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Salicylic acid regulated the antioxidant system of toon buds to improve preservation during cold storage

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ABSTRACT: Salicylic acid (SA) is a known plant hormone and a preservative. The postharvest loss of toon buds (*Toona sinensis* (A. Juss.) Roem.), an economically important woody vegetable, is one of the major constraints limiting its market value. Here, we investigated the postharvest quality attributes and physiological characteristics underlying the effect of SA on toon buds during cold storage (4 °C). Toon buds were soaked in SA at different concentrations and subsequently transferred to 4 °C conditions for 5 d. SA treatment delayed wilting, suppressed weight loss rate and water potential decrease, reduced respiration rate, slowed degradation of ascorbic acid (AsA) and anthocyanin, and inhibited malondialdehyde (MDA) and hydrogen peroxide accumulation. Furthermore, the activities of antioxidant enzymes, such as superoxide dismutase (SOD) and catalase (CAT), were enhanced by SA treatment; whereas peroxidase (POD) activity was inhibited. The most effective concentration of SA for treatment was 50 µM, which maintained the quality of the toon buds, provided a fresh appearance, and enhanced the accumulation of bioactive compounds. Taken together, these findings suggested that SA improves the quality of postharvest toon buds during cold storage by regulating the antioxidant system. Our study provided a theoretical basis for the application of SA in cold storage treatment of toon buds.

KEYWORDS: Chinese toon, salicylic acid, antioxidant enzyme activities, low-temperature storage, postharvest quality

INTRODUCTION

The Chinese toon (*Toona sinensis* (A. Juss.) Roem.), an economically important tree variety, is widely cultivated in China and Asia. Its fresh buds and young leaves, which are well known as toon buds, are famous for their distinctive flavor, color and aroma. In addition to its important nutrient and medicinal value, Chinese toon has become an ideal vegetable favored by consumers worldwide [1]. However, due to their tender texture, high water content, and vigorous respiratory metabolism, toon buds are notably prone to microbiological degradation, mechanical damage, and nutrient loss, resulting in a reduced edible value and shortened shelf life [2, 3]. Thus, maintaining quality and prolonging shelf life of toon buds have become important challenges that must be addressed after harvest.

Various storage technologies and great progress have been made in the preservation of postharvest toon buds [2–4]. The combination of ozone and polyethylene could maintain important characteristics of toon buds through enhancing the activity of antioxidant defense system [3]. Modified atmosphere packaging systems for postharvest toon bud storage have also been developed [5]. Exogenous glycine betaine treatment could significantly maintain freshness and extend the storage time of cold-stored toon buds [5]. In our previous study, the exogenous application of gibberellin A3 (GA3) enhanced preservation of postharvest toon buds by regulating the antioxidant defense system and reducing the peroxidation of lipids [2]. Although many postharvest technologies can prolong the shelf life of toon buds, very few operations are enforced by farmers; and the most widely used preservation method is still cold storage. However, physiological disorders always occur during cold storage [6]. Bursts of reactive oxygen species (ROS) and membrane peroxidation, which further lead to cell death, are common chilling injuries in fruits and vegetables exposed to low temperature [6]. Therefore, there is a need to continually seek other preservatives or chemicals to extend the postharvest life of toon buds during cold storage.

Salicylic acid (SA) is a simple and easy-to-use phenolic plant hormone that plays a crucial role in plant growth and development and in the context of environmental stress [7]. This compound is also considered an important preservative that is widely used for maintaining freshness, preventing microbiological degradation, delaying fruit ripening, and reducing the loss rate of nutritional value after harvest [8]. As a natural ingredient, SA is generally recognized as safe (GRAS) for postharvest use [9]. Therefore, the exogenous application of SA could be useful for prolonging the freshness of stored toon buds and maintaining their characteristics.

The exogenous application of SA and cold storage have been widely investigated for many types of fruits and vegetables. However, few reports have focused on the combination of SA treatment and cold storage of toon buds. Therefore, we investigated the postharvest physiological characteristics and quality of toon buds in response to the combination of SA treatment and cold storage. This study provided a theoretical basis for the application of SA in cold storage treatment of toon buds.

MATERIALS AND METHODS

Plant material and treatment

'Heiyouchun toon' buds were picked from a *T. sinensis* plantation in Taihe County, Anhui Province, China. The toon buds were then packed in foam boxes with ice bags and transferred to the laboratory. Toon buds in good condition without obvious damage were selected for experiments. After disinfection (1% NaClO, volume ratio, 2 min), the samples were treated for 20 min as follows: (1) control (distilled water), (2) 10 μM SA, (3) 50 μM SA, or (4) 100 μM SA. The treated toon buds were then dried and stored in a 4 °C refrigerator for 5 d. Each treatment was conducted in triplicate, with 10 toon buds per replicate.

Weight loss rate and water potential

The weight loss rate of the toon buds was measured by weighing the toon buds and expressed using the published method [10]. The water potential of the toon buds was measured according to the published protocol [11]. Toon buds were immersed in a graded series of solutions, and the solution that neither gained nor lost water was assumed to have a water potential equal to that of the toon buds [11]. The water potential was calculated as follows: $\Psi_w = -icRT$, where Ψ_w is the water potential of the toon buds, i is the dissociation coefficient (sucrose is set as 1), c is the mass molar concentration of the isotonic solution, R is the gas constant (0.00831 kg MPa mol^{-1}K^{-1}), and T is the thermodynamic temperature.

Respiration rate determination

Respiration rates were determined after 0, 3, and 5 d of storage using the small-skep method with minor modifications [12, 13]. In brief, 5 g of the toon bud sample was put into a 0.5-liter glass bottle connected to a closed-circuit system. The CO_2 from postharvest toon buds was absorbed using $Ba(OH)_2$ solution, and the residual $Ba(OH)_2$ was titrated with an oxalic acid solution. The amount of CO_2 could be calculated from the difference between the oxalic acid solution consumed by the blank and that consumed by the samples. The result was expressed as mg kg^{-1}h^{-1}. The respiration rate was measured based on the increase in CO_2 concentration in 1 h [13].

AsA and anthocyanin content determination

The AsA content in the toon buds was determined using the standard 2,6-dichlorophenol iodophenol titrimetric method described in our previous work [2]. The obtained results were expressed as mg AsA 100 g^{-1} sample. The quantification of anthocyanins was performed following the protocol of our previous work [14]. A total of 0.3 g of sample was immersed in 1 ml (1%, volume ratio) of HCl methanol solution. After centrifugation, the supernatant was drawn, diluted and assayed at 530 and 657 nm using a spectrophotometer. The anthocyanin content was calculated using the method described in a published protocol [15].

Malondialdehyde (MDA) content and hydrogen peroxide (H_2O_2) staining

The MDA concentration was determined using the thiobarbituric acid method [16]. H_2O_2 was detected by 3, 3′-diaminobenzidine (DAB) staining [17] and visualized as a brown color due to DAB polymerization. Samples of toon buds from different storage times were placed in DAB staining solution (1.25 mg/ml, pH 3.8). The stained plantlets were then bleached in an acetic acid-glycerol-ethanol (1:1:3, volume ratio) solution at 100 °C for 5 min and subsequently stored in a glycerol-ethanol (1:4, volume ratio) solution.

Soluble protein determination and antioxidant enzyme activity assays

The soluble protein concentration was measured according to the Bradford method [18]. A total of 1.0 g of toon bud sample was homogenized with 10 ml of cold 0.1 M sodium phosphate buffer containing 2% (ratio of weight to volume) polyvinylpolypyrrolidone (PVPP) in a cold bath and centrifuged at 4 °C for 30 min at 12000 rpm. The supernatant was collected and used for the assessment of peroxidase (POD) [19], superoxide dismutase (SOD), and catalase (CAT) activities [20]. POD activity was determined using a guaiacol assay. The reaction mixture contained 0.05 M phosphate buffer (pH 6.4), guaiacol and enzymes. One unit of POD activity is defined as an increase of 0.01 per min in absorbance at 470 nm during the assay. SOD activity was measured by inhibiting the photochemical reduction of nitrotetrazolium blue chloride (NBT) at 560 nm in the presence of riboflavin and L-methionine. The absorbance was recorded at 560 nm, and one unit of SOD activity was defined as a value at which the absorbance of the sample was reduced to 50% compared with the control without enzymes. CAT activity was measured according to a published method [21]. One unit of CAT activity was defined as a decrease of 0.01 in absorbance at 240 nm per min.

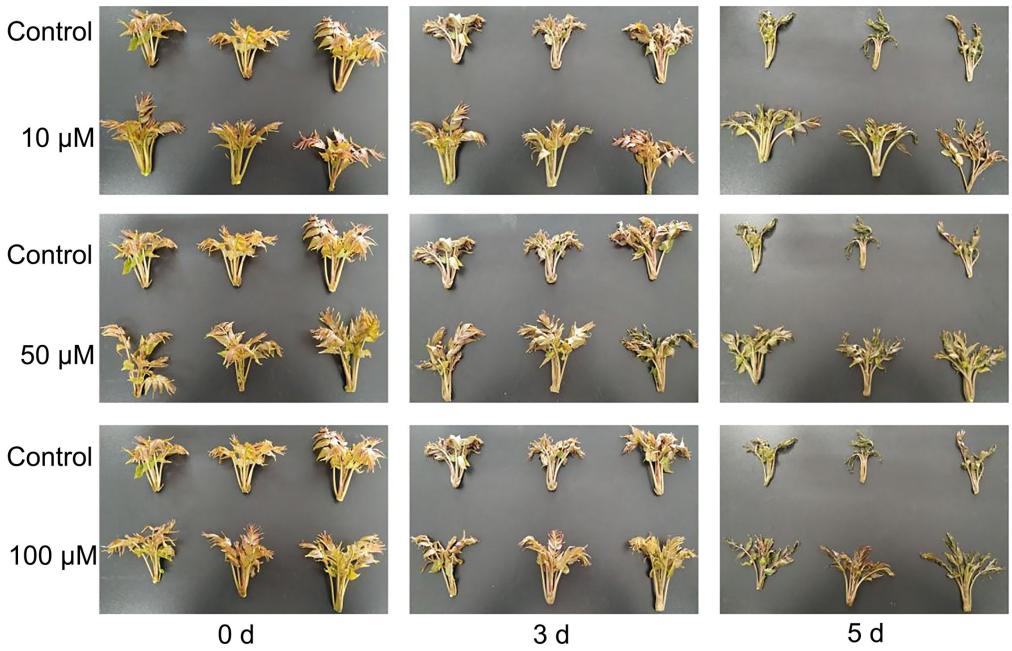

Fig. 1 Appearance of control and SA-treated postharvest toon buds during cold storage at 4 °C.

Statistical analysis

All statistical analyses were performed using IBM SPSS Statistics for Windows, version 19.0 software (IBM Corp., Armonk, NY, USA). The nonparametric Duncan's multiple range test was used for comparisons of means ± standard errors (means ± SEs). Means that were significantly different ($p < 0.05$) were represented by different letters.

RESULTS AND DISCUSSION

Changes in appearance of postharvest toon buds

Although all control and SA-treated postharvest toon buds during cold storage at 4 °C exhibited wilting symptoms, the former exhibited more severe wilting than the later (Fig. 1). After 3 d and 5 d of storage, the 50 µM SA-treated toon buds had a better appearance than the other groups (Fig. 1).

SA enhanced water holding capacity

The weight loss rates of toon buds in the control group after 3 d and 5 d of cold storage were significantly greater than the 10 µM, 50 µM and µM SA treated groups with the values of 26.6% and 35.6% (control), 15.7% and 21.8% (10 µM), 17.1% and 21.2% (50 µM), and 22.3% and 30.3% (100 µM), respectively (Fig. 2A). However, compared with the 10 and 50 µM SA treatments, the 100 µM SA treatment did not decrease the weight loss rate. The results indicated that SA inhibited weight loss at middle-low concentrations but enhanced weight loss at high concentrations.

The water potential of toon buds significantly decreased during postharvest cold storage (Fig. 2B). The water potential of the control group was lower than that of the 50 µM SA treatment group, especially after 5 d of cold storage. The results indicated that 50 µM SA could enhance the water holding capacity of postharvest toon buds during cold storage.

A decreased weight loss rate and an increased water potential are good qualities of toon buds. There was one study reporting that SA treatment improved the preservation of cut rose flowers with a slow decrease in relative fresh weight (FW) and an increase in water taken up by cut rose flowers treated with SA [22]. The improved water balance of toon buds after SA treatment could be due to its ability to act as antiseptics by inhibiting vascular blockage [23].

SA suppressed the respiration rate

As shown in Fig. 3, the respiration rate of the SA-treated samples was suppressed more strongly than that of the control samples during cold storage. In addition, with increasing SA concentration, the inhibitory effect on the respiration rate became more significant.

The respiration rate is closely related to nutrient loss, which decomposes organic matter such as stored sugar and releases energy. Thus, the lower respiration rate in the SA-treated groups might reflect the ability of SA to slow the metabolic consumption of toon buds. Moreover, a high respiration rate might lead to rapid wilting of toon buds, while a low respiration rate could be attributed to a reduction in fresh weight loss. It has been demonstrated that SA effectively suppressed

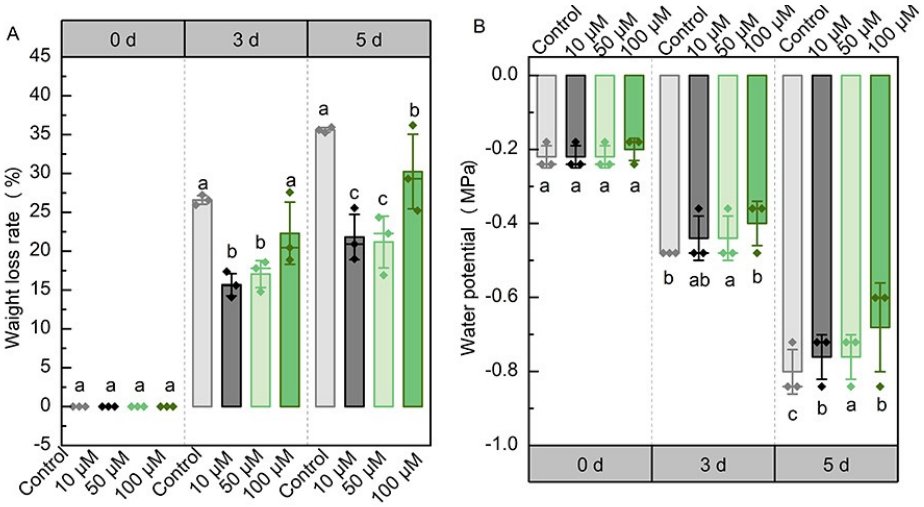

Fig. 2 Weight loss rate (A) and water potential (B) of control and SA-treated toon buds during cold storage at 4 °C.

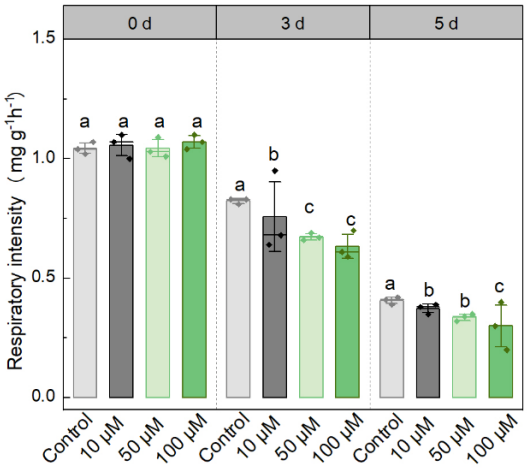

Fig. 3 Respiratory rate of control and SA-treated toon buds during cold storage at 4 °C.

respiration in harvested fruits [8]. Therefore, it is crucial to reduce respiration as much as possible to extend the shelf life of toon buds.

SA retarded oxidative damage

The degree of oxidative stress was determined by the MDA and H_2O_2 content. MDA is a marker of lipid membrane peroxidation [6]. As shown in Fig. 4A, the variation in the MDA contents in the control and SA-treated toon buds exhibited the same trend during postharvest storage. However, the MDA content in the control groups increased sharply, whereas the SA-treated samples had significantly lower concentrations of MDA.

H_2O_2 detection was performed by DAB staining. The light brown polymerization product of H_2O_2 appeared in the toon buds after 3–5 d of storage, and the staining was stronger in the control group than in the SA treated group (Fig. 4B). Moreover, a much weaker level of H_2O_2 in the 50 μM SA treated group than that in the other samples was observed after 5 d of cold storage (Fig. 4B).

The decreased accumulation of MDA and light DAB staining spots in the SA-treated samples could be attributed to the effects of SA on the cell lipid membrane resulting from ROS damage. Therefore, it could be inferred that the application of exogenous SA enhanced the ROS scavenging activity and subsequently contributed to the maintenance of antioxidant systems in toon buds.

SA prevented AsA loss and facilitated anthocyanin accumulation

AsA [19] and anthocyanins [24] are effective antioxidant substances in fruits and vegetables, as well as serving as nutrients. No obvious difference was observed in the amount of AsA in the control or SA treatment samples at the initial time; however, the 10 μM and 50 μM SA treated groups had higher AsA contents than the control group after storage for 3–5 d (Fig. 5A). Similarly, after 3 d and 5 d of storage, the AsA contents in the control group decreased by approximately 52.2% and 66.1%, respectively; which was significantly greater than those observed in the 50 μM SA treated group, which were 41.6% and 52.1%, respectively. In our previous study, many metabolites, including AsA, showed a downward trend when the cold storage time was prolonged [25]. A decrease in AsA in toon buds during storage was also observed in our present study. SA treatment can slow the

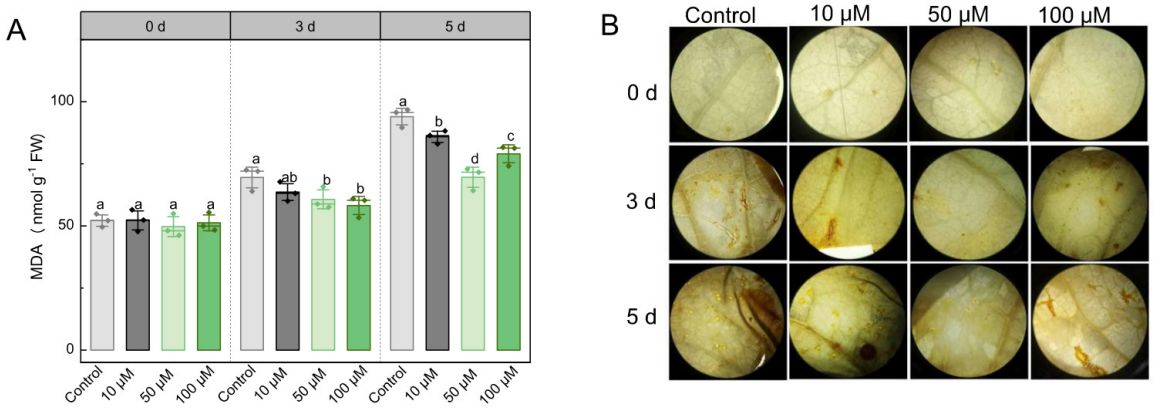

Fig. 4 MDA content (A) and histochemical detection of H_2O_2 via DAB staining (B) in control and SA-treated toon buds during cold storage at 4 °C.

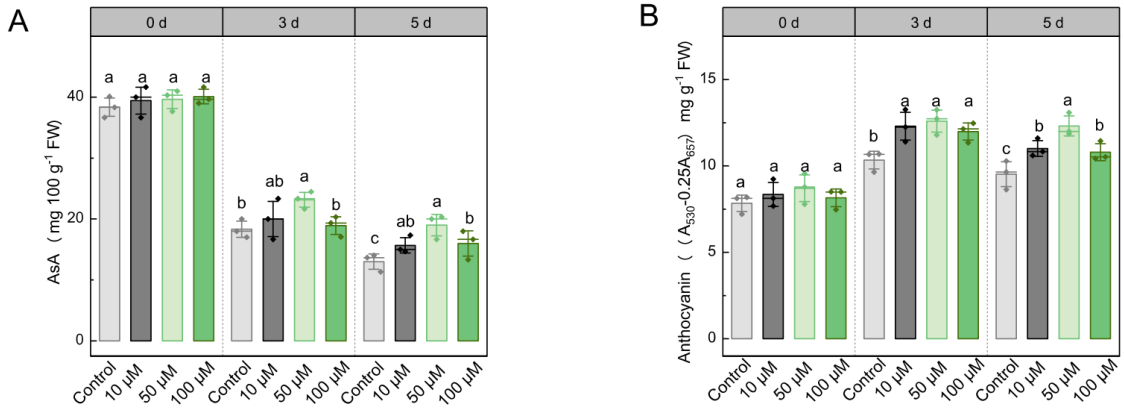

Fig. 5 AsA (A) and anthocyanin (B) content in control and SA-treated toon buds during cold storage at 4 °C. A_{530} and A_{657} are the absorptions at the wavelengths indicated, and FW is the fresh weight (in grams) of the plant tissue used for extraction.

degradation of AsA in a variety of fruits and vegetables, e.g., tomato (*Lycopersicon esculentum* Mill.) [26], and strawberry (*Fragaria* × *Ananassa* cv. Camarosa) [27]. These results revealed that appropriate SA treatment slowed the degradation of AsA and maintained the nutritional quality of the toon buds.

The anthocyanin levels increased in all the samples after 5 d of storage (Fig. 5B). After 3 d, the anthocyanin contents in all the SA-treated groups were greater than that in the control group. On 5 d of storage, the content of anthocyanin in the 50 μM SA-treated samples was much greater than that in the other samples.

Anthocyanin is a type of flavonoid. Previous study showed that total flavonoid content is affected by cold storage, and many flavonoid biosynthetic genes have been identified [28–30]. The increase in anthocyanin content in toon buds might be related to the upregulation of the flavonoid biosynthetic pathway, which is triggered by low temperature. Moreover, exogenous SA application could increase the flavonoid content by upregulating the expression of flavonoid biosynthetic genes [10, 31, 32], thus increasing the anthocyanin content.

SA promoted the accumulation and activity of antioxidant-related proteins

Previous studies showed that SA treatment could induce the accumulation of proteins (69 in total) at different levels in grape berry fruits [33]. Many defense-related proteins, such as heat shock proteins (HSPs) and antioxidant-related proteins, are also involved [33]. With increasing storage time, the soluble protein content decreased rapidly (Fig. 6A). However, toon buds treated with SA had higher soluble protein content than the control samples after 3 and 5 d of storage. SA is considered a key signaling molecule involved in inducing postharvest systemic resistance in fruits and vegetables [34]. We inferred that the application of SA improved the cold resistance of toon buds, and increased the content of soluble protein,

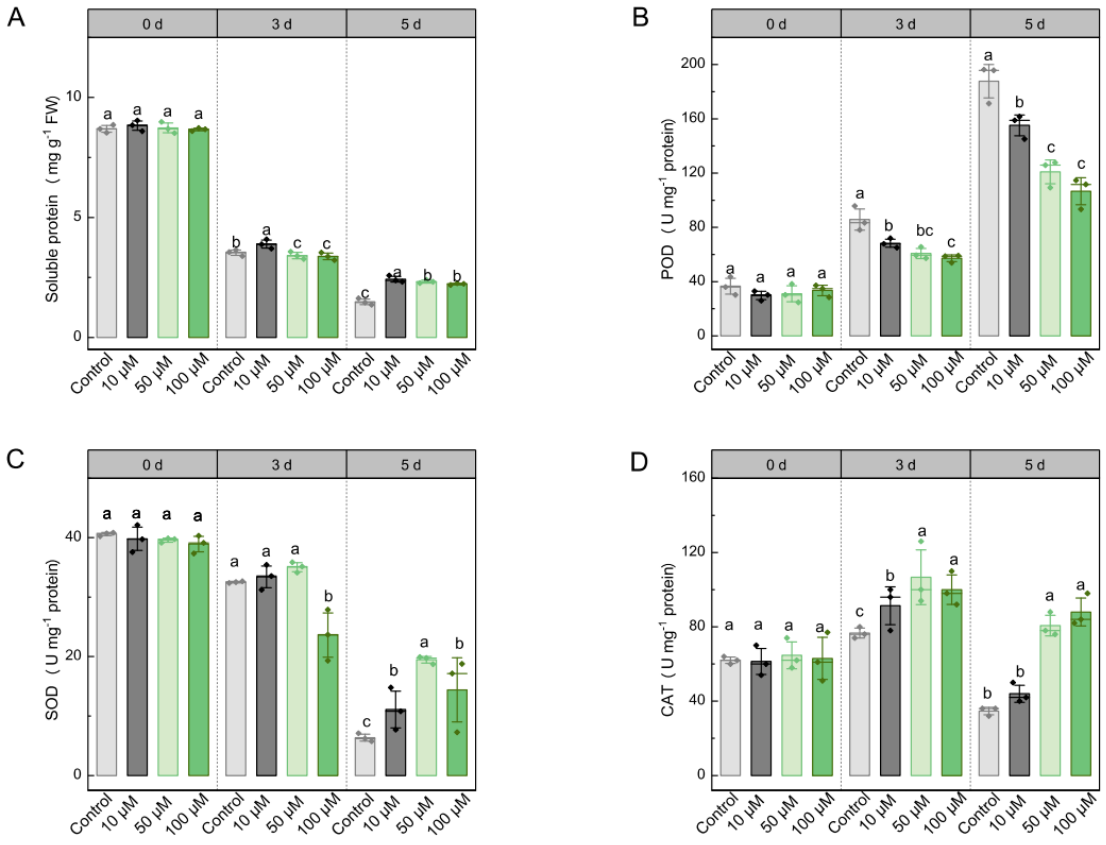

Fig. 6 Total soluble protein (A) and antioxidant enzyme activities (B–D) of control and SA-treated toon buds during cold storage at 4 °C.

which enabled osmotic adjustment.

SOD, POD, and CAT play key roles in scavenging ROS, such as H_2O_2, which induces oxidative stress, such as membrane lipid peroxidation, and triggers cell decay. In our present study, SA treatment significantly weakened the activity of POD during cold storage (Fig. 6B). Moreover, with increasing SA concentration, the increase in POD activity became weaker.

Unlike the changes in POD activity, the changes in SOD activity decreased during storage. In particular, after 5 d of storage, the 50 μM SA-treated samples exhibited a greater SOD activity than the control and the other SA-treated groups (Fig. 6C).

CAT activity in toon buds (both the SA-treated groups and the control group) increased at 3 d and then decreased at 5 d of cold storage (Fig. 6D). However, the changes differed between the SA-treated groups and control groups. The difference in CAT activity between the SA-treated samples and the control samples was more obvious, particularly at 5 d of storage. This difference might, at least partially, be due to SA, which had been reported to increase the expression levels of CAT genes in treated samples [35].

The antioxidant enzyme system can reduce damage to plants under stress, but there is a change threshold, and the different duration and intensity of cold stress can affect the change in enzyme activity. SOD converts O_2^- into H_2O_2 and is considered the first line of defense against oxidative damage [36]. H_2O_2 can be converted to H_2O by POD and CAT [37]. POD is also involved in respiration, ethylene synthesis, and many other processes in plants. SA has emerged as a key signaling component in the activation of certain plant defense responses [35, 38]. The application of SA has been reported to slow the rate of ethylene production [38]. Some members of the ethylene responsive factor (ERF) family are induced by SA [39, 40]. Therefore, it could be inferred that there was a close relationship between SA and ethylene signaling pathway in response and defense systems of cold stress. The effect of SA on POD might be related to the ethylene signaling pathway. The decreased POD activity in the SA-treated groups was influenced by many factors, for example, the application of SA retarded the rate of ethylene production and POD activity might be increased by ethylene.

A possible regulatory mechanism for SA in toon bud cold storage was proposed. Cold storage induced ROS, which might trigger membrane lipid oxidation. SA slowed the degradation of bioactive compounds such as AsA and anthocyanin. SA promoted the accumulation of defense- and antioxidant-related proteins. Subsequently, bioactive compounds and antioxidant-related proteins protected cells from ROS damage and enhanced the tolerance of toon buds.

CONCLUSION

The results of this work suggested that the use of SA (in particular, 50 μM) on Chinese toon buds was conducive to the preservation of toon under cold storage conditions. SA-treated toon buds had a better appearance, delayed weight loss, and a slowing degradation of bioactive compounds. Moreover, the positive effects of SA on toon bud freshness and quality were evident by the decreases of MDA and H_2O_2 levels, significant decreases in POD activity, and increases in SOD and CAT activities. Thus, in the present study, the ability of SA to maintain fresh toon buds might be attributed to its ability to regulate the antioxidant defense system under cold storage.

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