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Low-temperature conditioning enhances chilling tolerance and reduces damage in cold-stored eggplant (*Solanum melongena* L.) fruit

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ABSTRACT

Eggplant fruit are vulnerable to chilling injury (CI) after prolonged storage at temperatures below 12 °C. Here, we tested the effect of low-temperature conditioning (LTC) on chilling tolerance in eggplant fruit, in which fruit were stored at 13 °C for 2 d, and then held at 4 °C. Our results indicated that LTC maintained the appearance of eggplant fruit, and retarded the development of CI; the effect of LTC was characterized by inhibited sepal browning, and reduced loss of anthocyanins, and total phenolic compounds. The activity and relative gene expression of peroxidase (POD) and catalase (CAT) were increased by LTC, whereas the activity and relative gene expression of polyphenol oxidase (PPO) was reduced. In addition, the level of malondialdehyde (MDA) was significantly reduced. Our results suggest that LTC induces a range of physiological and molecular responses that enhance chilling tolerance in eggplant fruit.

1. Introduction

Eggplant (*Solanum melongena* L.) is an important economic crop in Asia and Mediterranean countries and has been ranked the 25th global commodity crop. In 2010, the data of food and Agriculture Organization showed that more than 80% of the global eggplant production was derived from China and India (Doğanlar et al., 2014). Eggplant fruit are rich in linoleic acid, fructose, malic acid, and a large number of antioxidants, including anthocyanins in the skin, that are known to offer several health benefits, including protection against vision impairment and some kinds of cancers (Ayaz et al., 2015; Jiang et al., 2016).

Postharvest storage of eggplants at room temperature rapidly reduces the quality of the fruit, mainly due to water loss, shrinkage of the skin, and discoloration, so cold storage is generally used to maintain postharvest fruit quality. However, eggplants are cold-sensitive and prone to chilling injury (CI) when stored at temperatures < 12 °C (Concellón et al., 2005), CI is a physiological disorder, with the main symptoms including rapid aging, skin shrinkage, and browning of the sepals and seeds (Fallik et al., 1995). As ROS scavengers, the activity of antioxidant enzymes in eggplant fruit can be decreased by low temperature (Zheng et al., 2008). The incidence of CI may be reduced using a number of techniques, includingoptimized storage conditioning (Abe and Chachin, 2007), and a fluctuating storage temperature (Ito and Nakamura, 1984). Low temperature conditioning (LTC) is the short-term storage of cold-sensitive plants above the damage-threshold temperature, to stimulate tolerance to subsequent storage at lower temperatures. Recently, studies of LTC in crops such as grapefruit (Chaudhary et al., 2017) and mango (Zhang et al., 2017) have indicated that it could significantly reduce CI and maintain product quality during low-temperature storage.

Here, we hypothesized that LTC may reduce CI in eggplants and we have explored its effect on metrics of eggplants quality.

2. Material and methods

2.1. Plant material and treatments

Undamaged, commercially mature eggplant fruit (*S. melongena* var. Brigitte), selected for uniform size, shape, and color, were collected from an organic vegetable farm in Xiaotangshan, Beijing, China, and were sent to the laboratory within three hours of harvest. The fruit were randomly allocated into two groups, each group contained 54 eggplant fruit, every six fruit being placed in a plastic tray and covered with polyethylene film. The control group was stored at 4 °C for 11 d, while the LTC treatment group was stored at 13 °C for 2 d, before subsequent storage at 4 °C for 9 d. Relative humidity (RH) for the two groups of eggplant was maintained at 90–95%. Six fruit were randomly collected

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from each treatment on days 0, 2, 5, 8, and 11, that is equal to the days on 0, 2, 5 (2 + 3), 8 (2 + 6), and 11 (2 + 9) in LTC, for evaluation of whole fruit appearance, CI index, and sepal browning index. Another six fruit were mixed to obtain homogeneous sample of the sepal, skin, and pulp, frozen using liquid nitrogen, and then stored at −80 °C prior to analysis. Three biological replicates were conducted within an experiment; each replicate was analyzed three times.

2.2. Appearance

Six fruit in each replicate were used to assess the appearance index. The appearance index of eggplant fruit were evaluated based on the development of browning on the sepals and black lesions and wrinkles on the skin. The scale was ranked as excellent (9), very good (7), good (5), fair (3), and poor (1) (Fan et al., 2016; Ghidelli et al., 2014). The appearance index was calculated as appearance index = (Appearance grade × Number of fruit at that level) / Total number of fruits × 100.

2.3. Chilling injury index

We modified the approach used by Concellón et al. (2007) to measure CI. On each sampling day, the effects of chilling on damage to the sepal and pulp were scored as none (1), slight (2), mild (3), moderate (4), or severe (5). Six fruit were evaluated on each sampling date. The CI index was calculated as:

$$\text{CI Index} = \frac{\sum (n_i \times i)}{N} \text{x}\,100$$

where n_i is the number of eggplant fruit with score i and N is the total number of fruit.

2.4. Sepal browning index

The degree of browning of the fruit sepals was visually evaluated, and the percentage of brown area was assessed based on the following scale: 1 = 0%–25%, 2 = 25%–50%, 3 = 50%–75%, 4 = 75%–100%. At each sample day, six fruit were select to evaluated browning index.The browning index was calculated by the following equation: browning index = (Browning level × Number of fruit at that level) / Total number of fruits × 100.

2.5. Phenolic content

Frozentissuepowder (2 g) of sepal and pulp were homogenized with 6 mL of ethanol, respectively, and then the mixture was centrifuged at 12,000 × *g* for 20 min at 4 °C and the total phenolic content of the supernatant was estimated using a colorimetric assay following a modified approach described by Hinneburg et al. (2006), where absorbance was measured at 760 nm. Phenol was used as a standard to calculate the level of total phenolic compounds and the total phenolic content was expressed as g kg^{-1}.

2.6. Anthocyanin content

We assessed total anthocyanin content of the skin, using the pH difference method, following a modified version of the technique used by Fan et al. (2016). Three replicates per treatment of frozen epidermal tissue (0.5 g) were homogenized in 5 mL of precooled ethanol solution containing 1% HCl and then centrifuged at 13,000 × *g* for 20 min at 4 °C. The change in absorbance at 530 nm and 600 nm was measured to determine the anthocyanin content. Absorbance readings were converted to gram of cyanidin 3-glucoside equivalents per kilogram of fresh weight.

2.7. Malondialdehyde content

MDA content was measured by a modification of the method of Wang et al. (2012). Frozen tissue powder of sepal and pulp (1 g) were homogenized in 5 mL of 5% (w/v) trichloroacetic acid, and centrifuged at 10,000 × *g* for 20 min at 4 °C. Then, 2 mL of 0.67% thiobarbituric acid was heated with 2 mL of the supernatant at 100 °C for 20 min, before the liquid was rapidly cooled and centrifuged at 10,000 × *g* for 15 min. The absorbance was measured at 450 nm, 532 nm, and 600 nm and the MDA content was expressed as μmol kg^{-1}.

2.8. Polyphenol oxidase, peroxidase, and catalase activity

For each of the two storage treatments, three replicates were determined three times in order to measure polyphenol oxidase (PPO) activity of sepal and pulp, peroxidase (POD) activity of pulp, and catalase (CAT) activity of pulp. Ice-cold extraction buffer (5 mL) - 100 mM sodium phosphate (pH 6.4) containing 0.2 g of polyvinylpyrrolidone was used for the PPO and POD assays, and 100 mM sodium phosphate (pH 7.8) containing 0.2 g of polyvinylpyrrolidone for the CAT assays. Pulp or sepal frozen tissue (1 g) was used for every assay. Centrifugal condition was 12,000 × *g* for 20 min at 4 °C then the supernatant was extracted for analysis.

To determine PPO and POD activity,a modification of the method of Hu et al. (2010) was used, in which 0.1mL of supernatant and 0.6 mL of catechol substrate (50 mM) were used to determine PPO activity, 0.9 mL of guaiacol (0.2%) and 1 mL of H_2O_2 (0.3%) were used to determine POD activity. The increase in absorbance was measured over 1 min at 410 nm (PPO) and 470 nm (POD), and the amount of enzyme required to cause an increase in one absorbance under the conditions of the assay in one minute was defined as one unit of activity.

To determine CAT activity, we used a modified approach of the technique used by Garcìa-Limones et al. (2002), in which 0.1 mL of supernatantand phosphate buffer solution at pH 7.8 (1.9 mL) were mixed with 0.3% H_2O_2 (1 mL); the change in absorbance at 240 nm was determined. One unit of activity was defined as the amount of enzyme required to cause a decrease of 0.01 absorbance under the conditions of the assay in one minute.

2.9. RNA extraction and quantitative reverse-transcription PCR (qRT-PCR) quantificationanalysis

Total RNA was extracted from eggplant tissue using Trizol reagent (Invitrogen Ltd., Carlsbad, CA, USA), and cDNA was synthesized by reverse transcription using the Invitrogen Super-Script ™ III First-Strand Synthesis System (Invitrogen, USA), and stored at −20 °C. The RT-PCR reaction system (20 μL) comprised 0.8 μL of diluted cDNA (100 ng), 10 μL of UltraSYBR mixture (CWbio.Co., Ltd., Beijing, China), 0.4 μL of each gene-specific primer, and 8.4 μL of RNase-free water and was analyzed using in a 96-well plate of a LightCycler1 480II real-time PCR system (Roche, Basel, Switzerland). Primer 5.0 (Applied Biosystem) was used to design specific primers based on the nucleotide sequence and qRT-PCR design principles of candidate internal reference genes: PPO (forward primer, 5′-GGCTTTTCTTCCCTTTC-3′; reverse primer 5′-TTA CTCTTCCATTGCGG-3′); POD (forward primer, 5′- AGCCATCTCCGTT TTGTG -3′; reverse primer 5′-CTGCTCGTGATTCCGTTC-3′); and CAT (forward primer, 5′- CGCATACGACACCCCTTTCT -3′; reverse primer 5′-AATCCCTTGGCACTAGCACC-3′). According to the formula $2^{-\Delta\Delta Ct}$ method (Livak and Schmitten, 2001), the relative value to control samples (0 d) was set, and the threshold constant (Ct) value was normalized to the Ct value of *Actin* (Zhou et al., 2014) to determine the relative fold differences of each sample.

2.10. Statistical analyses

SPSS version 22.0 (SPSS Inc., Chicago, IL, USA) was used to analyse

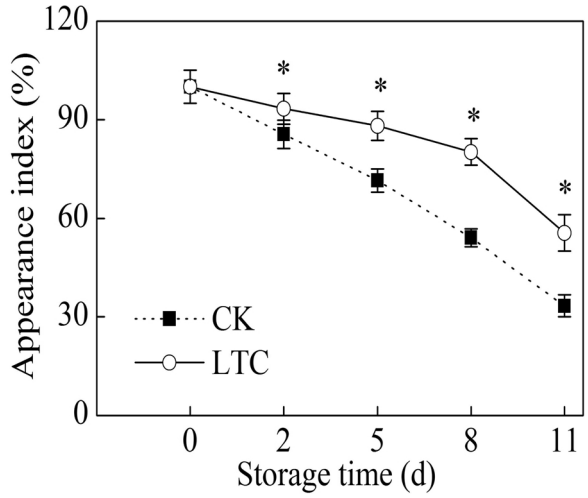

Fig. 1. Effect of LTC on appearance index of eggplant fruit during storage. CK: control; LTC: low-temperature conditioning. Vertical bars are SD (n = 3). The asterisk (*) represents statistical differences between treatments at each storage.

all statistic. The data from each analysis were test by one-way ANOVA. Means were performed by LSD. Differences at $P < 0.05$ were considered significant.

3. Results

3.1. Appearance

There was a clear reduction in the appearance of eggplant fruit during storage, and the rate of deterioration in appearance of LTC-treated fruit was less than for the untreated control fruit ($P < 0.05$; Fig. 1). The appearance of fruit in the LTC treatment was better than in the control ($P < 0.05$), which were classed as inedible after 11 d (2 + 9) of storage.

3.2. Chilling injury

CI of fruit in the LTC treatment and control increased during storage (Fig. 2). Both, in sepal and pulp, fruit stored only at 4 °C (control) exhibited CI symptoms from day 2, while fruit treated with LTC showed CI symptoms from day 5 (2 + 3) (Fig. 2). LTC slowed the rate of increase in CI and delayed the CI occurrence of fruit ($P < 0.05$) and by the end of the experiment, at day 11 (2 + 9), CI was 76% and 32 % lower in pulp and sepal of LTC treatment than those of the control, respectively (Fig. 2).

3.3. Sepal browning

Discoloration of sepals and senescence are part of the normal aging process in eggplants. Browning symptoms in the sepals began after one day of storage in both the LTC-treatment and control groups (Fig. 3); However, control fruit showed more severe sepal browning than LTC-treated fruit ($P < 0.05$).

3.4. Phenolic content

Although the levels phenolic content of eggplant fruit pulp in the LTC treatment remained stable from day 0 to day 5 (2 + 3), there was a general downward trend in total phenolic content of eggplant sepals and pulp in the control and LTC treatments during 11 d (Fig. 4). LTC treatment significantly slowed this decline, and at all sample dates, the total phenolic content of the sepals and pulp was higher in the LTC-treated fruit than in the controls. By the end of the experiments, at the 11th day (2 + 9), total phenolic contents in pulp and sepals were 1.74

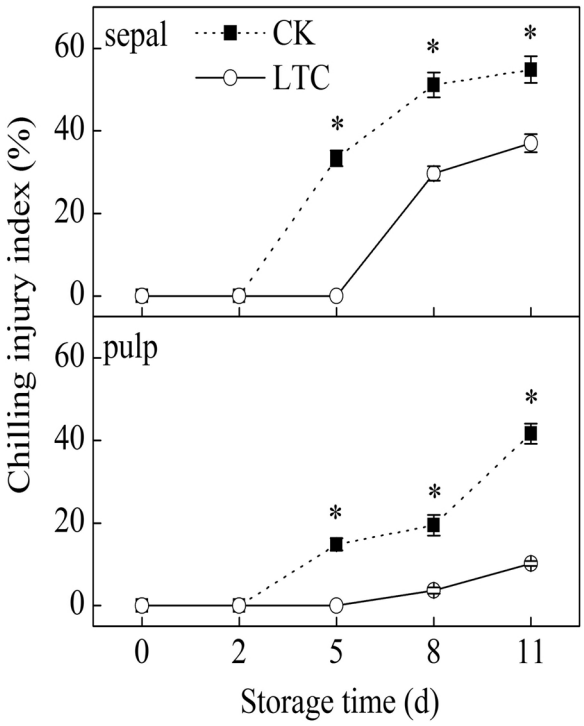

Fig. 2. Effect of LTC on chilling injury index of eggplant sepals (A) and pulp (B) during storage. CK: control; LTC: low-temperature conditioning. Vertical bars are SD (n = 3). The asterisk (*) represents statistical differences between treatments at each storage.

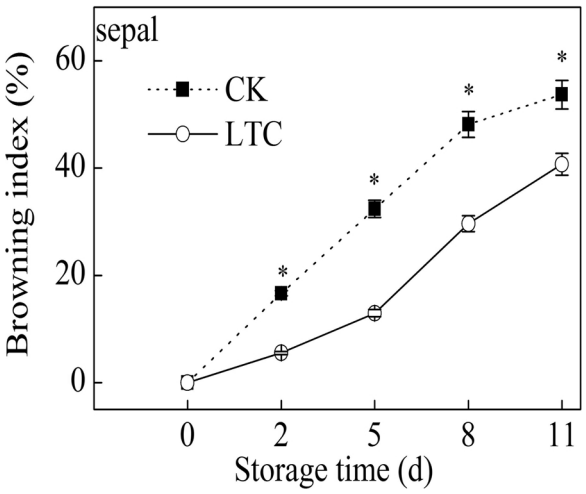

Fig. 3. Effect of LTC on browning index of eggplant sepals during storage. CK: control; LTC: low-temperature conditioning. Vertical bars are SD (n = 3). The asterisk (*) represents statistical differences between treatments at each storage.

and 1.45 fold higher, respectively, in the LTC treatment ($P < 0.05$).

3.5. Anthocyanins

The anthocyanin content in control and LTC-treated eggplant fruit skin significantly declined during storage (Fig. 5). There was a significantly higher anthocyanin content in the LTC treatment ($P < 0.05$) and, at day 11 (2 + 9), it was 70% higher than in the control.

3.6. MDA

We found that the MDA content gradually increased during the storage period in the treatment and control groups of sepal and pulp tissues (Fig. 6); however it was lower in the LTC-treated fruit. The

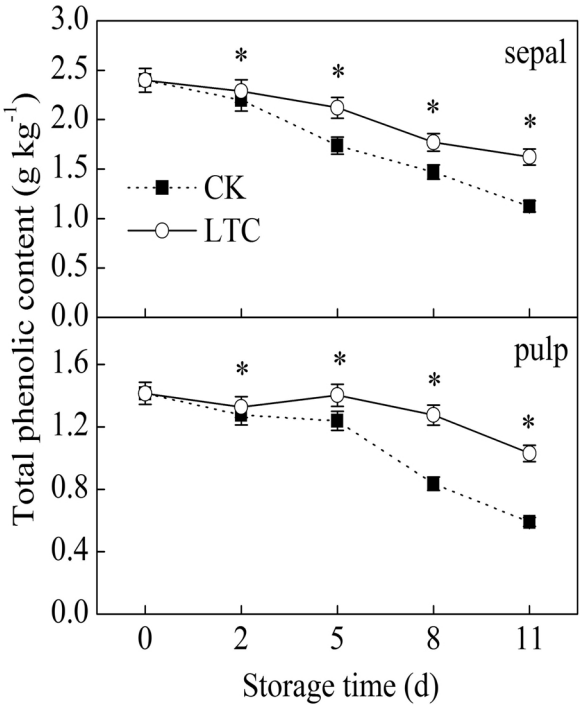

Fig. 4. Effect of LTC on total phenol content of eggplant sepals (A) and pulp (B) during storage. CK: control; LTC: low-temperature conditioning. Vertical bars are SD (n = 3). The asterisk (*) represents statistical differences between treatments at each storage.

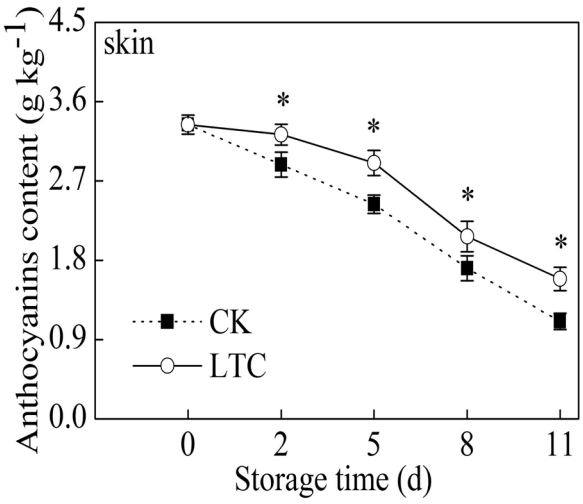

Fig. 5. Effect of LTC on anthocyanin content of eggplant skin during storage. CK: control; LTC: low-temperature conditioning. Vertical bars are SD (n = 3). The asterisk (*) represents statistical differences between treatments at each storage.

accumulation rate of MDA was higher in sepals than in pulp and by the 11th day (2 + 9) of storage, MDA content of the pulp and sepals was 26% and 29% lower, respectively, in the LTC treated fruit ($P < 0.05$).

3.7. PPO

We found that PPO activity gradually increased in sepals and pulp during the storage period (Fig. 7a, b), however it was lower in the LTC treated fruit ($P < 0.05$). The relative gene expression of PPO was similarly lower in the LTC treated fruit (Fig. 7A, B) ($P < 0.05$), and higher in sepals than in pulp.

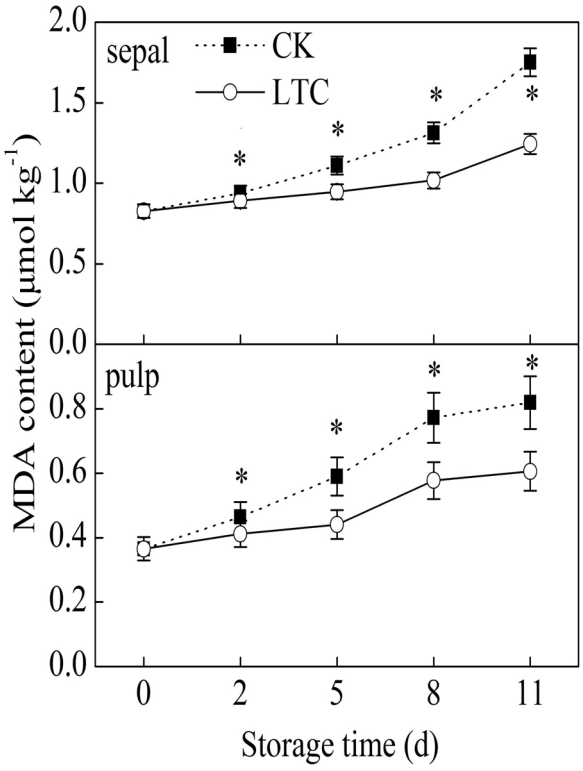

Fig. 6. Effect of LTC on MDA content of eggplant sepals (A) and pulp (B) during storage. CK: control; LTC: low-temperature conditioning. Vertical bars are SD (n = 3). The asterisk (*) represents statistical differences between treatments at each storage.

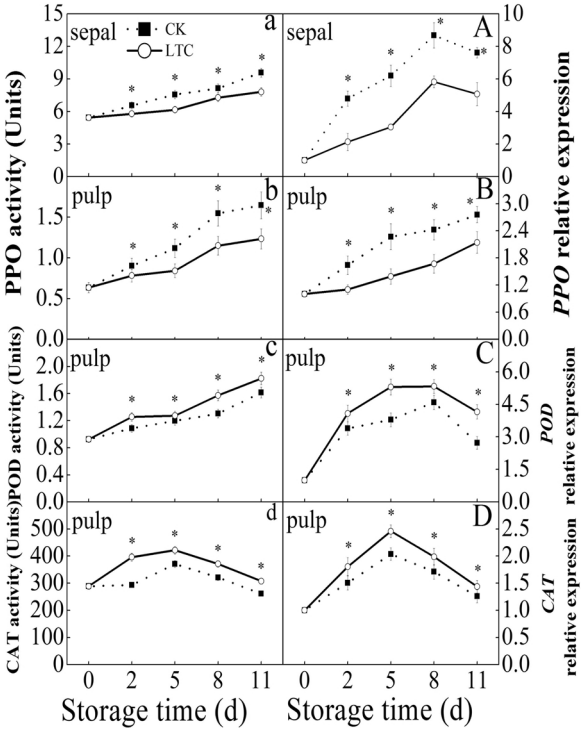

Fig. 7. Effect of LTC on PPO activity and gene expression of eggplant pulp (a and A, respectively) and sepals (b and B, respectively); POD activity and gene expression of eggplant pulp (c and C, respectively); CAT activity and gene expression of eggplant pulp (d and D, respectively) during storage. CK: control; LTC: low-temperature conditioning. Vertical bars are SD (n = 3). The asterisk (*) represents statistical differences between treatments at each storage.

3.8. Antioxidant enzymes: POD and CAT

During the whole storage period, the POD activity in both the treatment and control groups dramatically increased, however it was higher in the LTC treated fruit (Fig. 7). POD relative gene expression in control and LTC-treated fruit rapidly rose to a maximum during days 0–8 (2 + 6), before subsequently decreasing (Fig. 7C). There was higher POD gene expression in the LTC-treated eggplants ($P < 0.05$), and by day 11, mean relative gene expression of POD was 1.43% higher in the LTC treated fruit ($P < 0.05$). CAT activity and relative gene expression peaked at day 5 (2 + 3) (Fig. 7d, D) and were higher in the LTC treatment; by day 11 (2 + 9), relative gene expression was 13.78% higher in the LTC treated fruit ($P < 0.05$; Fig. 7D).

4. Discussion

Storage of postharvest crops at low temperature disrupts metabolism and results in cell necrosis, rapid fruit aging, and eventually decay (Watkins, 2003). Our study demonstrated that LTC of eggplants is a potentially powerful tool for enhancing chilling tolerance and improving postharvest fruit quality. LTC has been found to maintain higher fruit quality in chilling-sensitive fruit, such as loquat (Cai et al., 2006), pear (Chen et al., 2015), grapefruit (Chaudhary et al., 2017), mango (Zhang et al., 2017), avocado (Hofman et al., 2003), and pomegranate (Kashash et al., 2016).

Eggplant fruit is susceptible to CI during low-temperature storage, where the main visual symptoms include epidermal atrophy, and sepal deterioration and browning (Fallik et al., 1995). In our study, LTC of eggplant fruit reduced the severity of CI, and delayed CI onset by 3 d, showing that LTC is a useful technique for reducing the adverse effects of low-temperature storage. These favorable effects are due to LTC inducing cold tolerance by enhancing the antioxidant system, inducing lipid membrane unsaturation, and regulating the secondary metabolites and the relative expression of genes involved in antioxidation.

We found that the main visual indicator of CI during cold storage was sepal browning and the development of black lesions and wrinkles on the skin. Our study showed that LTC resulted in eggplant fruit with higher-quality appearance, as indicated by the lower CI and sepal browning indices. Sepal browning is a significant problem in eggplant storage that is usually associated with long-term storage or chilling injury and it greatly reduces fruit quality (Massolo et al., 2011). Eggplants contain high levels of phenolic compounds that facilitate enzymatic browning. Total phenolic content of eggplant fruit in both the control and the LTC treatment decreased significantly during storage, suggesting that phenolic compounds oxidize during the sepal browning process. Total phenolic content of the LTC-treated fruit decreased more slowly and remained higher than in the control fruit, indicating that LTC decreased phenolic compound content and its associated effect on sepal browning. These results are consistent with study reported by Saengnil et al. (2014), in which the reduction of total phenolic content in longan pericarp was slowed down by fumigation with chlorine dioxide.

PPO is essential in the enzymatic browning of several horticultural products (Kumar et al., 2013), including eggplant (Mishra et al., 2013), where it catalyzes the transformation of monophenol to *o*-diphenol, and subsequently to *o*-quinones, and results in the formation of brown, red, and black pigments characteristic of the browning process (Mai and Glomb, 2013) and CI. We suggest that the reduced PPO activity and relative gene expression in LTC-treated eggplant fruit resulted in lower levels of CI. The changes in PPO activity in our study were consistent with research that suggested that LTC treatment may slow down the reduction in total phenolic content, and inhibit PPO activity and PPO relative gene expression, thereby inhibiting the occurrence of browning reactions (Fan et al., 2016).

Anthocyanins in plants provide resistance to ultraviolet light, disease, and low temperature (Castellarin et al., 2007; Liu et al., 2013; Jiang et al., 2016) and are present at high levels in eggplant fruit, particularly in the skin. We found that delayed decreases in anthocyanin levels in eggplant skin caused by LTC were concomitant with a reduced level of discoloration.

Cold storage induced ROS production and accumulation involved in altering membrane integrity and causing phospholipid peroxidation, resulting in CI in many vegetable fruits (Jin et al., 2010). The plastids are found to be the sites of cold-induced peroxidation and the plastid membranes are susceptible to chilling (Concellón et al., 2012). MDA is an indicator of membrane damage and is a secondary end product of polyunsaturated fatty acid oxidation, and CI-associated membrane damage in fruit stored at low temperatures may be a result of lipid peroxidation. The content of MDA may therefore reflect the degree of CI (Hui et al., 2015) and in this study, we found that the MDA content in LTC-treated eggplant fruit remained at a lower level than in the control fruit. Some studies have suggested that LTC may inhibit MDA content in cold-stressed mango and pear (Chen et al., 2015; Zhang et al., 2017). The lower MDA content in LTC eggplants indicates that this technique may be appropriate in the suppression of oxidative damage and the maintenance of membrane integrity during cold storage. These results may be one explanation of LTC enhancing the chilling resistance in eggplant by regulating the activity of PPO, the production of MDA and secondary metabolites (total phenolic, anthocyanin) to increase resistance.

Plant cells are rich in antioxidants and have an efficient antioxidant system that reduces damage caused by reactive oxygen species (Pasquariello et al., 2015). However, antioxidant enzymatic activity of chilling sensitive cultivars can be reduced under the low temperature, which decreases their ability to treat with the increase of ROS (Valenzuela et al., 2017). We found that LTC stimulated the activity and relative gene expression of CAT and POD in eggplant fruit, which reduced the CI index. These findings may be another explanation of the alleviation of CI in eggplant by LTC. Antioxidant enzymes CAT and POD play important roles in H_2O_2 decomposition (Jihyun and Kwangdeog, 2011), higher activity and relative gene expression of CAT and POD contributes to the removal of ROS. These results were consistent with the effects of LTC on kiwifruit (Yang et al., 2013).

In conclusion, we found that LTC at 13 °C ± 0.5 °C and 90–95% RH for 2 d effectively maintained a best appearance quality of eggplant fruit, retarded sepal browning, reduced CI, and enhanced tolerance to chilling. The mechanism of enhanced chilling tolerance as a result of LTC may be due to improved expression and activity of antioxidant enzyme genes, and the maintenance of higher levels of anthocyanins and of total phenolics that protect against oxidative damage.

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