International Food Research Journal 30(4): 933 - 944 (August 2023)
Journal homepage: *http://www.ifrj.upm.edu.my*

Trehalose regulates the quality and antioxidant capacity of cherry tomato during postharvest ripening

*Fan, T. T., Xia, M. H., Cao, J. X., Zhang, J., Wang, T. and Cao, S. Q.

School of Food and Biological Engineering, Hefei University of Technology, 193 Tunxi Road, Hefei, Anhui 230009, P. R. China

Article history

Received:
22 February 2022
Received in revised form:
9 December 2022
Accepted:
10 February 2023

Keywords

trehalose,
cherry tomato,
decay,
antioxidant enzyme

Abstract

Trehalose has been extensively studied in the application of fruit preservation, but little has been reported in cherry tomato preservation. The present work investigated the effects of postharvest trehalose treatment on cherry tomato spoilage rate, antioxidant capacity, and fruit quality through the application of 0.5 and 1% (w/v) trehalose. Our results indicated that trehalose treatment could reduce rot from 44.5 to 18.5%, maintain the fruit flavour and quality, and delay the decrease in antioxidant content. At 15 d postharvest, the diphenyl-picryl hydrazide (DPPH) scavenging capacity, superoxide anion ($\cdot O_2^-$) production, and malonaldehyde (MDA) content were 78.1%, 1.04 $mmol \cdot min^{-1} \cdot kg^{-1}$, and 0.8 $\mu mol \cdot kg^{-1}$ in cherry tomato treated with 0.5% (w/v) trehalose, respectively. Trehalose-treated fruits maintained higher antioxidant capacities as compared to the control. Moreover, trehalose treatment increased the activities of superoxidase dismutase (SOD) and ascorbate peroxidase (APX), and inhibited the activity of lipoxygenase (LOX). The expression of encoding antioxidant genes was generally upregulated under trehalose treatment. However, the expression of *SlLOX* gene was significantly lower during storage, at only one-tenth of the control at 9 d. In conclusion, trehalose treatment had positive effects on decreasing decay incidence by increasing antioxidant capacity in cherry tomato.

DOI
https://doi.org/10.47836/ifrj.30.4.11

Introduction

Cherry tomato is a valuable fruit due to its unique flavour and variety of nutrients (Vinha *et al*., 2014). It has effects that include clearing heat and detoxifying, invigorating stomach and eliminating food, and nourishing blood (Badawy and Rabea, 2009). Vitamins, phenols, and carotenoids in cherry tomato have good antioxidant effects (Kim *et al*., 2002). The antioxidants in cherry tomato fruits have the ability to quench active agents, eliminate free radicals in the body, slow atherosclerosis, protect the cardiovascular system, and prevent many types of cancers (Sesso *et al*., 2003; Rissanen *et al*., 2003). However, cherry tomato is vulnerable to mechanical and microbial damage after harvesting due to its thin skin and high-water content, which leads to the deterioration of its sensory and nutritional qualities. At present, cherry tomato storage methods mainly include controlled atmosphere and chemical storage, both of which have shortcomings (Zhang *et al*., 2015). Therefore, the development and application of green and safe natural preservatives are in high demand.

Trehalose, also known as yeast sugar, was first extracted by Wiggers from the ergot fungus of rye in 1832, and it was later found to be widespread in plants, animals, and microorganisms (Alan and Elbein, 2003). Trehalose is a non-reductive disaccharide connected by two glucose molecules through α, α-1, and 1-glycan bonds (Ohtake and Wang, 2011). Its chemical properties are stable, and it does not undergo caramelisation or the Maillard reaction when heated (Alan and Elbein, 2003; Teramoto *et al*., 2008; Hengherr *et al*., 2011). Due to its special structure, trehalose could effectively protect the plasma membrane and protein structure of cells, maintain cell osmotic pressure, prevent the loss of intracellular nutrients, and preserve the normal structure of cells (Al-Naama *et al*., 2009).

Currently, trehalose has been applied to prevent food deterioration, maintain fresh flavour, and improve food quality in a variety of fruits and vegetables such as apples, strawberries, and peppers

*Corresponding author.
Email: fantting@hfut.edu.cn

(Jing *et al*., 2010; Zhao *et al*., 2013). Furthermore, Li and Tian (2006) cultured *Cryptococcus laurentii* with trehalose as the only carbon source, and the accumulation of endogenous trehalose was induced, enhancing the control of yeast on apple penicilliosis. Trehalose forms a protective membrane on the surface of fruits and vegetables to prevent external air from entering the cell membrane, and effectively inhibiting the respiration of fruits and vegetables. In addition, this adhesion slowed the evaporation of water and prevented the interaction between oxygen and enzymes in fruits and vegetables (Ali and Ashraf, 2011). Trehalose may have potential commercial value in reducing decay and improving antioxidant activity. However, little information is available on the effect of trehalose on the decay and antioxidant capacity in cherry tomato fruits. Therefore, the purpose of the present work was to explore the effects of trehalose treatment on cherry tomato spoilage rate, antioxidant capacity, and fruit quality at room temperature. The results would provide a theoretical basis for the application of trehalose as a new, safe, and effective preservative for cherry tomato.

Materials and methods

Samples and chemicals

Cherry tomato (*Lycopersicon esculentum* L. cv Xiunv) fruits were purchased from the fruit supermarket of Hefei University of Technology in Hefei, China. Fresh fruits with the same appearance and maturity, which were also free of disease, insect spots, and mechanical damage were selected. The selected fruits were randomly divided. Trehalose was purchased from Shanghai Yuanye Co. Ltd., China, and all other chemicals were analytically pure.

Trehalose treatment

In this experiment, 0.5 and 1% (w/v) trehalose solutions were prepared. The cherry tomato fruits were washed, drained, and soaked in the prepared solution (with or without trehalose) for 5 min. Then, the fruits were removed from the solutions, air-dried, and stored at 25°C with 80 - 85% humidity (Yao *et al*., 2018). The fruits were stored for 15 d, and each quality index was measured every 3 d. Seeds from the cherry tomato fruits were removed, and the pulp was immediately frozen with liquid nitrogen, and stored at -80°C until analysis. Each treatment was repeated three times.

Fruit quality measurements

Decay incidence of cherry tomato was assayed according to Aghdam and Fard (2017), and expressed as percentage. Sixty cherry tomato fruits were selected for each experiment. The rot index was calculated as follows: decay incidence (%) = (number of rotten fruits / number of total fruits) × 100. The weight loss rate was calculated as follows (Ge *et al*., 2019): weight loss rate (%) = (fruit weight before storage – fruit weight after storage) / fruit weight before storage × 100. The cherry tomato fruit was placed between two glass plates (10 × 10 cm), and the fruit hardness was measured by applying pressure above the equatorial part of the fruit with a fruit hardness tester (GY-3, Pride Instrument, Shanghai, China). Ten fruits were analysed for each determination, and the average value was calculated for three replicates. The total soluble solids (TSS) in the fruits were determined using a hand-held glucose meter (WYT-III, Flaig Magnetsysteme, Hardt, Germany). Ten cherry tomato fruits were pressed with a juicer to determine pH and titratable acid (TA). The pH of fruits was measured using a pH meter (PHS-25, Leici, Shanghai, China). The TA content was measured according to Jin *et al*. (2016) with slight modifications. Ten millilitres of juice were combined with two drops of phenolphthalein, and titrated to a red colour with 0.1 M NaOH. The reducing sugar content was determined by titration with Feilin's reagent, and the standard curve was constructed with glucose standard solutions (Davarpanah *et al*., 2016). The result was expressed as mg kg^{-1} of fresh fruit.

Total phenolic, flavonoid, vitamin C (Vc), and lycopene contents

The total phenolic and flavonoid contents in cherry tomato extracts were determined according to Toor and Savege (2005) with slight modifications. Gallic acid was used as the standard. The result was expressed as mg kg^{-1} gallic acid based on the fresh weight. For the total flavonoid assay, the absorbance was measured at 510 nm, and the result was expressed as mg kg^{-1} rutin based on the fresh weight. The Vc content was determined by 2,6-dichlorophenol indophenol dye titration method (Vahid, 2012). Ten grams of the sample was combined with 20 g L^{-1} oxalic acid solution, and ground in an ice bath. The mixture was centrifuged at 12,000 *g* for 10 min at 4°C, and 10 mL of the supernatant was reacted with

2,6-dichlorophenol indophenol to a reddish colour. The lycopene content was determined according to Goula and Adamopoulos (2005), and the absorbance at 475 nm was determined. The result was expressed as g kg^{-1} of fresh fruit.

Diphenyl-picryl hydrazide (DPPH), hydroxyl radical (·OH), and superoxide anion ($\cdot O_2^-$) radical scavenging capacities, reducing power, and malondialdehyde (MDA) contents

DPPH and the hydroxyl radical scavenging capacity were determined according to Cho (2016). The results were calculated as: DPPH scavenging capacity (%) = (1 – absorbance of the sample / absorbance of the control) × 100. Hydroxyl radical scavenging capacity (%) = (1 – sample absorbance / control absorbance) × 100. Superoxide anion production was determined according to Vo *et al*. (2021), measured spectrophotometrically and expressed as mmol min^{-1} kg^{-1} fresh weight. The reducing power was determined according to Saha and Verma (2016). The results were expressed as the absorbance of the mixture at 700 nm. The content of MDA in tomato fruits was determined by thiobarbituric acid (TBA) reaction (Ma *et al*., 2016). The absorbance at 450, 532, and 600 nm was measured. The concentration of MDA was calculated as $MDA = 6.45 \times (OD_{532} - OD_{600}) - 0.56 \times OD_{450}$. The amount of MDA in the fruits was calculated as MDA = concentration of MDA × volume of extracted liquid / fresh weight of plant tissue. The result was expressed as μmol kg^{-1} fresh weight.

Antioxidant enzyme measurements

Activity assays were performed on the superoxidase dismutase (SOD), ascorbate peroxidase (APX), and lipoxygenase (LOX) antioxidant enzyme systems. The SOD activity was analysed using a SOD activity assay kit (Yuanye, China). The activity of SOD in the sample was calculated by measuring the absorbance value at 560 nm. One unit of SOD activity is defined as the amount of enzyme that resulted in a 50% inhibition of nitroblue tetrazolium (NBT) reduction under assay conditions. The absorption values of the APX reaction system decreased at 290 nm, and the absorption values of the LOX reaction system decreased at 234 nm (Hu *et al*., 2012). For the determination of APX and LOX activities, the sample was mixed for 15 s, and then, the absorbance value was recorded immediately at 30 s intervals. The data of at least six points were obtained *via* continuous measurement. One unit of APX and LOX activity is defined as an absorbance change of 0.01 units per min.

Quantitative-RT-PCR analysis

Total tomato RNA was extracted by trizol RNA Reagent Kit (Takara, Japan). After the concentration was determined, RNA was reversely transcribed into cDNA using a reverse transcription kit, and stored at -20°C. The relative expression levels of the target genes were determined using the SYBR Premix Ex Taq (Vazyme, China). The total volume of quantitative PCR was 10 μL (5 μL of quantitative enzyme, 2.5 μL of primers, and deionised water to 10 μL). *SlTubulin* was selected as an internal reference gene for normalisation, and primers for antioxidant-related genes were designed by Yao *et al*. (2018) and Wang *et al*. (2017) (Table 1). The relative expression level of the target gene was calculated according to Schmittgen and Livak (2008). Three replicates were performed for each sample.

Table 1. Primer sequences for RT-qPCR of cherry tomato antioxidant genes.

Gene name	Forward primer (5'→3')	Reverse primer (5'→3')
SOD1	CTTGGAAAGGGAGGACATGAG	GTTAACCCTGGAGGCCAATAA
SOD2	TGGCCATGAACTCAGTCTTAC	CTGTTGTTGCTGCTGCATTTA
FeSOD	ACCTCATCCCTCCTCCTTATC	CATACGCCCTGTGATGCTT
CuZn-SOD	GGTAGGAGGAGGATAGAGACAA	CACTATCGTTCCCGGAGATTAC
APX1	TACAGTTGCCGTCAGACAAG	CCTCAGCATAGTCAGCAAAGA
APX2	GGCTCTTACAGTTGCCATCA	CATCTTCATCCGCAGCATATTTC
APX3	AGGTGTGCCGCATCTTAAA	GATGTGCCCTTCCTAGTGTATG
LOX	TTTACTCCTGGTCGCTATG	TACTGCCATCCCTCTTCG
Tubulin	TAGAGCCTGGTACGATGGATAG	CAACTCAGCGCCTTCAGTATAA

Statistical analysis

The experiment used a completely random design, and the parameters were measured in replicates of three. The data were graphed by Sigma Plot 14.0 and analysed by SPSS l9.0. Tukey's multiple comparison method was used for significant difference analysis, and the significance level was 0.05.

Results and discussion

Trehalose affected the quality of cherry tomato fruits

Cell wall disintegration and tissue softening during postharvest ripening make fruit more susceptible to pathogen infection, thus leading to a higher incidence of fruit decay (Ana *et al*., 2013). Trehalose treatment (spraying or soaking) on the surface of fruits and vegetables prolongs the shelf life (Cai *et al*., 2018). To investigate the effect of trehalose treatment on cherry tomato quality, we examined important quality indicators after fruit harvest. All fruits were stored at room temperature for 15 d, and their decay rate gradually increased. The fruit decay index of the trehalose-treated fruits was lower than the control group, and the effect was most obvious after 9 d (Figure 1A). The results of weight loss rate and decay index were consistent. There was no significant difference between the experimental and the control groups during the first 9 d of storage (Figures 1B and 1C). The weight loss rate of the control group was 16%, and 1% treatment group was only 11% at 15 d ($p < 0.05$). This is because trehalose forms a special coating on the surface of cherry tomato that decreases the invasion of pathogenic bacteria, and reduces the pathological decay of fruit. Similarly, Zhao *et al*. (2012) reported that the disease incidence of *Rhizopus* decay of strawberries treated with *Pichia caribbica* which was cultured in NYDB media containing 0.5% trehalose was significantly lower than that of the control strawberries.

Hardness is the most direct indicator of fruit firmness, which directly determines the acceptance of cherry tomato fruits by consumers (Ji *et al*., 2020). With the extension of storage time, fruit hardness gradually decreased, but both trehalose concentrations delayed the decrease in fruit firmness (Figure 1D). In addition, the pH value of the fruit increased gradually. This might have been due to some organic acids in cherry tomato fruits being converted to sugars during storage, which led to an increase in the sugar-acid ratio and a gradual increase in pH. Trehalose treatment resulted in a lower pH when compared with the control group in the later stage of storage, and the lower pH delayed fruit ripeness (Figure 1E). Due to the absence of external nutritional sources, respiration mainly occurs through the consumption of soluble sugars in the fruit during storage, thus resulting in a decrease in TSS content in each group. When compared with the control group, trehalose treatment resulted in higher TSS contents during cherry tomato ripening. In particular, TSS contents were higher in the treatment groups at 9, 12, and 15 d, when compared with the control group (Figure 1F, $p < 0.05$). Similarly, Cao *et al*. (2018) reported trehalose osmotic dehydration as a pre-treatment for grapes, and the authors observed an increase in TSS content. Furthermore, the TA content of fruits in all treatment groups gradually decreased, and the TA content of trehalose treatment was higher than the control group after 12 d (Figure 1G). As shown in Figure 1H, the results of reducing sugar and TA content were consistent. Overall, trehalose treatment of cherry tomato inhibited fruit decay, and maintained the quality of the fruits.

Trehalose increased the amount of antioxidants in cherry tomato fruits

The defence system against free radical oxidative damage in fruits and vegetables mainly includes enzymatic and non-enzymatic antioxidant substances (Gonzalez *et al*., 2010). Cherry tomato fruits mainly contain antioxidant substances such as total phenols, total flavonoids, Vc, and carotenoids. These antioxidants are closely related to the removal of reactive oxygen free radicals, and an increase in disease resistance in fruit (Suttirak and Manurakchinakorn, 2014). Trehalose treatment affected not only the nutrients of cherry tomato fruits but also the antioxidant content. As shown in Figure 2A, the total phenolic content of cherry tomato decreased gradually during storage. The total phenolic content of trehalose-treated fruits was higher than the control in the late stage of storage, and there was no difference between the 0.5 and 1% treatments. The content of total flavonoids and Vc increased initially, and then decreased gradually. Trehalose treatment delayed the peak in flavonoid content, which occurred at 9 d in the control group and at 12 d in the treatment group (Figure 2B). Trehalose treatment had the most significant inhibitory effect on

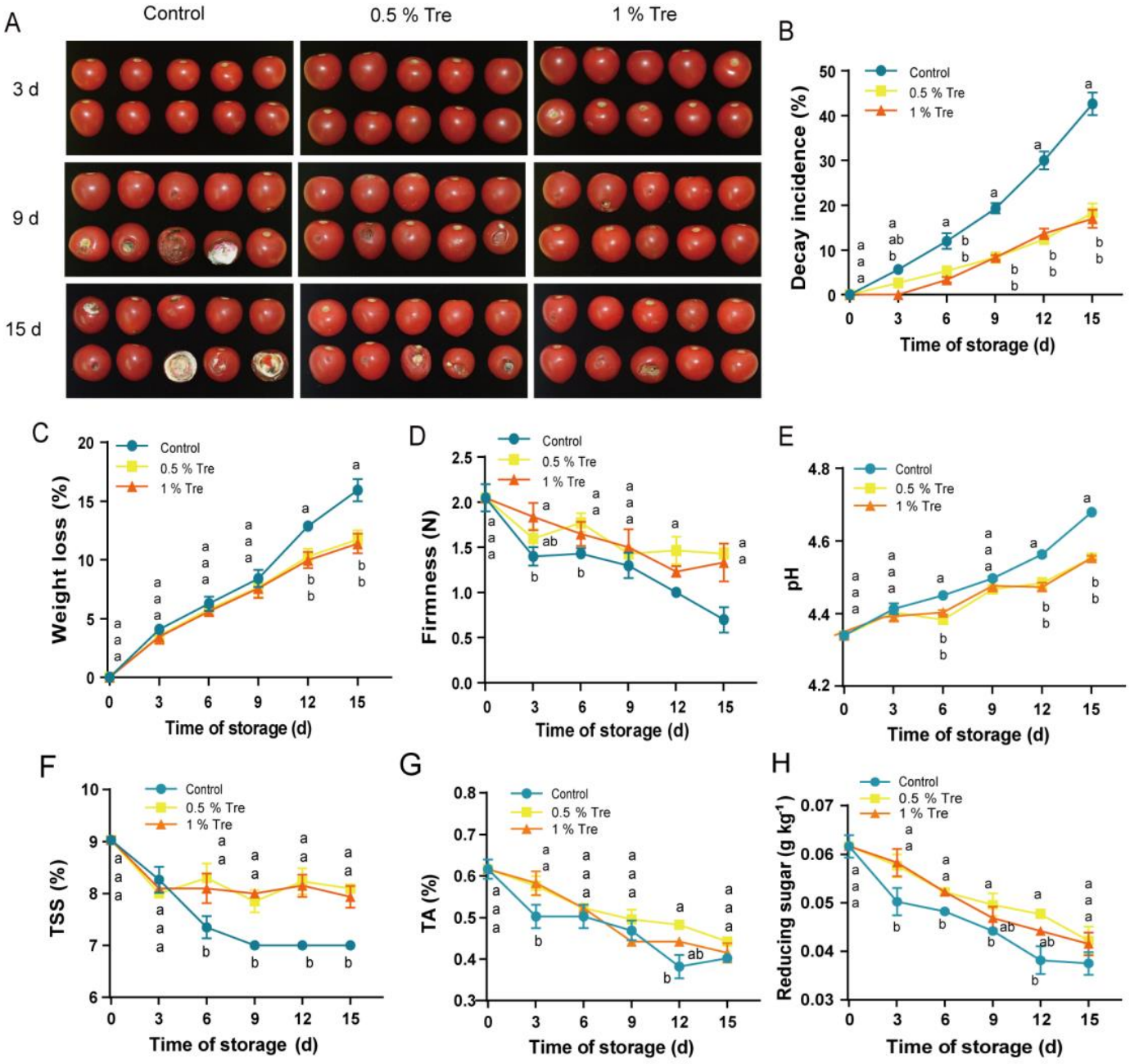

Figure 1. Trehalose affected the phenotype **(A)**, decay incidence **(B)**, weight loss **(C)**, firmness **(D)**, pH **(E)**, TSS **(F)**, TA **(G)**, and reducing sugar content **(H)** during cherry tomato ripening. Vertical bars are the standard deviation (SD, $n = 3$). Different lowercase letters indicate significant differences at $p < 0.05$ between trehalose-treated and control fruits.

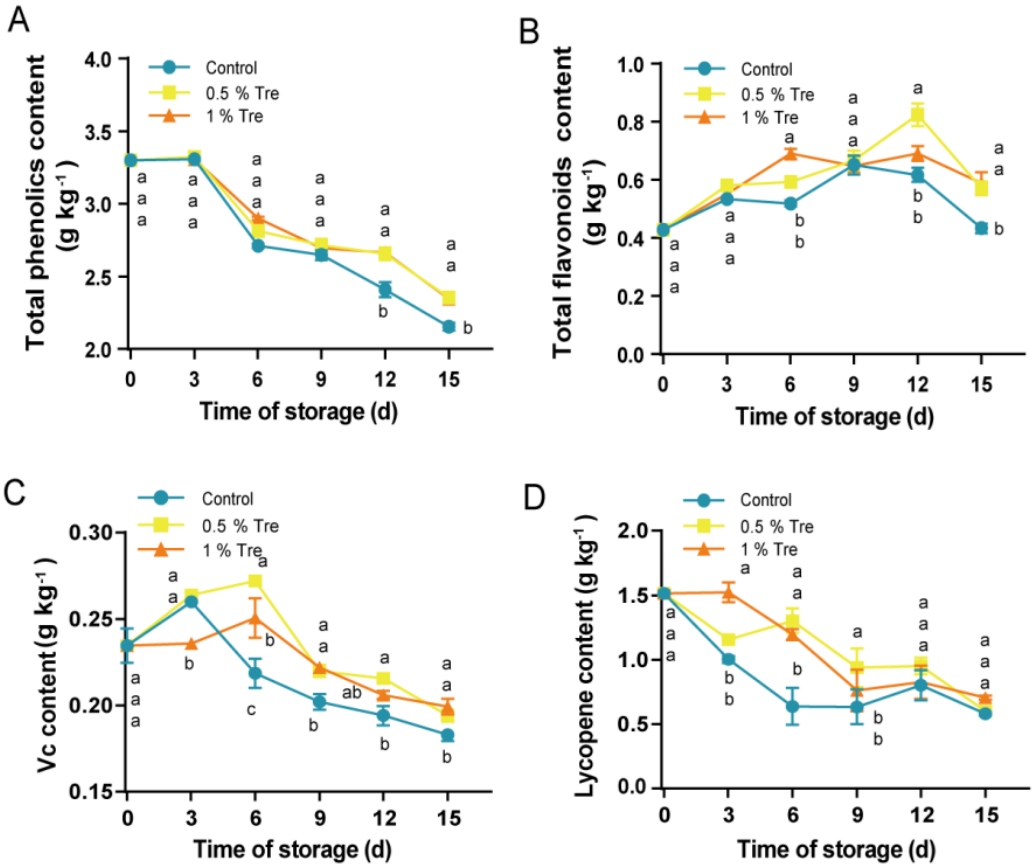

Figure 2. Trehalose affected the content of total phenols **(A)**, flavonoids **(B)**, Vc **(C)**, and lycopene **(D)** during cherry tomato ripening. Vertical bars are the standard deviation (SD, n = 3). Different lowercase letters indicate significant differences at $p < 0.05$ between trehalose-treated and control fruits.

Vc content on the 6th day (Figure 2C, $p < 0.05$). Vc contents in the 0.5%, 1%, and the control groups were 0.273, 0.242, and 0.22 g·kg^{-1}, respectively. In addition, trehalose treatment inhibited the decrease in lycopene content in the early stage of storage (Figure 2D). The content of lycopene in the 1% treatment group was two times higher than the control group at 6 d ($p < 0.05$). This may be due to the fact that trehalose adhered to the fruit surface, thus delaying the aging process *via* the inhibition of respiration. Consequently, the results showed that trehalose improved the antioxidant content of the fruits.

Trehalose improved the antioxidant capacity of cherry tomato fruits

Fruits and vegetables continue to ripen and evolve even after picking, and a series of enzymatic reactions such as glycolysis, tricarboxylic acid cycle (TCA), and respiration continue to occur (Carla, 2012). The heat released from these reactions affects the storage temperature, and enhance life activities of fruits and vegetables, thus accelerating the consumption of nutrients. With prolonged storage, large amounts of reactive-oxygen-species (ROS) gradually accumulate in cherry tomato fruits. ROS have strong oxidising power, thus leading to plasma membrane damage, irreversible metabolic disorders, cell death, and the acceleration of fruit senescence (Ji *et al*., 2020). The antioxidant activity cannot be evaluated using only one method because of the complexity of the composition of fruits and vegetables (Valadez-Carmona *et al*., 2016). Therefore, we evaluated the antioxidant capacity of the fruits *via* five parameters: DPPH scavenging capacity, superoxide anion production, MDA content, reducing power, and hydroxyl radical scavenging capacity.

The DPPH scavenging capacity of cherry tomato fruits decreased gradually during storage. The DPPH scavenging capacity was higher in the trehalose treatment groups as compared to the control group at 9 and 15 d (Figure 3A, $p < 0.05$). Similar results were found by Davila-Avina *et al*. (2014), who studied the effects of mineral oil and carnauba

treatment on DPPH radical-scavenging activity in tomato fruits. The mineral oil and carnauba treatment resulted in an increase in antioxidant capacity. In addition, superoxide anions accumulated continuously during cherry tomato ripening. The production of superoxide anions was lower in the trehalose treatment groups than in the control group, and the 0.5% concentration had the best effect (Figure 3B). MDA, which is the final product of membranous antioxidant reactions, was negatively correlated with the antioxidant activity of fruits. The continuous aggravation of membrane peroxidation leads to an increase in plasma membrane permeability, and increased electrolyte outflow, which directly affected the degree of damage to the cell membrane (Mikail *et al*., 2016). As shown in Figure 3C, the results of MDA content and superoxide anion production were consistent. MDA accumulation in the trehalose treatment groups was lower than that in the control group. The reducing power of each treatment group gradually increased, and then decreased, while the hydroxyl radical scavenging capacity continually decreased (Figures 3D and 3E). There were no significant differences in the reducing power and hydroxyl radical scavenging rate among groups. These results indicated that trehalose treatments could reduce free radical accumulation, and maintain the balance of ROS metabolism, thus delaying the senescence of cherry tomato products.

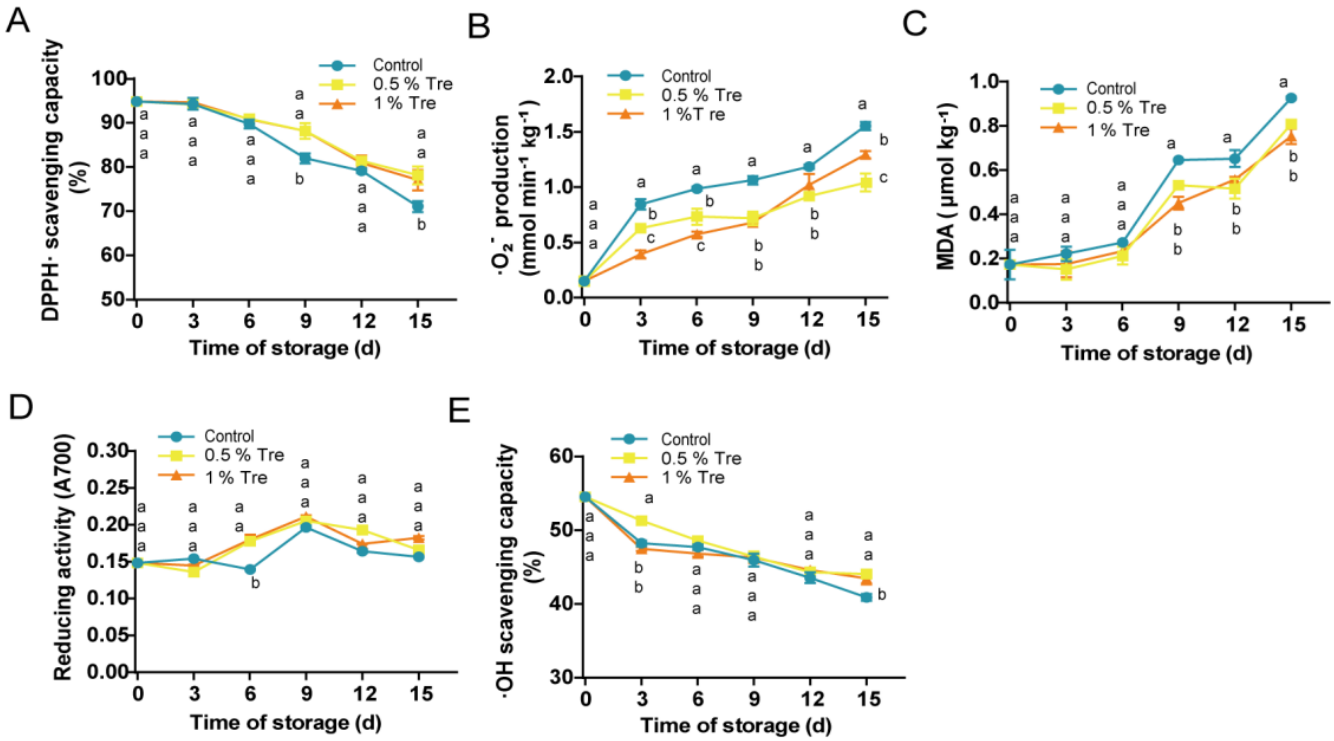

Figure 3. Trehalose affected the DPPH scavenging capacity **(A)**, $\cdot O_2^-$ production **(B)**, MDA **(C)**, reducing power **(D)**, and ·OH scavenging capacity **(E)** during cherry tomato ripening. Vertical bars are the standard deviation (SD, n = 3). Different lowercase letters indicate significant differences at $p < 0.05$ between trehalose-treated and control fruits.

Trehalose affected enzyme activities of cherry tomato fruits

Berry fruits have been reported to have high levels of antioxidants, which resist oxidative damage to cell lipids, proteins, and nucleic acids. Effective antioxidant activity is essential for maintaining relatively low ROS levels (Manganaris *et al*., 2014). SOD, APX, and LOX are important antioxidant-related enzymes in the cherry tomato fruits. SOD and APX are necessary enzymes in the scavenging system of ROS. As an antioxidant metalloenzyme in living organisms, SOD plays a role in maintaining $\cdot O_2^-$ balance. Maintaining high enzyme activity is beneficial to scavenging superoxide anions and reducing oxidative damage (Petriccione *et al*., 2018). SOD reduces $\cdot O_2^-$ to H_2O_2, which is decomposed into H_2O and O_2 under the action of APX and CAT, thus mitigating its toxicity to cells (Ramasarma, 2012).

LOX specifically catalyses the oxygenation of polyunsaturated fatty acids. Therefore, it is an important enzyme in fruit post-ripening and senescence (Petriccione *et al*., 2018). During fruit storage, the activity of antioxidant enzymes SOD, APX, and LOX increased gradually at first, and then decreased slowly. The activity peaked on the third day, and when compared with the control group, SOD and APX activities in the trehalose treatment groups were maintained at a higher level. Overall, the 0.5% concentration had the best effect (Figures 4A and 4B, $p < 0.05$). Jiang *et al*. (2022) demonstrated that UV-B pre-irradiation activated the activity of SOD enzymes in cold-stored tomato fruits. As shown in Figure 4C, the activity of LOX in trehalose-treated fruits was lower than that in the control group, and the most effective inhibition was observed in the 0.5% treatment group. These results demonstrated that trehalose treatment maintained the activity of antioxidant enzymes, improved antioxidant capacity, and slowed the aging of cherry tomato fruits.

Trehalose affected gene expressions of cherry tomato fruits

To study the activities of antioxidant enzymes SOD, APX, and LOX, we examined the expression levels of the cherry tomato antioxidant-related genes *SlSOD1*, *SlSOD2*, *SlFeSOD*, *SlCuZnSOD*, *SlAPX1*, *SlAPX2*, *SlAPX3*, and *SlLOX* between trehalose-treated and the control groups, as shown in Figure 5. The expression of *SlSOD1* after trehalose treatment was higher than in the control group at 9 and 15 d (Figure 5A, $p < 0.05$). As shown in Figures 5B and 5C, the changes in the expression of *SlSOD2* and *SlFeSOD* were similar, and the expression levels were higher in the trehalose treatment group, as compared to the control group at 3, 9, and 15 d ($p < 0.05$). The expression levels of *SlCuZnSOD* sharply declined on day 3, and then sustained lower levels under both treatments (Figure 5D). As shown in Figure 5E, the expression of *SlAPX1* after trehalose treatment was higher than the control group at 9 and 15 d ($p < 0.05$). As shown in Figures 5F and 5G, the increased expression of *SlAPX2* and *SlAPX3* was similar between the trehalose-treated and the control groups, and the trehalose-treated groups maintained higher *SlAPX2* and *SlAPX3* expression levels than the control group in the late stage of storage. Similarly, Yao *et al*. (2018) showed that exogenous H_2S could enhance the expression of *SlCuZnSOD*, *SlAPX2*, *SlCAT1*, and *SlPOD12* by inhibiting the effects of ethylene. As shown in Figure 5H, the expression of *SlLOX* increased constantly during storage. *SlLOX* expression was higher in the control group than the experimental groups ($p < 0.05$). Moreover, there were strongly positive correlations between the *SlFeSOD* expression level and SOD activity, *SlAPX2* expression level and APX activity, and *SlLOX* expression level and LOX activity. This further supported the supposition that the upregulation of genes, such as *SlFeSOD*, *SlAPX2*, and *SlLOX*, was responsible for the increased activities of these enzymes. Therefore, our data suggested that trehalose treatment could increase enzyme activity by upregulating their encoding genes at the transcriptional level.

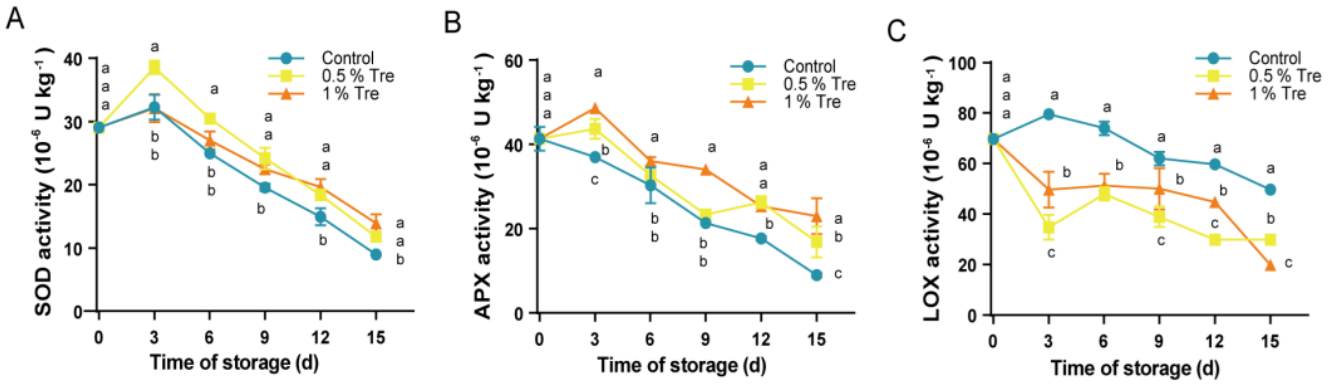

Figure 4. Trehalose affected SOD **(A)**, APX **(B)**, and LOX **(C)** activities during cherry tomato ripening. Vertical bars are the standard deviation (SD, $n = 3$). Different lowercase letters indicate significant differences at $p < 0.05$ between trehalose-treated and control fruits.

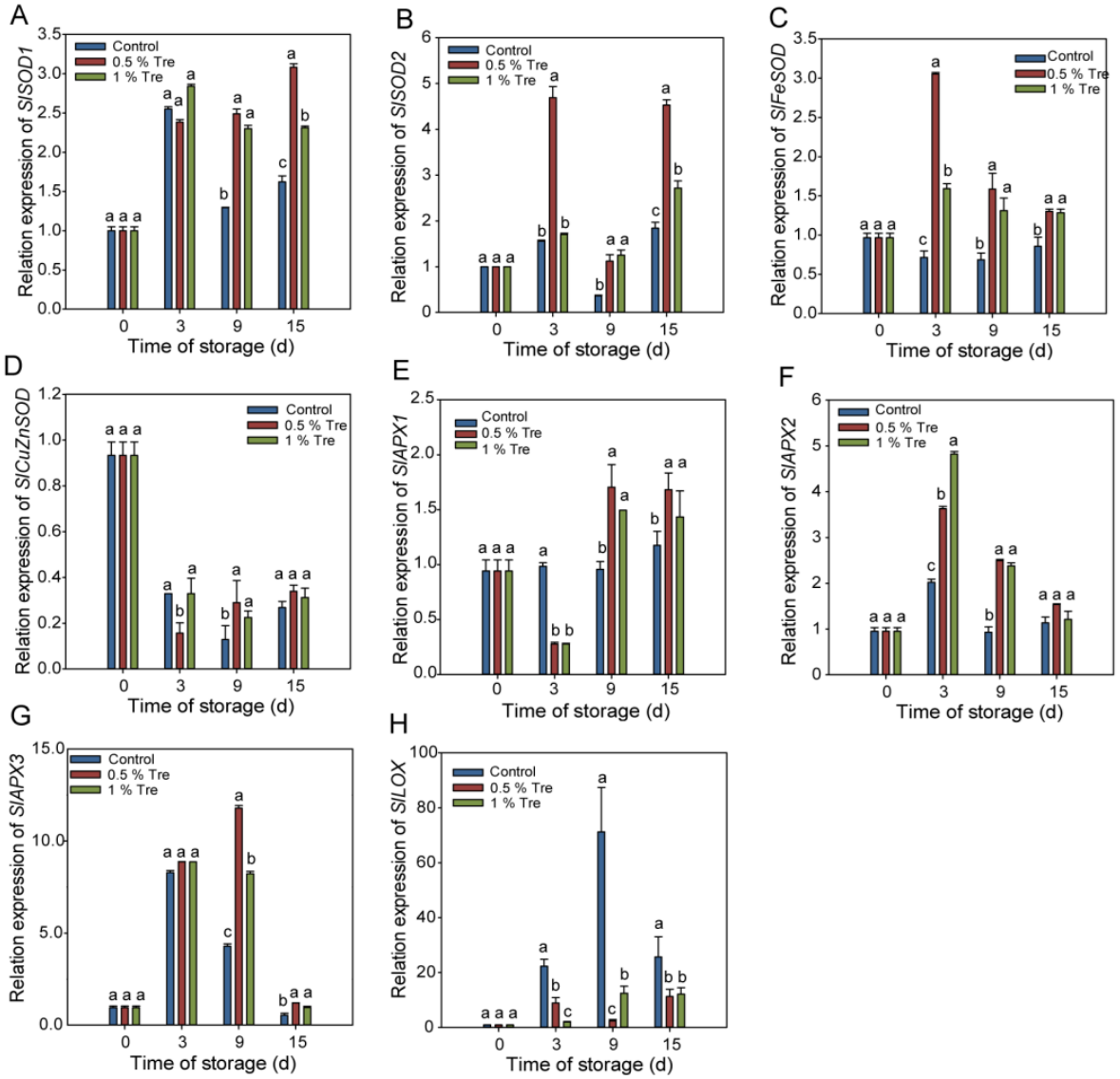

Figure 5. Trehalose affected antioxidant-related genes (*SlSOD1*, *SlSOD2*, *SlFeSOD*, *SlCuZnSOD*, *SlAPX1*, *SlAPX2*, *SlAPX3*, and *SlLOX*) expression during cherry tomato ripening. Vertical bars are the standard deviation (SD, n = 3). Different lowercase letters indicate significant differences at $p < 0.05$ between trehalose-treated and control fruits.

Conclusion

Based on the results, 0.5 and 1% trehalose treatment solutions had a significant effect on fruit quality of cherry tomato. At the later stages of storage, the decay rate of the 0.5% group was 50% less than that of the control group. At 6 d, the reducing sugar and Vc content of the 0.5% group were both the highest among the three groups. Additionally, the lycopene content of the 0.5% group was twice that of the control group. In terms of antioxidant activity, the production of superoxide anions, and the activity of LOX enzyme in the treatment groups were lower than in the control, and the 0.5% group was the most significant. The same results were obtained for the expression levels of antioxidant enzyme-related genes. In summary, 0.5% trehalose solution had the most significant effect on maintaining the content of antioxidant substances, antioxidant enzyme activity, and the antioxidant capacity of cherry tomato. Therefore, trehalose has potential value in reducing decay and preserving the quality of cherry tomato.

Acknowledgement

Thanks to Guiran Xiao, Xiaofeng Tang, and Min Miao for their instrument and equipment support. The present work was financially supported by the Fundamental Research Funds for the Central Universities (grant no.: JZ2018HGTB0248).

References

Aghdam, M. S. and Fard, J. R. 2017. Melatonin treatment attenuates postharvest decay and maintains nutritional quality of strawberry fruit (*Fragaria* × *anannasa cv. Selva*) by enhancing GABA shunt activity. Food Chemistry 221(2): 1650-1657.

Alan, D. and Elbein, Y. T. 2003. New insights on trehalose: A multifunctional molecule. Glycobiology 13(4): 17-27.

Ali, Q. and Ashraf, M. 2011. Induction of drought tolerance in maize (*Zea mays* L.) due to exogenous application of trehalose: Growth, photosynthesis, water relations and oxidative defence mechanism. Journal of Agronomy and Crop Science 197(4): 258-271.

Al-Naama, M., Ewaze, J. O., Green, B. J. and Scott, J. A. 2009. Trehalose accumulation in *Baudoinia compniacensis* following abiotic stress. International Biodeterioration and Biodegradation 63(6): 765-768.

Ana, F. V., Sérgio, V. P. B., Ana, C., Anabela, C. and Beatriz, P. 2013. Influence of the storage conditions on the physicochemical properties, antioxidant activity and microbial flora of different tomato (*Lycopersicon esculentum* L.) cultivars. Journal of Agricultural Science 5(2): 118-128.

Badawy, M. and Rabea, E. I. 2009. Potential of the biopolymer chitosan with different molecular weights to control postharvest gray mold of tomato fruit. Postharvest Biology and Technology 51(1): 110-117.

Cai, X., Seitl, I., Mu, W., Zhang, T., Stressler, T., Fischer, L. and Jiang, B. 2018. Biotechnical production of trehalose through the trehalose synthase pathway: Current status and future prospects. Applied Microbiology and Biotechnology 7: 2965-2976.

Cao, X., Zhang, F. and Zhu, D. 2018. Effect of different sugars on the freezing characteristics of Kyoho grape. Journal of Texture Studies 49(6): 604-611.

Carla, A. N. 2012. Biological control of postharvest diseases of fruit. European Journal of Plant Pathology 133(1): 181-196.

Cho, K. S. 2016. Inhibitory effect of DPPH radical scavenging activity and hydroxyl radicals (OH) activity of *Hydrocotyle sibthorpioides* Lamarck. Journal of Life Science 26(9): 1022-1026.

Davarpanah, S., Tehranifar, A. and Davarynejad, G. 2016. Effects of foliar applications of zinc and boron nano-fertilizers on pomegranate (*Punica granatum* cv. Ardestani) fruit yield and quality. Scientia Horticulturae 210: 57-64.

Davila-Avina, J. E., Villa-Rodríguez, J. A., Villegas-Ochoa, M. A., Tortoledo-Ortiz, O., Olivas, G. I., Ayala-Zavala, J. F. and Gonzalez-Aguilar, G. A. 2014. Effect of edible coatings on bioactive compounds and antioxidant capacity of tomatoes at different maturity stages. Journal of Food Science and Technology 51(10): 2706-2712.

Ge, Y., Chen, Y., Li, C., Wei, M., Li, X. and Li, S. 2019. Effect of trisodium phosphate dipping treatment on the quality and energy metabolism of apples. Food Chemistry 274(14): 324-329.

Gonzalez, A. G. A., Villa-Rodriguez, J. A., Ayala-Zavala, J. F. and Yahia, E. M. 2010. Improvement of the antioxidant status of tropical fruit as a secondary response to some postharvest treatments. Trends Food Science Technology 21(10): 475-482.

Goula, A. M. and Adamopoulos, K. G. 2005. Stability of lycopene during spray drying of tomato pulp. LWT - Food Science and Technology 38(5): 479-487.

Hengherr, S., Heyer, A. G., Brümmer, F. and Schill, R. O. 2011. Trehalose and vitreous states: Desiccation tolerance of dormant stages of the crustaceans *Triops* and *Daphnia*. Physiological and Biochemical Zoology 84(2): 147-153.

Hu, L. Y., Hu, S. L., Wu, J., Li, Y. H., Zheng, J. L., Wei, Z. J., … and Zhang, H. 2012. Hydrogen sulfide prolongs postharvest shelf life of strawberry and plays an antioxidative role in fruit. Journal of Agricultural and Food Chemistry 60(35): 8684-8693.

Ji, Y. R., Hu, W. Z., Liao, J., Jiang, A. L., Xiu, Z. L., Gaowa, S. R., … and Liu, C. H. 2020. Effect of atmospheric cold plasma treatment on antioxidant activities and reactive oxygen species production in postharvest blueberries during storage. Journal of the Science of Food and Agriculture 100(15): 5586-5595.

Jiang, Z., Xu, M., Dong, J., Zhu, Y., Lou, P. P., Han, Y. D., … and Xu, M. J. 2022. UV-B pre-

irradiation induces cold tolerance in tomato fruit by *SlUVR8*-mediated upregulation of superoxide dismutase and catalase. Postharvest Biology and Technology 185: 111777.

Jin, Z. X., Sun, H. and Sun, T. Y. 2016. Modifications of 'Gold Finger' grape berry quality as affected by the different rootstocks. Scientia Horticulturae 210(21): 130-137.

Jing, W., Tu, K. and Shao, X. F. 2010. Effect of postharvest short hot-water rinsing and brushing treatment on decay and quality of strawberry fruit. Journal of Food Quality 33: 262-272.

Kim, D. O., Lee, K. W., Lee, H. J. and Chang, Y. L. 2002. Vitamin C equivalent antioxidant capacity (VCEAC) of phenolic phytochemicals. Journal of Agricultural and Food Chemistry 50(13): 3713-3717.

Li, B. Q. and Tian, S. P. 2006. Effects of trehalose on stress tolerance and biocontrol efficacy of *Cryptococcus laurentii*. Journal of Applied Microbiology 100(4): 854-861.

Ma, Q., Zhang, T., Zhang, P. and Wang, Z. Y. 2016. Melatonin attenuates postharvest physiological deterioration of cassava storage roots. Journal of Pineal Research 60(4): 424-434.

Manganaris, G. A., Goulas, V. and Vicente, A. R. 2014. Berry antioxidants: Small fruit providing large benefits. Journal of the Science of Food and Agriculture 94(5): 825-833.

Mikail, M. A., Ahmed, I. A., Ibrahim, M., Hazali, N., Abdul Rasad, M. S., Abdul Ghani, R., … and Adros Yahya, M. N. 2016. *Baccaurea angulata* fruit inhibits lipid peroxidation and induces the increase in antioxidant enzyme activities. European Journal of Nutrition 55(4): 1435-1444.

Ohtake, S. and Wang, Y. J. 2011. Trehalose: Current use and future application. Journal of Pharmaceutical Science 100(60): 2020-2053.

Petriccione, M., Pagano, L. and Forniti, R. 2018. Postharvest treatment with chitosan affects the antioxidant metabolism and quality of wine grape during partial dehydration. Postharvest Biology and Technology 137: 38-45.

Ramasarma, T. 2012. In praise of H_2O_2, the versatile ROS, and its vanadium complexes. Toxicology Methods 22(5): 336-346.

Rissanen, T. H., Voutilainen, S., Nyyssönen, K., Salonen, R., Kaplan, G. A. and Salonen, J. T. 2003. Serum lycopene concentrations and carotid atherosclerosis: The Kuopio Ischaemic Heart Disease Risk Factor Study. American Journal of Clinical Nutrition 77(1): 133-138.

Saha, S. and Verma, R. J. 2016. Antioxidant activity of polyphenolic extract of *Terminalia chebula* Retzius fruit. Journal of Taibah University for Science 10(6): 805-812.

Schmittgen, T. D. and Livak, K. J. 2008. Analyzing real-time PCR data by the comparative C_T method. Nature Protocols 3(6): 1101-1108.

Sesso, H. D., Liu, S., Michael, G. J. and Buring, J. E. 2003. Dietary lycopene, tomato-based food products and cardiovascular disease in women. Journal of Nutrition 133(7): 2336-2341.

Suttirak, W. and Manurakchinakorn, S. 2014. *In vitro* antioxidant properties of mangosteen peel extract. Journal of Food Science and Technology 51(12): 3546-3558.

Teramoto, N., Sachinvala, N. D. and Shibata, M. 2008. Trehalose and trehalose-based polymers for environmentally benign, biocompatible and bioactive materials. Molecules 13(8): 1773-1816.

Toor, R. K. and Savage, G. P. 2005. Antioxidant activity in different fractions of tomatoes. Food Research International 38(5): 487-494.

Vahid, B. 2012. Titrimetric determination of ascorbic acid contents in plant samples by 2,6-dichlorophenolindophenol method. Journal of The Chemical Society of Pakistan 34(6): 1510-1512.

Valadez-Carmona, L., Cortez-García, R. M., Plazola-Jacinto, C. P., Necoechea-Mondragón, H. and Ortiz-Moreno, A. 2016. Effect of microwave drying and oven drying on the water activity, color, phenolic compounds content and antioxidant activity of coconut husk (*Cocos nucifera* L.). Journal of Food Science and Technology 53(9): 3495-3501.

Vinha, A. F., Alves, R. C., Barreira, S. V. P., Castro, A., Costa, A. and Oliveira, M. 2014. Effect of peel and seed removal on the nutritional value and antioxidant activity of tomato (*Lycopersicon esculentum* L.) fruit. LWT - Food Science and Technology 55(1): 197-202.

Vo, Q. V., Hoa, N. T., Thong. N. M. and Mechler, A. 2021. The hydroperoxyl and superoxide anion radical scavenging activity of anthocyanidins in physiological environments: Theoretical insights into mechanisms and kinetics. Phytochemistry 192: 112968.

Wang, L., Chen, L., Li, R., Zhao, R. R., Yang, M. J., Sheng, J. P. and Shen, L. 2017. Reduced drought tolerance by CRISPR/Cas9-mediated *SlMAPK3* mutagenesis in tomato plants. Journal of Agricultural and Food Chemistry 65(39): 8674-8682.

Yao, G. F., Wei, Z. Z., Li, T. T., Tang, J., Huang, Z. Q., Yang, F., … and Zhang, H. 2018. Modulation of enhanced antioxidant activity by hydrogen sulfide antagonization of ethylene in tomato fruit ripening. Journal of Agricultural and Food Chemistry 66(40): 10380-10387.

Zhang, D., Wang, H. and Yi, H. 2015. Chitosan controls postharvest decay on cherry tomato fruit possibly *via* the mitogen-activated protein kinase signaling pathway. Journal of Agricultural and Food Chemistry 63(33): 7399-7404.

Zhao, L., Zhang, H., Li, J., Cui, J., Zhang, X. and Ren, X. 2012. Enhancement of biocontrol efficacy of *Pichia caribbica* to postharvest diseases of strawberries by addition of trehalose to the growth medium. International Journal of Molecular Science 13(3): 3916-3932.

Zhao, L., Zhang, H., Lin, H., Zhang, X. and Ren, X. 2013. Effect of trehalose on the biocontrol efficacy of *Pichia caribbica* against post-harvest grey mould and blue mould decay of apples. Pest Management Science 69(8): 983-989.