per kilogram of fresh weight (U kg^{-1} FW).

Gene expression analysis by real-time quantitative PCR (RT-qPCR)

Total RNA from taro slices was extracted using an RNA extraction kit (DP441, TianGen, China), and one strand of cDNA used for PCR amplification was synthesized using an cDNA synthesis kit (11123ES60, Yeasen, China) following the manufacturer's instructions (Xiao et al., 2022). RT-qPCR was used to analyze the expression of specific gene. RT-qPCR was performed through an iCyeler iQTM/Clooo system (Bio-Rad, USA) and a Hieff® qPCR SYBR Green Master Mix (No Rox) kit was employed (11201ES03, Yeasen, China). Taro *Actin7* (GenBank: MQM19396.1) was used as the internal control to normalize relative expression level of each target gene. mRNA sequences of candidate genes for qRT-PCR analysis were isolated from the taro genome (https://www.ncbi.nlm.nih.gov/genome/12429) using BLAST searcher against published sequences. Primer information was listed in Supplementary Table 1.

Statistical analysis

All experiments in this study were randomly designed, and were repeated at least twice for each analysis under the same conditions. The results presented in this study was from one set of experiment. In all figures, data were presented as means and the vertical line above each column represents the standard error (*SE*) from nine or three replications. Statistical analysis on the data were performed by Duncan's multiple range test to determine significant differences between treatments ($P < 0.05$) in the SPSS software (version 25). Correlation analysis for control samples between browning-related indices was analyzed in the Microsoft Excel software (version 2016). Plots of correlation analysis was made by TBtool software (Chen et al., 2020) using the HeatMap lllustrator tool.

Results

Effects of citronellal treatments in different concentrations on FCT browning during cold storage

L^*, a^*, and b^* values are suitable indicators for evaluating browning degree of fresh-cut products (Qiao et al., 2021). Higher L^* but lower BI values mean that the product has less browning (Kim et al., 2014; Kan et al., 2019). In the present study, FCT browning was represented as the color values (L^*, a^*, b^*, and BI) on cut-surfaces. To determine suitable CA treatment concentration reducing FCT browning, we first conducted a preliminary experiment using three concentrations (0.2, 0.5, and 1 mL/L).

The L^* values of FCT tended to decline with increasing storage days (Figure 1A). Two CA treatments (0.5 and 1 mL/L) did not exhibit significant influences on L^* values between the control (DW) (Figure 1A). However, the decline rate of L^* values in 0.2 mL/L CA treatment were evidently lower than that in DW-treated samples (control). 0.2 mL/L CA-treated FCT showed significantly higher L^* values than DW-treated taros after 3 days of cold storage (Figure 1A).

a^*, b^*, and BI values of FCT in this study showed similar patterns during cold storage (Figures 1B–D). The values tended to raise with increasing storage duration. The raising rate of three browning indicators were significantly lower in the cut taros treated with 0.2 mL/L CA than in the other treatments (Figures 1B–D). The a^* values were obviously higher in the slices treated with 0.5 and 1 mL/L CA during the last 6 days. These results together show that 0.2 mL/L CA treatment had a significant effect on maintaining fresh color of FCT. Therefore, CA concentration of 0.2 mL/L was used in the following experiment to investigate diverse effects of CA on FCT during cold storage.

To confirm the inhibitory effects of 0.2 mL/L CA treatment, a repeated experiment was conducted under the same conditions in accordance with those of the above experiment. As compared with the control, CA treatment at 0.2 mL/L concentration significantly reduced FCT browning, reflecting at higher L^* values but lower a^* and b^* and BI values in CA-treated taros (Figures 2A–D). Microbial development was observed on the

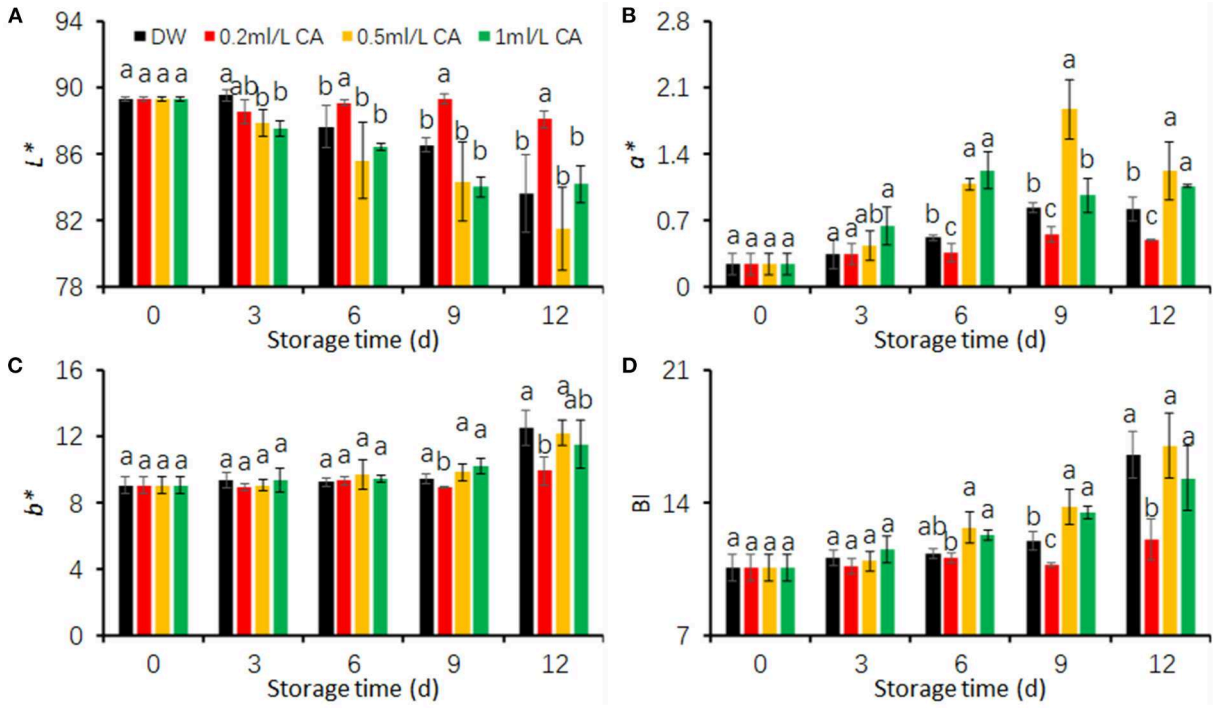

FIGURE 1
Effects of different concentrations (0.2, 0.5, and 1 mL/L) of citronellal (CA) treatments on the browning of fresh-cut taros during cold storage. **(A)** *L** value; **(B)** *a** value; **(C)** *b** value; **(D)** browning index (BI). Fresh-cut taros were stored at 5°C during the entire storage. DW, distilled water. Each value is presented as the mean ± *SE* ($n = 9$). Statistical differences ($p \leq 0.05$) are indicated using different letters above the bars.

cut-surface of control slices (Figure 2E), implying that CA treatment also had adverse effects on pathogen growth especially mold. In the control, visual browning symptoms far from disease spot on the surface of taro disks were occurred at day 6 of storage at 5°C, but progressively aggravated during the remaining storage period. However, taro slices treated with 0.2 mL/L CA had a bright appearance throughout the whole storage period (Figure 2E). These results strongly demonstrate that 0.2 mL/L CA is effective in preventing FCT browning.

Effects of citronellal treatment on phenolic oxidation in taro slices

In the control, TPC contents increased after peeling, from the initial value of 203.58–215.33 mg/kg at 12 d. However, CA (0.2 mL/L) treatment strongly inhibited the increase in TPC contents (Figure 3A). SQ contents in FCT tended to increase with increasing storage period. SQ contents in the control quickly increased during cold storage, whereas that in CA treatment increased slowly (Figure 3B). CA treatment (0.2 mL/L) significantly reduced SQ contents in FCT comparing with the control.

PPO activities of FCT exhibited an overall increased trend during the entire storage (Figure 3C). Nevertheless, CA treatment significantly prevented the increase of PPO activity during the entire cold storage when compared with the control. The effects of CA treatment on the expression of three *PPO* genes were also assessed. CA treatment effectively repressed *PPO1* and *PPO2* expression during the entire storage, *PPO3* expression during cold storage excepting at 6 d (Figures 3D–F).

In the control, POD activities drastically increased during the first 3 days and maintained at high levels during the later storage (Figure 3G). In CA treatment, POD activity mildly increased at 3 d, then suddenly dropped into very low levels at 6 d and sharply increased at 9 d. POD activity in CA treatment was significantly lower than that in the control group during the entire storage duration (Figure 3G). CA treatment markedly repressed *POD1* expression in the first 9 days (Figure 3H), *POD72* expression at 3 d and 12 d (Figure 3I).

Effects of citronellal treatment on the phenolic biosynthesis in FCT

Our previous studies suggested that taro browning may be associated with phenolic biosynthesis induced by cutting

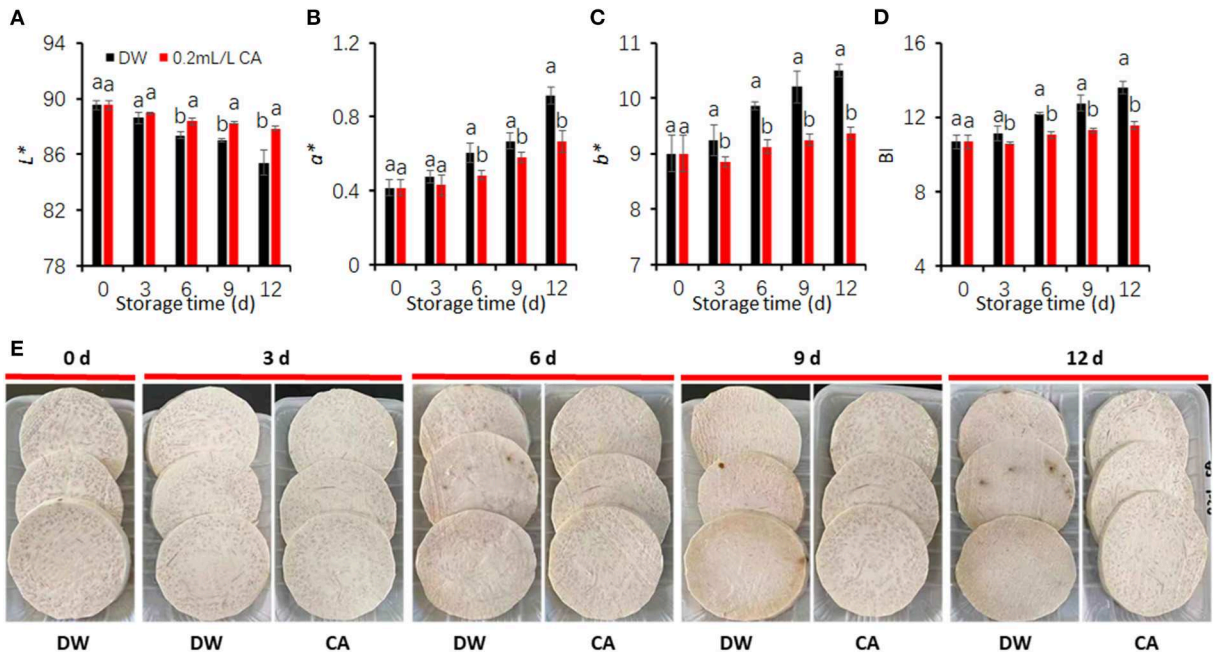

FIGURE 2
Inhibitory effects of 0.2 mL/L citronellal (CA) treatment on the browning of fresh-cut taros. **(A)** *L** value; **(B)** *a** value; **(C)** *b** value; **(D)** browning index (BI); **(E)** representative pictures from DW and CA treated taros during cold storage. DW, distilled water. Each value is presented as the mean ± *SE* ($n = 9$). Statistical differences ($p \leq 0.05$) are indicated as different letters above the bars.

operations (Xiao et al., 2022). The phenylpropanoid pathway is the major approach to the synthesis of various phenols (Yao et al., 2021). To examine whether CA mitigator reduced taro browning by suppressing the phenolic biosynthesis, the effects of CA treatment on the activity and gene expression of key enzymes in the phenylpropanoid pathway were investigated.

PAL activities in both the control and CA treatment declined during the first 6 days and increased thereafter. PAL activities of CA treatment were significantly lower than that of the control during the last 9 days (Figure 4A). Additionally, CA treatment also restricted the expression of two *PAL* genes during storage excepting at 9 d (Figures 4B,C).

In the control group, the expression of three genes coding cinnamic acid-4-hydroxylase (C4H) were increased after cutting (Figures 4D–F). CA treatment markedly restricted the expression induction of three *C4H* genes during cold storage (Figures 4D–F) comparing with the control.

In both the control and CA groups, the expression of two genes encoding 4-coumarate: CoA ligase (C4L), *C4L1*, and *C4L2*, decreased with prolonging storage period (Figures 4G,H). The expression levels of *C4L3* in the control first peaked at 3 d and fell hereafter, while that in CA treatment was decreased throughout storage (Figure 4I). Compared with the control, CA treatment significantly reduced the expression levels of three taro *C4L* genes (Figures 4G–I).

In the control group, the expression of three chalcone synthase (CHS) genes was induced by cutting at 3 d of storage at 5°C (Figures 4J–L). CA treatment significantly downregulated *CHS1* during the first 9 days, and *CHS2* expression at 3 d, and *CHS3* expression during the whole storage (Figures 4J–L). The results suggest that CA treatment reduced the activities of key enzymes in the phenylpropanoid pathway by down-regulating the expression of coding genes.

Effects of citronellal treatment on MDA concentration and LOX activity

In two treatments, MDA concentrations continuously increased with storage time progressed (Figure 5A). However, CA treatment effectively prevented the increase in MDA concentrations during storage. Consequently, MDA contents in CA-treated samples were markedly lower than that in DW-treated samples (Figure 5A). Taro slices subjected to CA solutions showed 26.88% less MDA contents at day 12 when compared to the control.

Similar to MDA content, LOX activity progressively increased with prolonging storage time in two treatments (Figure 5B). CA treatment significantly decreased LOX activities during the first 9 days comparing with the control (Figure 5B).

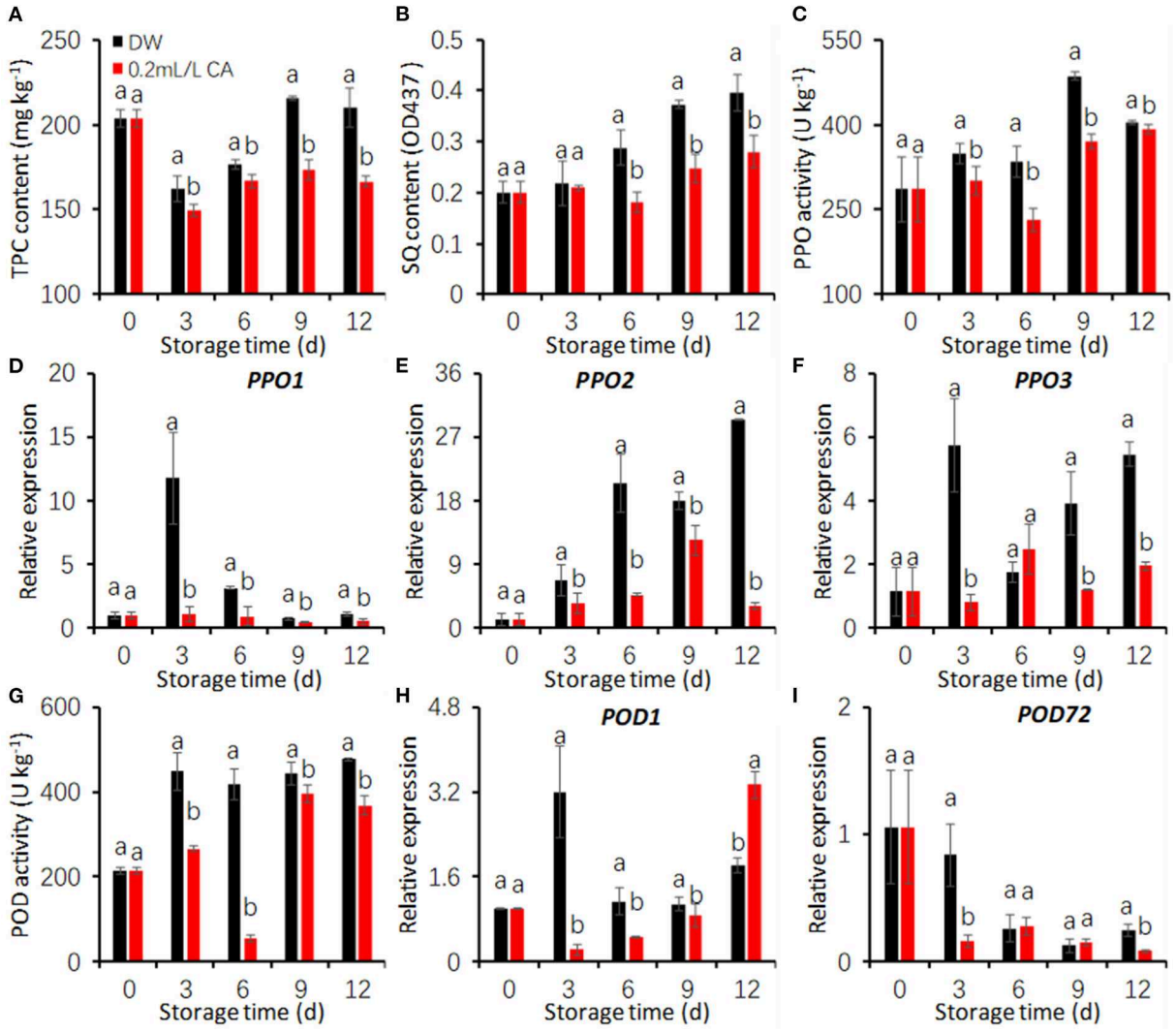

FIGURE 3
Effects of 0.2 mL/L citronellal (CA) treatment on the oxidation of phenolics in fresh-cut taros. **(A)** Total phenolic compound (TPC) content; **(B)** soluble quinone (SQ) content; **(C–F)** PPO activity and gene expression; **(G–I)** POD activity and gene expression. DW, distilled water. The expression levels were all normalized to 100% (1.0) at 0 d (before treatment). Each value is presented as the mean ± *SE* ($n = 3$). Statistical differences ($p \leq 0.05$) are indicated as different letters above the bars.

In addition, the expression of two *LOX* genes, *LOX1* and *LOX2*, were also repressed by CA treatment during cold storage (Figures 5C,D). The time-course trends of LOX activity and gene expression are opposite, suggesting that other member of *LOX* family genes could complement this and contribute to the higher enzyme activity during the late storage, as LOX is encoded by a multigene family (Porta and Rocha-Sosa, 2002).

Correlation analysis of browning-related indicators

Browning-related indices including L^*, a^*, b^* and BI values, TPC and SQ and MDA content, and PPO, POD, PAL, and LOX activity from the control samples were employed to perform correlation analysis. As shown in Figure 6, the BI, a characteristic index of FCT browning, was positively correlated with the parameters of a^* and b^* values, MDA and SQ and TPC contents, and POD and LOX and PPO and PAL activities, but negatively correlated with L^* value. BI had the highest Pearson correlations with b^* value ($r = 1.00$) and L^* ($r = -0.99$) and MDA content ($r = 0.99$) in the FCT, followed by a^* value and SQ content ($r = 0.98$; Figure 6). The correlation coefficients between BI and LOX activity, POD activity, PPO activity, and PAL activity were 0.87, 0.72, 0.72, and 0.55, respectively (Figure 6). These results imply that the key enzymes involving in FCT browning were LOX, followed by PPO and POD, and PAL was the secondary factor affecting taro browning.

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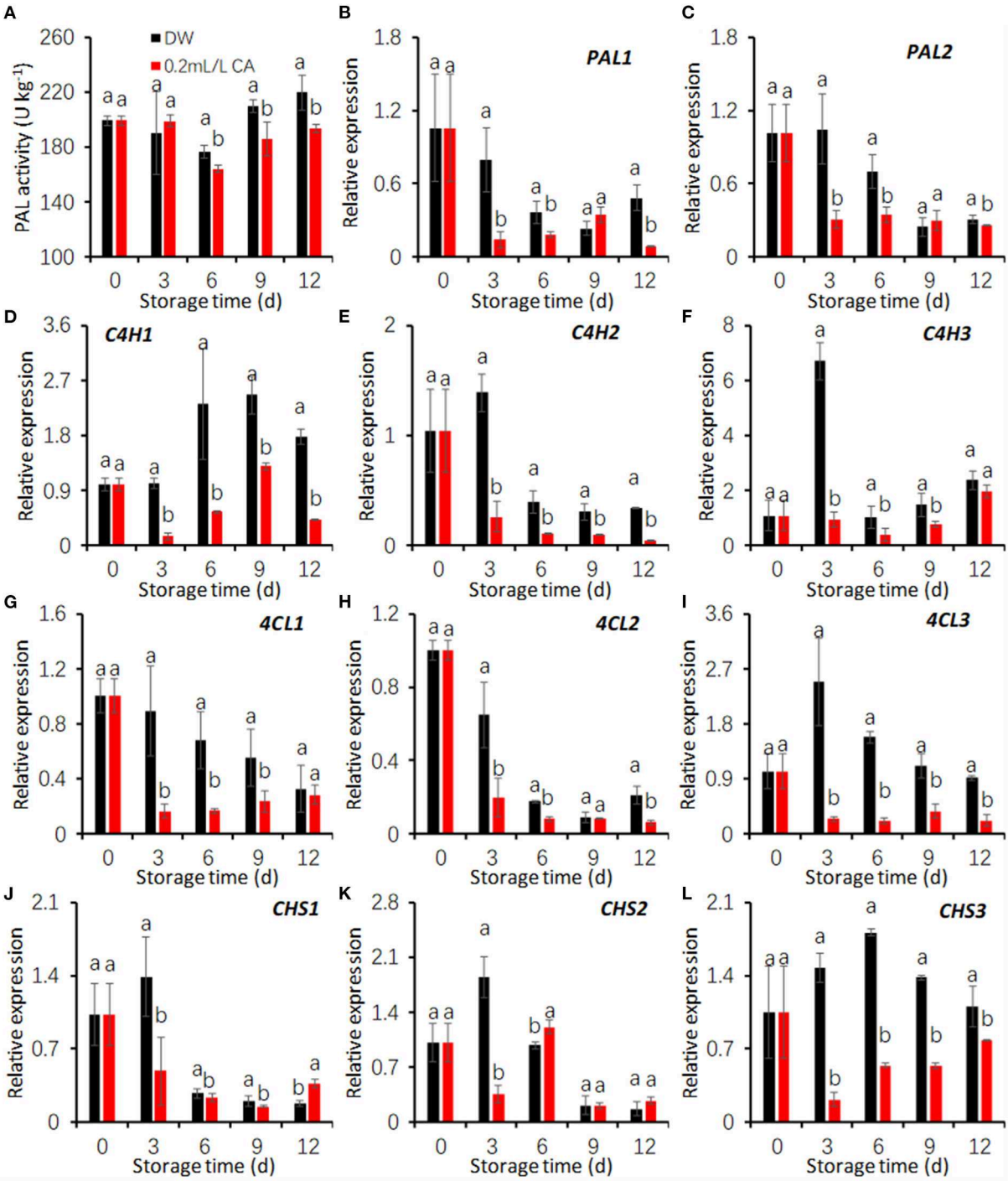

FIGURE 4
Effects of 0.2 mL/L citronellal (CA) treatment on the phenolic biosynthesis in fresh-cut taros. **(A–C)** PAL activity and gene expression; **(D–F)** relative expression of *C4H* genes; **(G–I)** relative expression of *4CL* genes; **(J–L)** relative expression of *CHI* genes. DW, distilled water. The expression levels were all normalized to 100% (1.0) at 0 d (before treatment). Each value is presented as the mean ± *SE* ($n = 3$). Statistical differences ($p \leq 0.05$) are indicated as different letters above the bars.

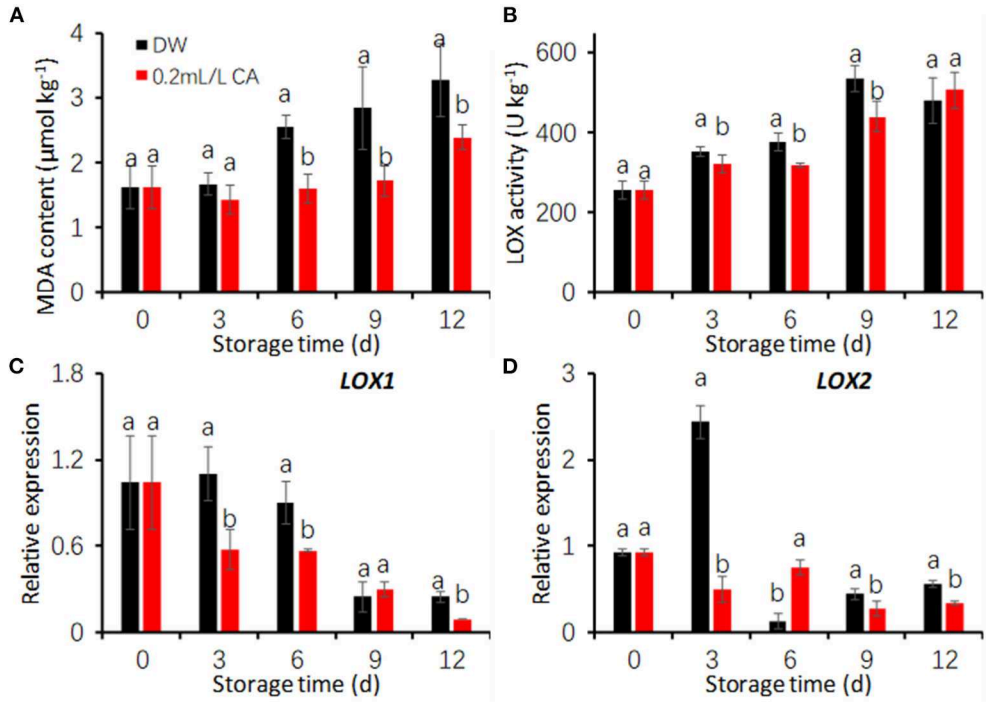

FIGURE 5
Effects of citronellal (CA) treatment on malondialdehyde (MDA) content **(A)** and LOX activity **(B)** and gene expression **(C,D)** in fresh-cut taros. DW, distilled water. The expression levels were all normalized to 100% (1.0) at 0 d (before treatment). Each value is presented as the mean ± *SE* ($n = 3$). Statistical differences ($p \leq 0.05$) are indicated as different letters above the bars.

Discussion

Taro is the fifth root crop and the 14th vegetable in the world (Bellinger et al., 2020). However, the cut surface browning is one of the major causes for the deterioration of FCT roots during processing and storage (Xiao et al., 2022). Here, the inhibitory effects of different concentrations of CA treatments on taro browning were investigated during cold storage. The results presented in this study showed that 0.2 mL/L CA significantly prevented the development of enzymatic browning of taro corm slices (Figures 1, 2), suggesting that this concentration might be suitable for the browning prevention. More investigations are needed to determine whether lower CA concentration is effective. It also noted that CA treatments in 0.5 and 1 mL/L concentration displayed slightly aggravated browning (Figure 1). We guessed that high concentration of CA solution treatments might cause chemical injuries on FCT tissues, as CA could impair the integrity of plasma membrane of living organisms (Wu et al., 2016) and cause a severe phytotoxicity on some plants (Singh et al., 2006) at a high concentration.

The growth and development of pathogens, mainly bacteria and mold, on the surface of fresh-cut produce negatively affect the microbial safety (Fan and Wang, 2022), as many pathogens in food are capable of secreting a wide range of exotoxins which severely threaten consumers' health (Liu et al., 2022). Numerous studies have demonstrated that CA possesses strong antifungal activities against many pathogens in food (Sharma et al., 2019). The mechanisms of CA inhibiting pathogen development are probably that it causes plasma membrane damage (Wu et al., 2016) and inhibits the biosynthesis of ergosterol, an integral component of the cell membrane (OuYang et al., 2021), and inhibits hemolytic activities of pathogens (Zhang et al., 2022). In this study, we observed that 0.2 mL/L CA treatment seemed to restrict some pathogens development on the FCT slices (Figure 2E), suggesting that low-dose CA treatment improved the microbial safety of FCT under cold storage condition by directly inhibiting pathogen development. However, how CA treatment restrains pathogen development on the surface of FCT and it restricts which kind of specific pathogen should be investigated in the future.

The browning on cut-surface in most fresh-cut products is generally attributed to the oxidation of phenolic compounds by two oxidases, PPO and POD (Altunkaya and Gokmen, 2010; Kasnak, 2020). In the current study, 0.2 mL/L CA treatment reduced POD and PPO activities and gene expression and SQ contents in FCT (Figure 3), suggesting that CA treatment restricted phenolic oxidation to form black-dark quinones by inactivating PPO and POD activity. Correlation analysis for

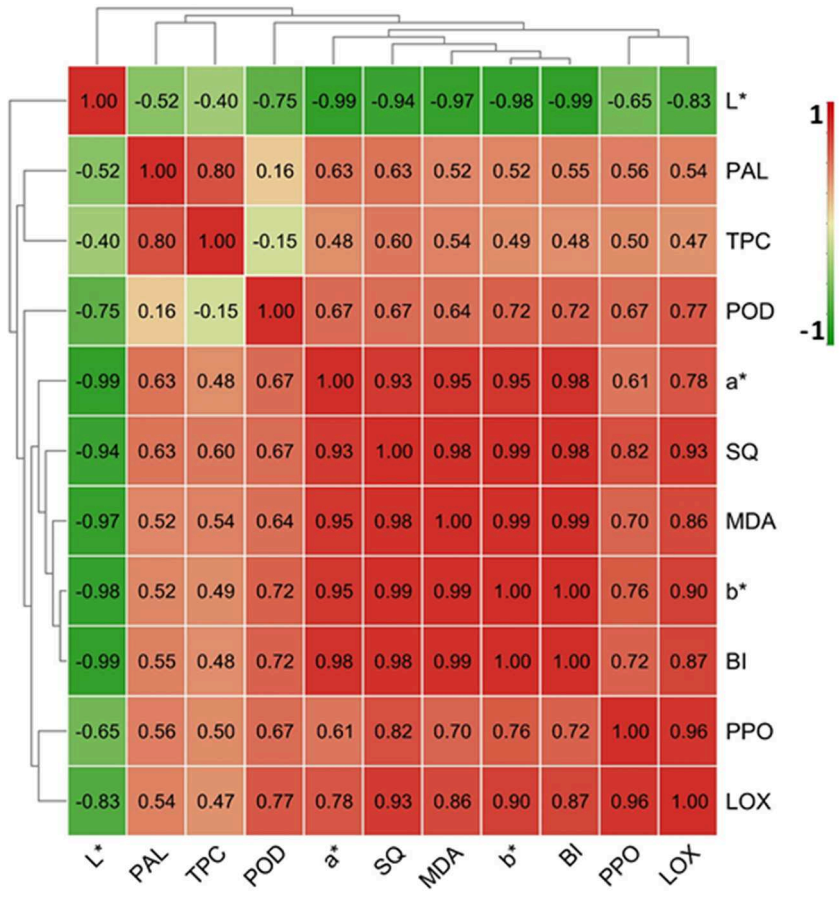

FIGURE 6
Correlation analysis of browning-related indicators in fresh-cut taro during cold storage. The map was made by TBtool software (Chen et al., 2020). The correlation coefficient between two browning-related indices was indicated in the map. The color code depicted at the right side of the image ranged from −1.0 (green) to 1.0 (red).

control samples in this study showed positive correlations between BI and both SQ contents ($r = 0.98$) and PPO ($r = 0.72$) and POD activities ($r = 0.72$; Figure 6). The application of 4-hexylresorcinol completely inhibited PPO activity and the browning of fresh-cut pears (Oms-Oliu et al., 2010). Ascorbic acid treatment prevented the oxidation of phenolics and flavonoids in fresh-cut apples by inhibiting PPO and POD activities (Wen et al., 2021). These investigations concur with our study and suggest that CA treatment prevented FCT browning by retarding the oxidation of phenolic compounds.

The *de novo* biosynthesis of phenlics induced by cutting and peeling through the phenylpropanoid pathway was suggested to be related to the browning of several fresh-cut foods (Song et al., 2019) including taros (Xiao et al., 2022). In plant, PAL, 4CL, C4H, and CHS are the four key enzymes responsible for phenolic biosynthesis through the phenylpropanoid pathway (Dong and Lin, 2021). Briefly, PAL catalyzes the deamination of L-Phenylalanine, and resulting in the formation of cinnamic acid (Medda et al., 2020). Cinnamic acid is subsequently hydroxylated by C4H to form *p*-coumaric acid (Zhang et al., 2020a). 4CL catalyzes the formation of CoA esters for some phenolics including ferulic acid, 4-coumaric acid, benzoic acid and caffeic acid (Klempien et al., 2012). CHS can use 4-coumaroyl-CoA to produce naringenin-chalcone, which can spontaneously isomerize into naringenin (Liu et al., 2019). In this study, CA treatment significantly reduced total phenolic contents (Figure 3A), PAL activity and the expression of nine *C4H*, *4CL*, and *CHS* genes in FCT (Figure 4), suggesting CA treatment reduced cutting-induced phenolic biosynthesis by suppressing the activities of key enzymes in the phenylpropanoid pathway. The repressed phenolic biosynthesis by CA treatment might contribute to a delay in FCT browning.

The stability and integrity of the cell membrane has been suggested to be closely associated with the browning of fresh-cut foods (Li et al., 2017; Worarad et al., 2021). LOX is a lipid peroxidizing enzyme involving in the oxygenation of polyunsaturated fatty acids into lipid hydroperoxides, and locates in the cell membrane (Shewfelt and del Rosario, 2000;

Lv et al., 2021). Fresh-cut operations usually induce LOX activity, and the enhanced LOX activity accelerates membrane lipid peroxidation (Gao et al., 2017; Zhao et al., 2021). MDA is generally supposed to be an indicator of membrane lipid peroxidation in plant (Dhindsa et al., 1981). LOX is proposed to promote the browning through inducing oxidative damages to cell membrane as seen in fresh-cut pears (Hu et al., 2014; Li et al., 2017), lotus roots (Gao et al., 2017), lily bulbs (Kan et al., 2019), as well as taros (Xiao et al., 2021). In the current study, CA treatment significantly reduced MDA contents and LOX activities and gene expression in FCT under cold condition (Figure 5). These results suggest that CA treatment reduced the membrane lipid peroxidation of FCT by restricting LOX activity, and thus maintaining an intact compartmentation for enzymes and substrates resulting in taro browning. In addition, correlation analysis indicated that there were positive correlations between BI and both MDA content ($r = 0.99$) and LOX activity ($r = 0.87$; Figure 6). The results suggest that MDA content and LOX activity could be browning indicators in FCT.

Now the question is: how can CA reduce the activities of browning-related enzymes? The answer may hide behind its chemical attributes. CA is a monoterpene aldehyde which has the ability to react with amino group (Han et al., 2017). The aldehyde compounds such as citral from citrus essential oil can directly react with the amino group in mushroom PPO to form a Schiff base (Lante and Tinello, 2015). A comparison of inhibitory activity for PPO by several aldehydes indicated that the stability of the Schiff base formed between PPO and one aldehyde was correlated with PPO activity (Kubo and Kinst-Hori, 1999). These results suggest that, at protein level, CA agent could directly inactivate the activities of browning-related enzymes by forming a Schiff base with amino group inner enzymes. Apart from regulations at protein level, CA treatment also suppressed the expression of 18 genes coding browning-related enzymes (Figures 3–5). The expression levels of all the 13 ergosterol biosynthesis genes were repressed after citronellal treatment (OuYang et al., 2021). These results suggest that CA treatment regulates gene expression *via* an as yet unknown mechanism. In all, the results suggest that CA treatment regulates the activities of browning-related enzymes at both protein and gene levels.

In conclusion, CA treatment in 0.2 mL/L showed a strong anti-browning activity against FCT browning. It could restrict the activity and gene expression of browning-related enzymes including PPO, POD, PAL and LOX, reduce TPC, SQ, and MDA contents in FCT during cold storage. The results of this study demonstrated that CA was a novel anti-browning agent at preserving high quality of FCT for processing. Further studies are required to investigate the detailed mechanisms behind the effects of CA on the browning reduction of FCT. Additionally, whether CA treatment could affect the aroma quality of FCT and consumers' acceptability should be thoroughly evaluated in future studies. Moreover, how CA treatment influences the microbial attributes of fresh-cut produce and which microbe is restrained need in-depth investigations.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: https://www.ncbi.nlm.nih.gov/protein/MQM19396.1.

Author contributions

BW: writing—original draft, data curation, investigation, resources, and methodology. YW: writing—original draft and data curation. YH: investigation and methodology. YJ: writing—original draft. JH: conceptualization, funding acquisition, and writing—review and editing. YX: writing—review and editing. All authors contributed to the article and approved the submitted version.

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Conflict of 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.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2022.1001362/full#supplementary-material

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