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RESEARCH

Effects of Short-Term High Oxygen Pre-Stimulation on Browning Resistance and Low-Temperature Tolerance of Fresh-Cut Potatoes in Supercooled Storage

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Abstract

In this study, the anti-browning effectiveness of short-term high oxygen pre-stimulation (SHOP), supercooled (SC) storage, or combined (SHOP + SC) treatment for fresh-cut potatoes was explored by evaluations on surface color, texture, phenolic anabolism, membrane integrity, antioxidant capacity, and reactive oxygen species (ROS) balancing. Furthermore, enzyme activity ratios (EA ratios) were further proposed to assess the effect of SHOP on enzymatic browning, which were defined as ratios between defense enzymes, including peroxidase (POD), phenylalanine ammonia-lyase (PAL) or catalase (CAT), and attacked enzymes including polyphenol oxidase (PPO) or lipoxygenase (LOX). As a result, SHOP + SC treatment retarded the browning and delayed the softening of fresh-cut potatoes by inhibiting the activities of related enzymes, restraining the accumulation of malondialdehyde (MDA), and promoting the synthesis of phenolic substances against their oxidation in potatoes. Besides, higher POD activities and lower BI were observed in SHOP + SC compared with SC, but PPO activities were non-statistically significant in both. At the early storage stage, the antioxidant capacities of fresh-cut potatoes treated with SHOP and SHOP + SC were enhanced, and the ROS accumulation was inhibited. Moreover, EA ratios and their changing amplitude of the SC group ranked top, followed by the control, SHOP, and SHOP + SC. Results suggested that the antioxidant capacity was reinforced by SHOP in fresh-cut potatoes due to enhanced resistance against membrane lipid damage resulting from mechanical cutting and persistent SC stimulation.

Keywords Fresh-cut potatoes · Short-term stimulation · High oxygen · Supercooled storage · Enzyme activity ratios

Introduction

There has been a growing demand for fresh-cut vegetables from consumers in recent years due to the convenience and high nutritional value (Kou et al., 2014). The COVID-19 outbreak spurred a boom in the prepared food and dishes market (Zarbà et al., 2022). As reported, the processed fruits and vegetable industry is projected to exceed USD 115 billion by 2026 (Global Market Insights, 2021). The potato (*Solanum tuberosum*) is one of the most popular vegetables in the world (Zhou et al., 2019). Potatoes that are washed, peeled, cut into pieces or slices, and cooked are suitable and convenient as main and side dishes for consumers (Haverkort et al., 2022). However, fresh-cut processing might cause quality losses such as surface shrinkage, browning, and off-odor, thus shortening the shelf life of potatoes (Shen et al., 2020).

Texture and appearance play a crucial role in food selection preference by affecting taste threshold, pleasantness, and acceptability (Toivonen & Brummell, 2008; Rico et al., 2007; Xylia et al., 2022). The major problem that reduces the commercial value of fresh-cut fruits and vegetables is browning (Fan et al., 2021; Martín-Diana et al., 2008). The leading cause of browning in fresh-cut potatoes was enzymatic browning, which had been widely reported. Once cut, phenols would be released from vacuoles and contacted with polyphenol oxidase (PPO) in the cell membrane to form quinones. Later, the quinones are dehydrated and polymerized to form dark substances (Feumba Dibanda et al., 2020; Ru et al., 2020). Phenylalanine ammonia-lyase (PAL) is also directly associated with enzymatic browning (Liu et al.,

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2019). PAL (as a defense enzyme) would be activated once the surrounding environment emerges and stimulates fruits and vegetables. In addition, PAL also involves in controlling the synthesis of phenolic substances. The browning substrate content assessed by total phenolic content (TPC) and the browning intermediates determined by soluble quinone content (SQC) is two leading paths for evaluating the enzymatic browning process (Zhang et al., 2022). Moreover, cutting disrupts the dynamic balance between scavenging and producing reactive oxygen species (ROS), leading to excessive accumulation of ROS and malondialdehyde (MDA) to damage plant cell membrane function. Catalase (CAT) and peroxidase (POD) are the primary enzymes in ROS enzymatic scavenging systems (Das & Roychoudhury, 2014; Suman et al., 2021). Lipoxygenase (LOX) catalyzes the generation of reactive oxygen species and oxygen free radicals from unsaturated fatty acids (generated by phospholipase D degradation of plasma membrane phospholipids). These ROS and oxygen free radicals directly act on the unsaturated fatty acids that bind with membrane phospholipids and therefore damage the phospholipid bilayer membrane (Liu et al., 2011; Mao et al., 2007). Hence, modulation of PPO, POD, PAL, CAT, and LOX activities is a fundamental strategy for many anti-browning approaches. Our previous study has revealed that enzyme activity ratios (EA ratios) systematically evaluate the differences in the effects of treatments on attack enzymes (promoting browning) and defense enzymes (preventing browning) in fresh-cut apples (Li et al., 2022).

High oxygen (super-atmospheric oxygen) has recently been widely used in meat, fruit, and vegetable preservation as a green preservation technology (Chen et al., 2015; Garcia-Lomillo et al., 2016; Helena Gomes et al., 2010; Li et al., 2014). At present, it has been confirmed that high oxygen works as abiotic stress, which preserves fruits and vegetables by regulating the PAL metabolic pathway and polyphenol synthesis in the process of fruits and vegetables postharvest. As a result, the fruits and vegetables turn into an induced resistance state (ISR), thereby maintaining the cell membrane integrity and enhancing the resistance to browning (Liu et al., 2019). Generally, most metabolic processes are temperature-dependent, such as microbial growth, respiration, and ethylene production (Koide et al., 2019a). Therefore, decreasing the storage temperature as low as possible without ice crystallization would be the utmost to maintain the texture, flavor, and biologically active substances of fruits and vegetables by reducing metabolic activities (Ahmed et al., 2022; Nadeem et al., 2022). Supercooled (SC) storage is a method without freezing where the storage temperature is below the freezing temperature but above the nucleation temperature (Osuga et al., 2021). SC has been reported to extend the shelf life of garlic, shallots, fresh-cut cabbages, and fresh-cut apples by 1–2.5 folds (James et al., 2009; James & James, 2011; Koide et al., 2019a). Hruschka (1961) suggested that SC storage is possible for fresh-cut potatoes with lower enzyme activities. Adversely, an undercooled environment would promote membrane lipid-related enzyme activities, generate more MDA, and accelerate browning in the storage (Koide et al., 2019b).

Opportunely, SHOP treatment has been proven to control browning by maintaining membrane integrity (Li et al., 2022). Therefore, the combination of SHOP and SC storage is expected to have an enhanced anti-browning effect. In this study, physicochemical changes and quality evaluations of SHOP-treated fresh-cut potatoes were observed and analyzed during 9 days of SC storage. Specifically, the anti-browning effects and cold injury resistance of fresh-cut potatoes after pre-stimulation with high oxygen (80% O_2 for 30 min) before SC storage was further explored. In addition, the EA ratios were used to study and confirm that SHOP could counteract the SC stress to fresh-cut potatoes, improve the resistance to quality deterioration, and prolong the shelf life of fresh-cut potatoes.

Materials and Methods

Vegetable Materials

The yellow-fleshed potatoes were obtained from Jiaohe City (Shandong province, China) and then transported through the cold chain to the laboratory. Potatoes without disease, blemishes, or mechanical damage were selected for pre-cold treatment at 4 °C for 18 h.

Determination of Freezing and Supercooling Points

The supercooling point of potatoes was assessed by the method by Koide et al. (2019b) with minor modifications. A T-type thermocouple was positioned at the geometric center of each potato sample (2 × 2 × 2 cm), which was then placed in a polystyrene box in a freezer (BC-142FQD, TCL Technology Group Co. LTD). Temperatures were recorded every 3 s by a datalogger (FLUKE 2638A, Fluke Electronic Instruments Co, USA) until the temperature of samples cooled down to –20 °C (Fig. S1). The time–temperature distribution of the fresh-cut potatoes ($n = 10$) was used to ascertain the initial freezing point and the supercooling point as the description by Kaale et al. (2011).

Experimental Design

The experimental design of this study is demonstrated in Fig. 1. In sealed bottles, half of the 8 kg selected potatoes were treated with 80% O_2 + 20% N_2 for 30 min, while the other half was immersed in 21% O_2 + % N_2 for 30 min. An O_2/CO_2 analyzer was used to measure the oxygen

concentration (Checkpoint II, PBI Dansensor Denmark). After that, potato tubers were peeled and cut into slices (4 mm thick) by a slicer with adjustable thickness. All potato slices were rinsed by distilled water, then wiped the distilled water on the surface and packaged in food ziplock bags (Polyethylene, 140 × 200 mm, 0.7 mm thick, oxygen transmission rate is 1500–2700 mL m^{-2} day^{-1}, Heyuan Huafeng Plastic Co., Ltd.) (Heo et al., 2019; Norrrahim et al., 2013; Yaptenco et al., 2007). Subsequently, potato slices were stored at –2 ± 0.5 °C (SC storage) or 4 ± 0.5 °C for 9 days. In summary, a total of 4 groups of samples were evaluated and analyzed on days 0, 2, 4, 6, and 9, namely the control (21% O_2, 4 °C), SHOP (80% O_2, 4 °C), SC (21% O_2, –2 °C), and SHOP + SC (80% O_2, –2 °C) (Fig. 1).

Browning Index (BI) and ΔE

A chromameter (HP-200, Hanpu Photoelectric Technology Co., Ltd, Shanghai, China) was used to measure the surface color in values of L^* (light), a^* (reddish-greenish), b^* (yellowish-bluish), and ΔE (CIE, 1976). Browning index (BI) was calculated to assess browning degrees (Buera et al., 1986).

Firmness and Fracturability

The firmness and fracturability were evaluated by a texture Analyzer (TA-XT plus, Stable Micro Systems, Surrey, UK) equipped with a 100-mm-diameter-cylindrical probe for texture profile analysis (TPA) (Phinney et al., 2017). Potato slices were cut into round flakes (10 mm in diameter, 4 mm in thickness). The trigger type was "auto force" with a test speed of 15 mm s^{-1}, and a trigger force of 1.5 N until 75% strain.

MDA Content

MDA was measured according to the method by Hu et al. (2021) and expressed as μmol kg^{-1} on a fresh weight basis. Briefly, trichloroacetic acid (w/v, 10%, 5 mL) was homogenized with frozen potato samples (5 g) at 0 °C. The mixture was centrifuged at 6000 × g at 4 ℃ for 20 min. Supernatant or trichloroacetic acid solution (2 mL) was mixed with 0.6% (w/v) thiobarbituric acid solution (2 mL) and then incubated in a boiling water bath for 20 min. After cooling to room temperature, absorbances were measured at 532 nm, 600 nm, and 450 nm.

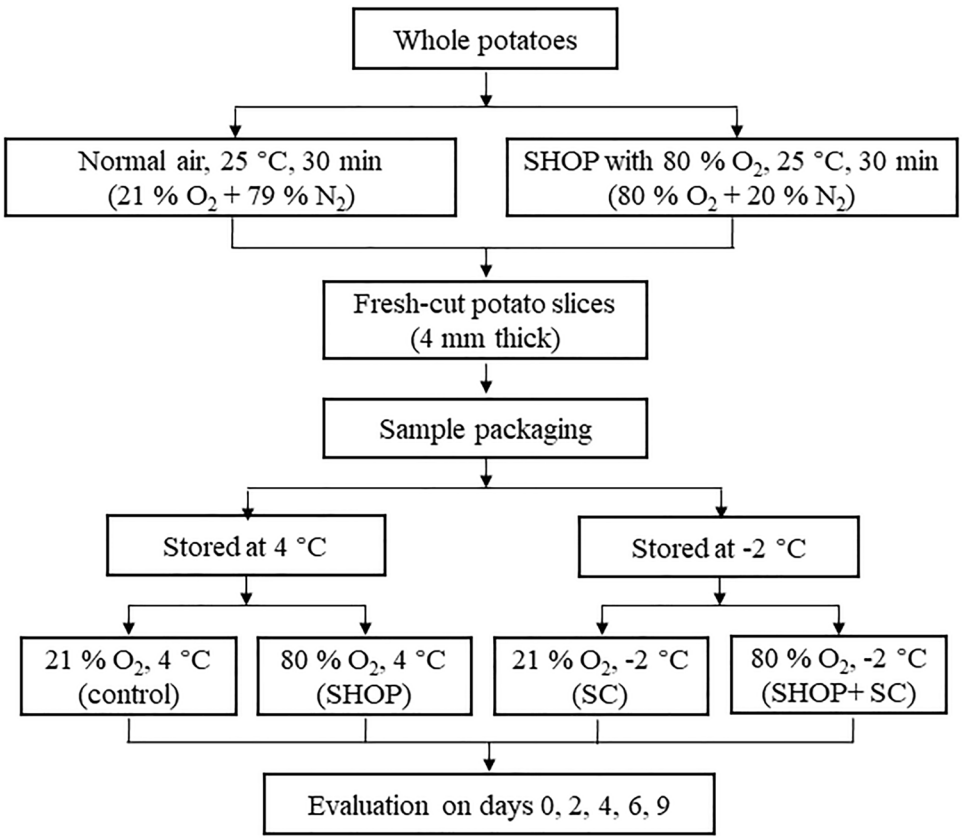

Fig. 1 Experimental design to study effects of short-term high oxygen pre-stimulation (SHOP) and/or supercooled (SC) storage on fresh-cut potatoes

Antioxidant Capacity

According to the method reported by Tang et al. (2015), the phenols extraction method in fresh-cut potatoes was slightly modified. The frozen potato samples were lyophilized in a vacuum freeze dryer for 24 h and then ground to powder for further use. Potato freeze-dried powder (1 g) and 70% methanol containing 0% glacial acetic acid (v/v, 5 mL) were mixed evenly, extracted at room temperature with a shaker (HY 60, Wuhan Huicheng Biotechnology Co., LTD, Wuhan, China) in the dark for 2 h, then sonicated for 30 min. The mixture was centrifuged at 6000 × g for 20 min. Three extractions were performed, and the supernatant was pooled to 15 mL. The supernatant was used as a crude extraction for further use.

The Folin-Ciocalteu method was used to assay TPC with minor modifications (Tang et al., 2015). Each sample or standard (25 μL) was transferred to a 96-well plate and mixed with freshly diluted Folin-Ciocalten reagent (1 mol L^{-1} Folin-Ciocalten:water = 1:4, 125 μL). After 10 min reaction, 125 μL of 7.5% Na_2CO_3 was added. After 30 min, the absorbance was read at 765 nm and methanol was the blank (Spectra Max190, Molecular Devices Corporation, USA). TPC was expressed as grams of gallic acid equivalents per kilogram on a dry weight basis (g GAE kg^{-1}) ($y = 0.0049\,x + 0.0736$, $r^2 = 0.9999$). A previously reported method was used to determine SQC (Qiao et al., 2021).

1,1-Diphenyl-2-trinitrophenylhydrazine (DPPH) free radical scavenging activity and Ferric reducing antioxidant power (FRAP) assay were evaluated by the method by Tang et al. (2015). DPPH free radical scavenging activity was expressed on a fresh weight basis as mmol Trolox equivalents per kilogram (mmol TE kg^{-1}) ($y = -0.0009\,x + 0.0555$, $r^2 = 0.9999$). The FRAP antioxidant activity was expressed on a dry weight basis as mmol ascorbic acid equivalent per kilogram (mmol AAE kg^{-1}) ($y = 0.0017\,x + 0.0032$, $r^2 = 0.9996$).

Production of H_2O_2 was measured by the hydrogen peroxide assay kit (Beijing Solarbio Science & Technology Co. Ltd., Beijing, China). The superoxide anion ($O_2^{\cdot-}$) scavenging activity was assessed by a superoxide anion assay kit (Shanghai Yuanye Bio-Technology Co., Ltd., Shanghai, China).

Enzyme Activity Assay

PPO, POD, PAL, and CAT activities were evaluated referring to the method by our lab (Du et al., 2021). The 1 absorbance change per minute at 420 and 470 nm was denoted as one unit for PPO and POD activity, respectively. One unit of CAT and PAL activity was defined as 0.01 absorbance changes per minute at 240 and 290 nm, respectively. The results were expressed as U kg^{-1} on a fresh weight basis.

LOX activity was determined according to the method by Qiao et al. (2021) with minor modifications. A total of 5.0 g potato tissues and 5.0 mL extraction buffer were ground and homogenized in ice bath condition. Then the mixture was centrifuged at 12,000 × g at 4 °C for 30 min. Subsequently, 2.7 mL phosphoric acid buffer (0.1 mol L^{-1}, pH 6.8) and 100 μL 0.5% linoleic acid solution were incubated at 30 °C for 10 min. Then 200 μL crude enzyme extract was added, mixed evenly, and immediately measured for absorbance. LOX activity was defined as 0.01 absorbance changes per minute at 234 nm. The results were expressed as U kg^{-1} on a fresh weight basis.

Enzyme Activity Ratio

The definition of EA ratio refers to our previous work (Li et al., 2022), while the scope of its definition was further extended as follows formulas in this study, which was used to reflect the resisting capacity against the cutting and chilling injury.

$$\mathrm{Ratio}_1 = \frac{\mathrm{POD}_n - \mathrm{POD}_0}{\mathrm{PPO}_n - \mathrm{PPO}_0} \quad \mathrm{Ratio}_2 = \frac{\mathrm{PAL}_n - \mathrm{PAL}_0}{\mathrm{PPO}_n - \mathrm{PPO}_0} \quad \mathrm{Ratio}_3 = \frac{\mathrm{CAT}_n - \mathrm{CAT}_0}{\mathrm{PPO}_n - \mathrm{PPO}_0}$$

$$\mathrm{Ratio}_4 = \frac{\mathrm{POD}_n - \mathrm{POD}_0}{\mathrm{LOX}_n - \mathrm{LOX}_0} \quad \mathrm{Ratio}_5 = \frac{\mathrm{PAL}_n - \mathrm{PAL}_0}{\mathrm{LOX}_n - \mathrm{LOX}_0} \quad \mathrm{Ratio}_6 = \frac{\mathrm{CAT}_n - \mathrm{CAT}_0}{\mathrm{LOX}_n - \mathrm{LOX}_0}$$

$_0$—values on day 0; $_n$ — values on days 2, 4, 6, and 9.

Statistical Analysis

Data were expressed as mean ± SD. Origin 2018 (OriginLab Corp., USA) and SPSS 19 (IBM, USA) were used for plotting figures and experimental data analysis. The initial freezing and supercooling points were 10 replicates, and BI, ΔE, firmness, and fracturability were 5 replicates, which were analyzed by Tukey's test with $P \leq 0.05$. The other indicators were 3 replicates and analyzed by the least significant difference (LSD) method with $P \leq 0.05$.

Table 1 Initial freezing point and supercooling point of fresh-cut potatoes

	Initial freezing point (°C)	Supercooling point (°C)
Mean	−1.6	−3.3
SD	0.4	0.8
Min	−2.6	−4.9
Max	−1.3	−2.5

SD standard deviation, *Min* minimum, *Max* maximum, $n = 10$

Results and Discussion

Freezing and Supercooling Points

As shown in Table 1 and Fig. S1, the average initial freezing point was –1.6 ± 0.4 °C, and the minimal supercooling point was –2.5 °C in fresh-cut potatoes, which suggests that fresh-cut potatoes can be stored at −2 °C. This result was in line with the previously reported initial freezing point in whole potatoes (–2 °C) (Comandini et al., 2013; Hruschka, 1961), leaf lettuces (–0.2 °C), carrot (–1.6 °C), parsnip (–2.2 °C), and broccoli (–2.1 °C) (James & James , 2011; Nguyen Quang et al., 2017). Therefore, the SC storage temperature in this study was set at −2.0 ± 0.5 °C.

Overall Visual and Textural Quality

Surface color is a crucial sensory parameter of fresh-cut potatoes. Browning occurrence lowers the purchase desirability of consumers directly (Osuga et al., 2021). The BI and ΔE usually evaluate the change of surface color in fresh-cut fruits and vegetables. The higher BI and ΔE are generally considered more severe browning (Toivonen & Brummell, 2008). It has been reported that the surface color of fresh-cut potatoes without any treatment changed drastically within 4 days at 4 °C (Liu et al., 2019; Zhou et al., 2019). In this study, SHOP, SC, and SHOP + SC postponed the increase of ΔE (Fig. 2b) and BI (Fig. 2c) and delayed the decline of firmness (Fig. 2d) and fracturability (Fig. 2e) of fresh-cut potatoes. From Fig. 2b, c, the surface color of potato samples from all groups gradually got darker (higher BI and ΔE) throughout the storage duration. In this study, the serene browning of the control and SHOP (6 days) occurred earlier than SC (9 days), while SHOP + SC maintained the lowest BI (113.10) and ΔE (10.26) with a light bright appearance after 9-day storage. The trends above were consistent with the study by Liu et al. (2019), where SHOP inhibited browning by activating PAL to enhance the antioxidant ability in fresh-cut potatoes. In addition, the SC and SHOP + SC maintained higher firmness (53.2 N, 55.3 N) and fracturability (56.8 N, 53.6 N) compared with the control and SHOP on day 9 (Fig. 2d, e). Similar effect as supercooled preservation controlled the microbial population and maintained color parameters and firmness has been previously reported in fresh-cut apples (Osuga et al., 2021). Therefore, the combination of SHOP and SC treatment is believed to be more effective than SHOP or SC alone in maintaining the storage quality and regulating the browning process.

Phenolic Compound Metabolism and Lipid Peroxidation

PPO is a critical enzyme for controlling the enzymatic browning in plants. After exposure to oxygen, phenols were catalyzed by PPO to form quinones, which polymerize themselves in plants or interact with amino acids and proteins in cells and finally produce black or brown deposits (Shen et al., 2020). As a wound-inducing enzyme, PAL is easily activated after cleavage (Qiao et al., 2022). The TPC (Fig. 3a), SQC (Fig. 3b), and PAL activity (Fig. 3c) of fresh-cut potatoes were increased, but the PPO activity (Fig. 3d) was inhibited by SHOP on day 0. On day 2, the PAL and POD activities (Figs. 3c and 4a) of SC were 35.6–49.2% lower than SHOP + SC. Moreover, the increment of TPC in SHOP + SC was 0.85–0.90 times that of the control and SC during the storage. Those results pointed out that SHOP inhibited enzymatic browning by activating the phenylpropane metabolic pathway, synthesizing secondary metabolites, and inhibiting the activity of PPO at conventional refrigeration temperature (4 °C). High oxygen ($O_2 \geq 75\%$) pre-stimulation and high oxygen packaging were used to block the browning of fresh-cut watercored apples, fresh-cut eggplants, and mushrooms, which were consistent with this study (Li et al., 2014, 2017, 2022). In addition, the TPC of SHOP and SHOP + SC increased sharply from day 4 to day 6 and from day 6 to day 9, respectively. This result was consistent with the changes in photos (Fig. 1a), BI (Fig. 1b), and ΔE (Fig. 1c). From day 4 to day 9, non-statistically significance was observed in PPO activities between SC and SHOP + SC, while the highest POD activity and the lowest BI were obtained in SHOP + SC. Sun et al. (2015) reported that in the presence of H_2O_2, POD catalyzed the oxidation of phenolic substances, leading to tissue browning. This suggested that the main pathway of browning in SHOP + SC might be mediated by POD. In addition, the lower PAL activity and TPC in SHOP + SC in this study indicated that SHOP alleviated the stress of the SC environment on fresh-cut potatoes, maintained a lower biochemical reaction activity, and achieved the purpose of inhibiting browning.

Cell membrane integrity plays an essential part in browning development. MDA is a reference index to evaluate the degree of membrane lipid peroxidation, and higher MDA content generally means more severe damage to the cell membrane (Aghdam & Bodbodak, 2014; Zheng et al., 2019). LOX catalyzes the oxidation of polyunsaturated fatty acids,

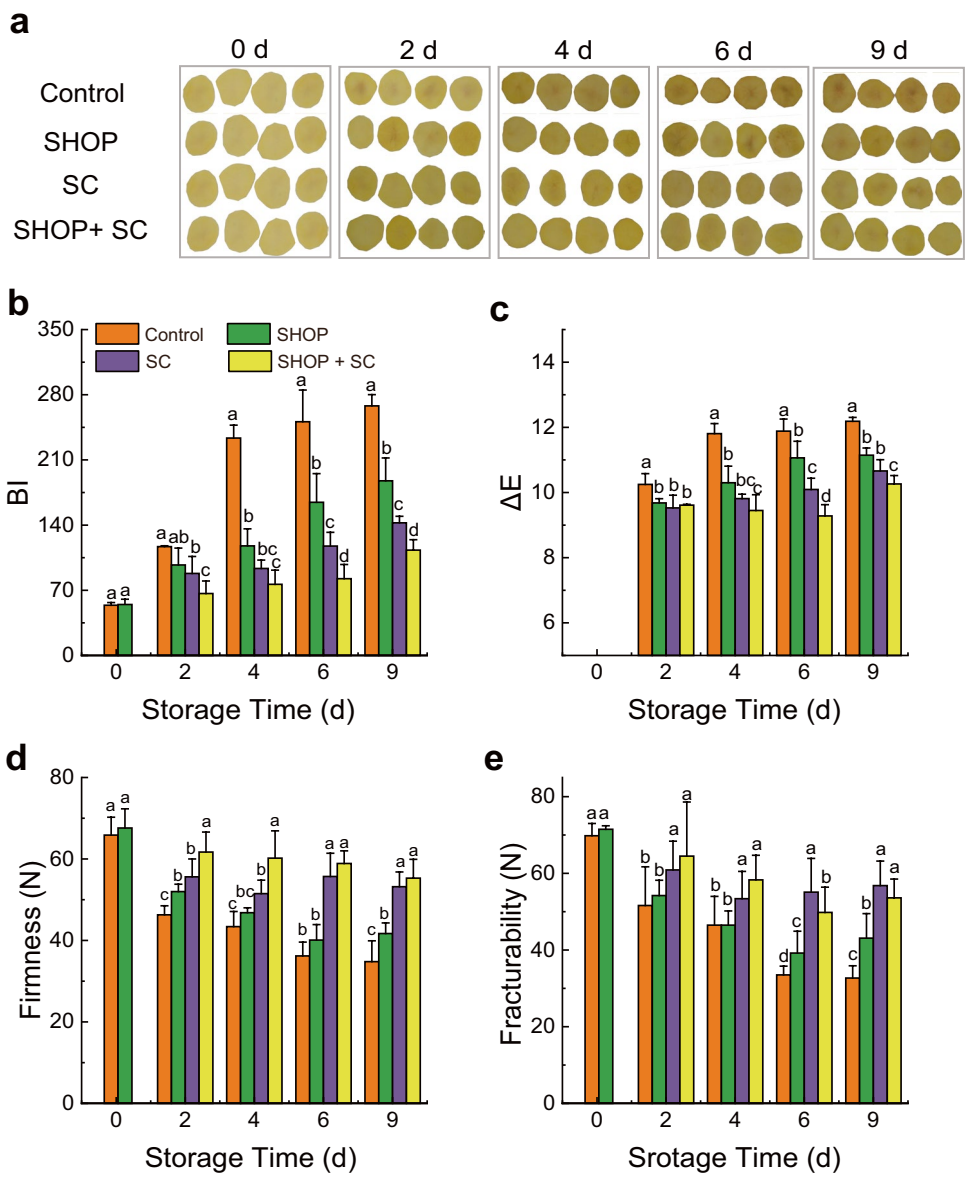

Fig. 2 SHOP combined with SC storage maintained the surface color and texture of fresh-cut potatoes at –2 °C for 9 days. Photographs of fresh-cut potatoes (**a**), BI (**b**), ΔE (**c**), firmness (**d**), and fracturability (**e**). Vertical bars indicate standard errors ($n = 5$). Different letters denote significant differences between treatments within each time interval ($P \leq 0.05$)

commonly observed in browning and chilling injury phenomena (Liu et al., 2011). In this study, the MDA content (Fig. 3e) of SC and SHOP + SC rose and then decreased throughout the storage process, while the MDA content of the control and SHOP continued to increase. The samples of SC group had the highest MDA content (Fig. 3e) and LOX activities (Fig. 3f) compared with the other three groups on day 2 and day 4, followed by SHOP + SC. Ma et al. (2022) reported that cold shock treatment regulated the membrane lipid metabolism of peach fruits to alleviate the chilling injury. Similarly, heat treatment protects against cold injury by improving the unsaturated/saturated fatty acid ratio (unSFA/SFA) and maintaining the membrane integrity of cold-sensitive fruits and vegetables (Aghdam & Bodbodak, 2014). Besides, severe browning was associated with higher MDA content and LOX activity in fresh-cut pears, potatoes, lettuce, and other fruits and vegetables (Li et al., 2014; Martín-Diana et al., 2008; Qiao et al., 2021; Zheng et al., 2019). In this study, the lowest MDA content (Fig. 3e) and LOX activity (Fig. 3f) and a relatively steady changing trend were found in SHOP + SC, which indicated the synergetic role of SHOP and SC in maintaining membrane integrity.

Antioxidant Capacity

The homeostasis between ROS production and elimination will be disrupted and induce severe accumulation of ROS under the stress conditions, such as drought, mechanical damage, and cold or heat shock (Aghdam & Bodbodak, 2014; Imahori et al., 2008). Excessive ROS ($O_2^{\cdot -}$ and H_2O_2) accelerates membrane lipid peroxidation, ultimately aggravating tissue chilling injury and browning (Imahori

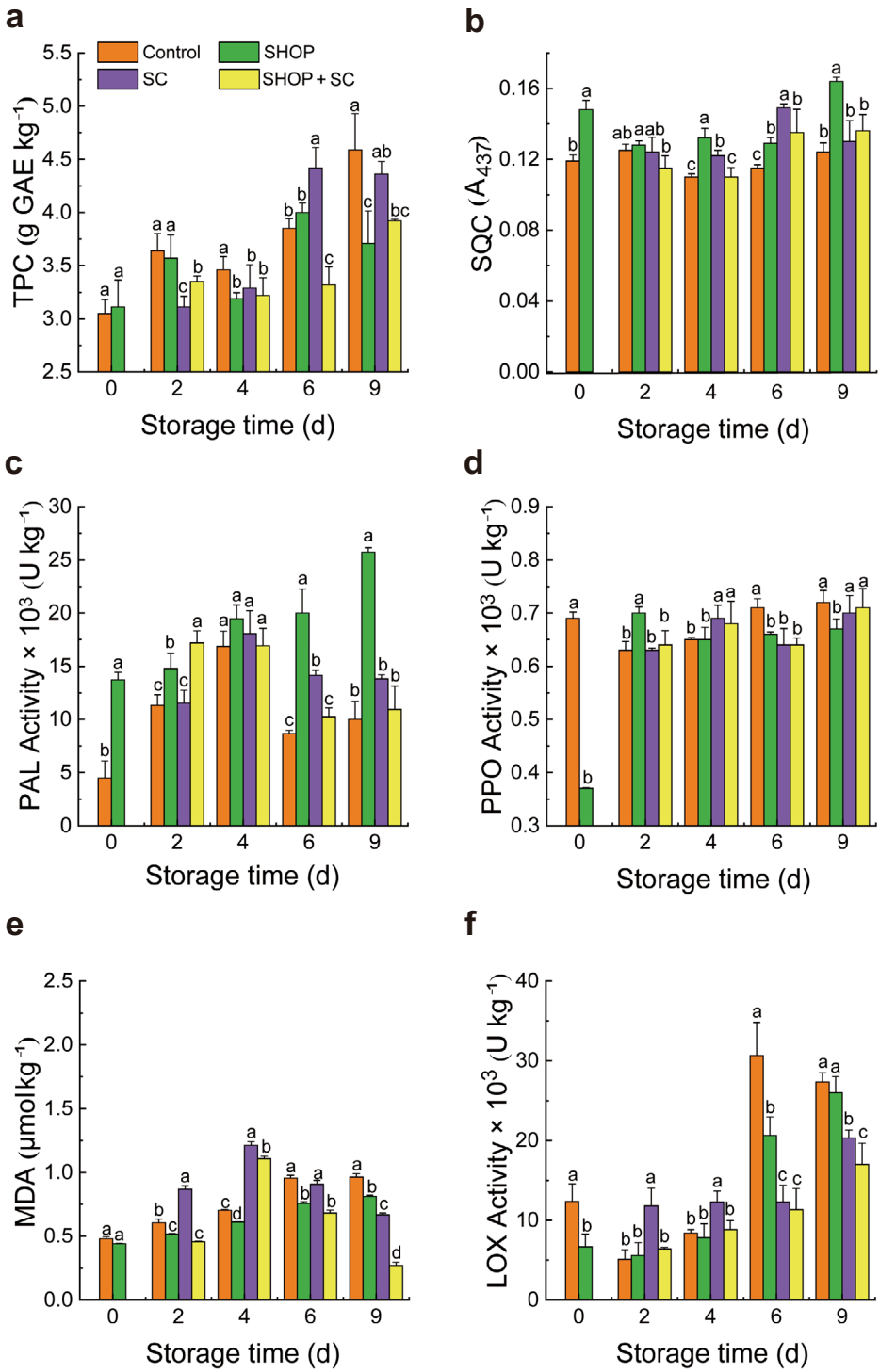

Fig. 3 SHOP combined with SC delayed the synthesis of phenolic substances, reduced phenolic oxidation, and delayed the lipid peroxidation of fresh-cut potatoes at –2 °C for 9 days. TPC (**a**), SQC (**b**), PAL activity (**c**), PPO activity (**d**), MDA (**e**), and LOX activity (**f**). Vertical bars indicate standard errors ($n = 3$). Different letters denote significant differences between treatments within each time interval ($P \leq 0.05$)

et al., 2008). $O_2^{\cdot-}$ leads to high local free radical concentration. However, SOD catalyzes $O_2^{\cdot-}$ into H_2O_2, which passes through the cell membrane to all parts of the cell to reduce the oxidative damage caused by excessive local ROS (Das & Roychoudhury, 2014). Due to the vigorous SOD activity and widespread presence in various parts of cells, H_2O_2 is the true representative of reactive oxygen species in tissue cells (Sies et al., 2022). H_2O_2 induced a plant defense system and activated the activity of defense enzymes (POD, PAL, and CAT) (Jaafar et al., 2012). H_2O_2 catalyzed by CAT to H_2O and O_2, which would reduce the oxidative damage caused by free radicals as well. Within the early 4 days of storage,

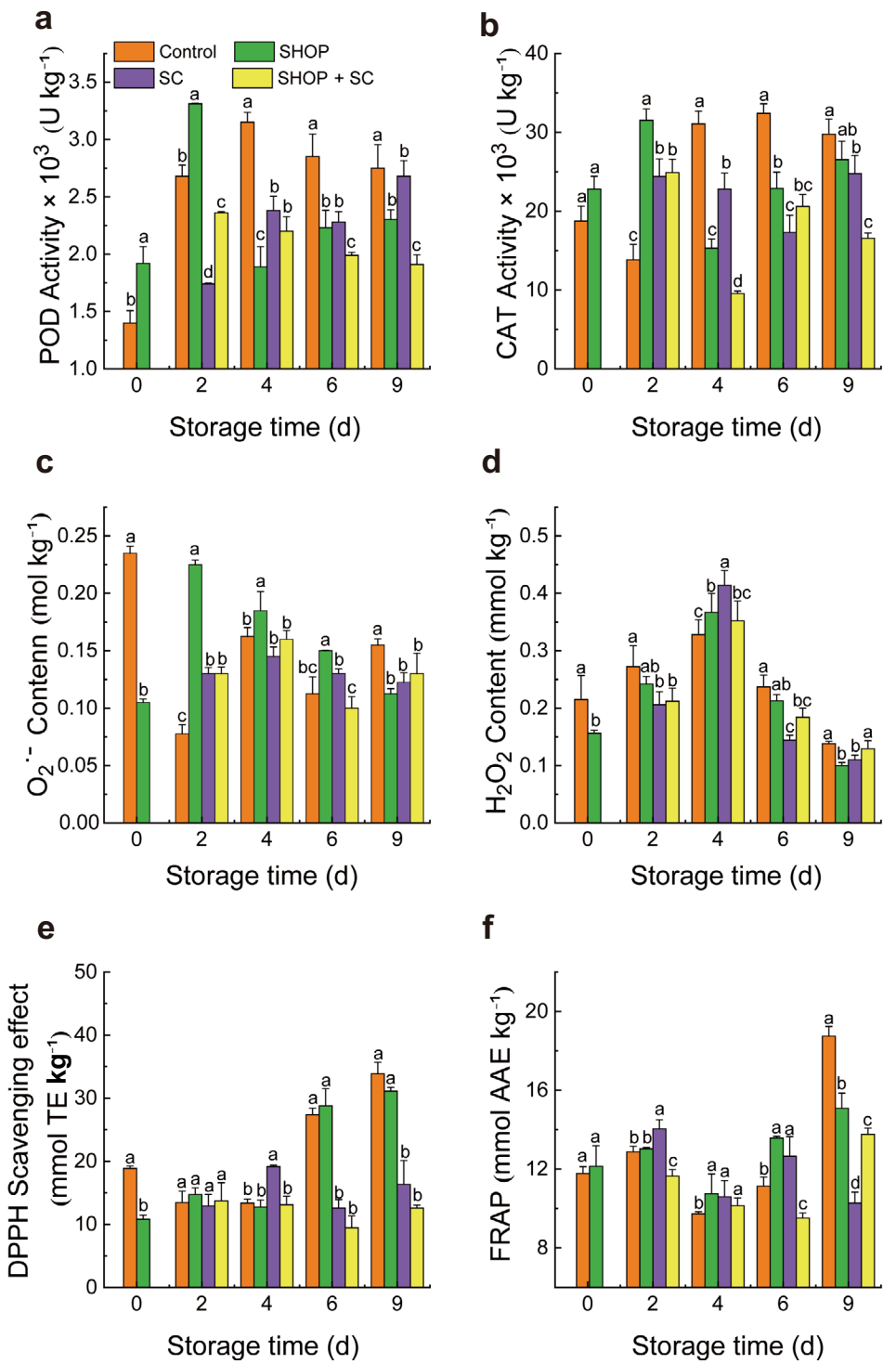

Fig. 4 SHOP combined with SC improved the antioxidant capacity and inhibited the accumulation of ROS of fresh-cut potatoes at –2 °C for 9 days. POD activity (**a**), CAT activity (**b**), $O_2^{\cdot-}$ content (**c**), H_2O_2 content (**d**), DPPH scavenging effect (**e**), and FRAP (**f**). Vertical bars indicate standard errors ($n = 3$). Different letters denote significant differences between treatments within each time interval ($P \leq 0.05$)

the $O_2^{\cdot-}$ and H_2O_2 contents (Fig. 4c, d) of SHOP, SC, and SHOP + SC increased sharply, and then the H_2O_2 content gradually decreased on day 6 and was lower than that of the control. However, after 4 days of storage, the $O_2^{\cdot-}$ content in each treatment group was generally inhibited compared with the control (Fig. 4d). Those changes were similar to MDA content and LOX activity (Fig. 3e, f). This indicated that $O_2^{\cdot-}$ and H_2O_2 were induced by SHOP treatment to cause transient stress increase, and then it acted as a signaling molecule to regulate downstream related metabolic systems and other physiological and biochemical reaction processes, which enhanced the cold resistance and browning resistance of fresh-cut potatoes. Zheng et al. (2019) and Bai et al. (2022) found that melatonin and eugenol treatment reduced

the ROS content of fresh-cut pears and fresh-cut yams to inhibit their browning, a pathway similar to this study.

Many studies have found that POD manifests itself as two mechanisms of action in fruits refrigeration. One mechanism is expressed in large quantities in the early stages of cold adversity, manifesting itself as a protective effect (Magri et al., 2022). Another mechanism is activated late in refrigeration adversity and manifests itself as a harmful effect, thereby reducing the storability of fruits (Li et al., 2019). Figure 4a, b shows that POD and CAT activities were increased by SHOP in fresh-cut potatoes from day 0 to day 2, while these enzyme activities decreased to 22.4 – 50.7% of the control on day 4. The POD and CAT activities of SHOP + SC gradually decreased lower than SC with the passage of storage time, which can be inferred that POD and CAT are non-key factors of the antioxidant system in the late refrigeration stage. Those results may be caused by POD and CAT metabolism disorders in long-term low-temperature storage (Boonyaritthongchai & Supapvanich, 2017). Overall, SHOP increased the activity of potato tubers and fresh-cut potato defense enzymes at the early stage of storage and inhibited the metabolic disorders of POD and CAT caused by supercooling.

Two chemical model systems, the DPPH scavenging effect and FRAP were used to evaluate the antioxidant activities of fresh-cut potatoes (Yu et al., 2019). SHOP had higher DPPH free radical scavenging and iron ion reducing ability, consistent with that of Liu et al. (2019), who tested that the DPPH free radical scavenging rate of fresh-cut potatoes was 53% after 80% O_2 pretreatment, which was higher than 49% in the control (21% O_2). However, the combined treatment did not enhance the antioxidant capacity of fresh-cut potatoes. In addition, the fluctuations of the DPPH scavenging effect (Fig. 4e) of the control, SHOP, SC, and SHOP + SC within 9 days of storage were 20.48, 18.37, 6.57, and 4.28 mmol TE kg^{-1}, respectively. Moreover, the fluctuations in FRAP (Fig. 4f) of the control, SHOP, SC, and SHOP + SC were 9.01, 4.32, 3.77, and 4.25 mmol AAE

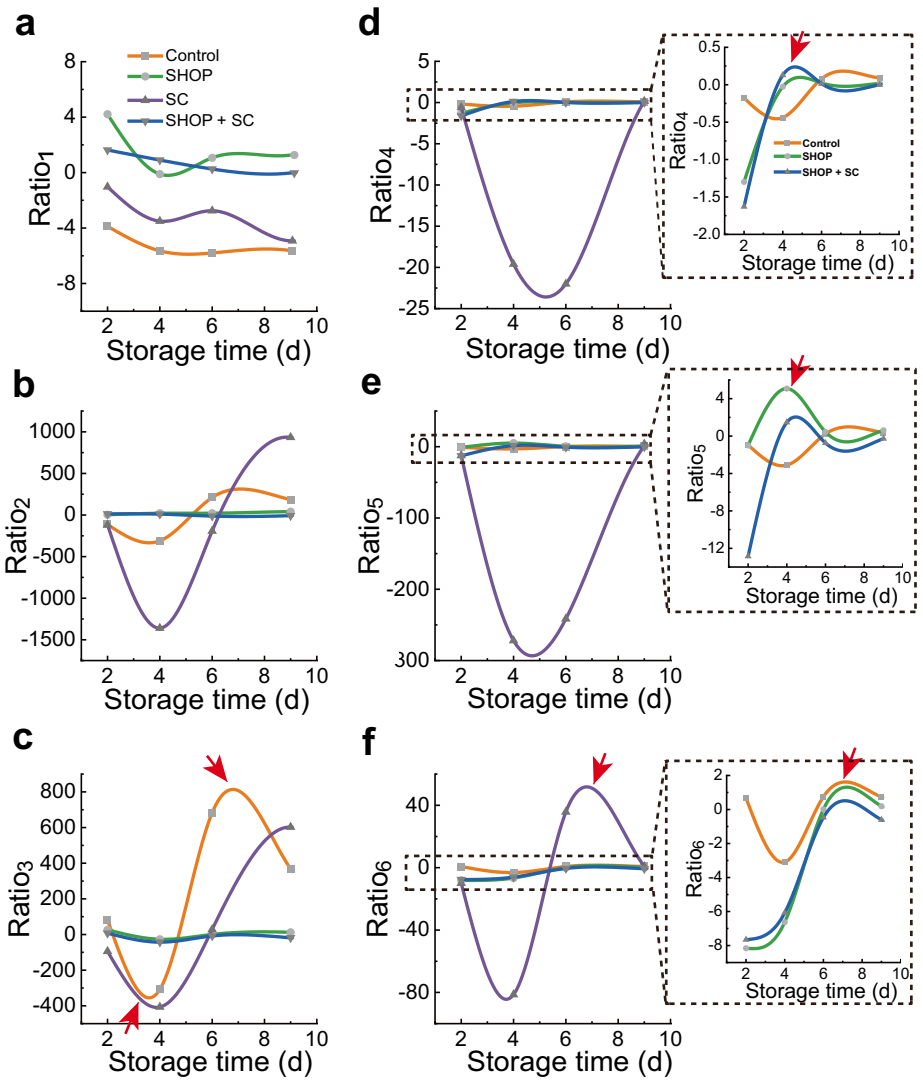

Fig. 5 SHOP combined with SC storage showed a slight fluctuation on $Ratio_1$, $Ratio_2$, $Ratio_3$, $Ratio_4$, $Ratio_5$, and $Ratio_6$ of fresh-cut potatoes at –2 °C for 9 days. $Ratio_1$ ($(POD_n\text{-}POD_0)/(PPO_n\text{-}PPO_0)$, (**a**)), $Ratio_2$ ($(PAL_n\text{-}PAL_0)/(PPO_n\text{-}PPO_0)$, (**b**)), $Ratio_3$ ($(CAT_n\text{-}CAT_0)/(PPO_n\text{-}PPO_0)$, (**c**)), $Ratio_4$ ($(POD_n\text{-}POD_0)/(LOX_n\text{-}LOX_0)$, (**d**)), $Ratio_5$ ($(PAL_n\text{-}PAL_0)/(LOX_n\text{-}LOX_0)$, (**e**)), and $Ratio_6$ ($(CAT_n\text{-}CAT_0)/(LOX_n\text{-}LOX_0)$, (**f**)). Data are represented by means

kg^{-1}, respectively. The above results may be due to persistent damage to fresh-cut potatoes caused by SC, but SHOP provided potato tubers with excellent resistance against minimal processing and supercooled storage, resulting in less damage in SHOP + SC than in SC after day 4, which failed to induce higher defense enzyme activities and antioxidant capacity.

Enzyme Activity Ratios

It has been reported that the enzyme activity (EA) ratio was applied as an overall and direct indicator to express the effectiveness of fresh-cut watercored apples in anti-browning ability (Li et al., 2022). The EA ratio refers to the proportion of the increments of the attack enzyme and the defense enzyme per unit of time, which can express the intensity of the life activity of the samples during storage. The trends of changes in the activities of various enzymes measured in this experiment were fluctuant within 9 days of storage. Still, after reprocessing the enzyme activity data by EA ratio, the differences and trends of changes in each treatment group gradually became clear. The $Ratio_1$ (Fig. 5a), $Ratio_2$ (Fig. 5b), and $Ratio_3$ (Fig. 5c) of SHOP and SHOP + SC had minor variations than the control and SC. Moreover, the $Ratio_4$ (Fig. 5d), $Ratio_5$ (Fig. 5e), and $Ratio_6$ (Fig. 5f) of the control and SC, and SHOP and SHOP + SC had the same trends. In Fig. 5a, $Ratio_1$ was higher in SHOP and SHOP + SC than in the control and SC. Among them, the fluctuation ranges of $Ratio_1$ values of SC and SHOP + SC within 9 days of storage were 3.9 and 1.7, respectively. In contrast, $Ratio_2$ and $Ratio_3$ (Fig. 5b, c) in SC and SHOP + SC showed a smaller variation range than the control and SC. The values range of SC in $Ratio_4$, $Ratio_5$, and $Ratio_6$ was 12.6–47.5, 19.1–72.17, and 14.0–29.2 times higher than the other three treatment groups, respectively. Those results have shown that SHOP inhibited the persistent damage to fresh-cut potatoes caused by the storage environment and maintained the fresh-cut potatoes in a stable state of lower biological activity. In addition, except for $Ratio_1$, the ratios of other enzyme activities in the control reached the maximum on day 6, while $Ratio_1$ and $Ratio_2$, $Ratio_3$, $Ratio_4$, and $Ratio_5$ (Fig. 5a–e) of SC were on day 9. Overall, SHOP induced a more extraordinary ability to resist supercooling and cutting injury for the cell membrane within 4 days of storage. We also found that the change point of EA ratios was consistent with the color mutation point of fresh-cut potatoes, supporting those ratios as comprehensive and direct indicators of when the quality of fresh-cut potatoes reaches the plateau.

According to our results and previous studies, the mechanism of SHOP treatment to inhibit browning and chilling injury of fresh-cut potatoes was summarized in Fig. 6 (Li et al., 2014, 2022; Mao et al., 2007; Sies et al., 2022). The surface color, texture, phenolic compounds anabolism, membrane integrity, antioxidant capacity, ROS balancing, and EA ratios in fresh-cut potatoes were comprehensively considered in this study. The results demonstrated that

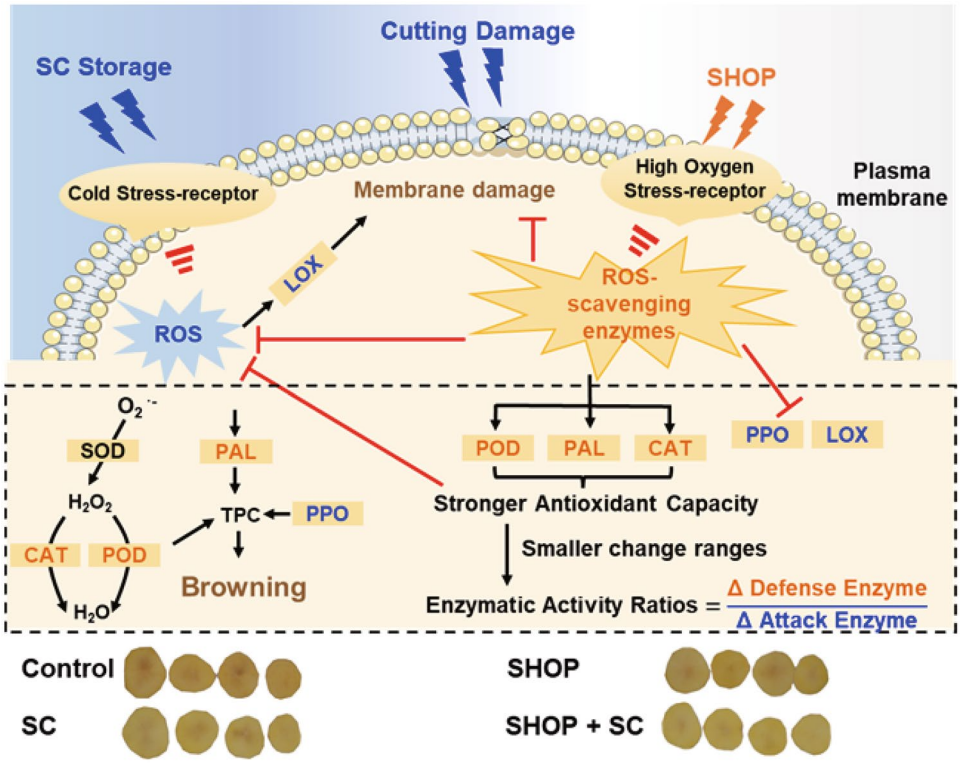

Fig. 6 Schematic overview of the proposed model for SHOP-induced cold tolerance and anti-browning. ↓: Stimulatory effect; ⊥: Inhibitory effect; enzyme abbreviations in blue and orange: attack enzymes and defend enzymes, respectively. The photographs at the bottom exhibit the appearance of fresh-cut potatoes at –2 °C for 9 days after treatment with SHOP combined with SC storage

SHOP treatment enhanced the antioxidant capacity in the early stage of storage, promoted the synthesis of phenolic compounds, and inhibited PPO activity and phenolic oxidation, thereby maintaining the stability of the cell membrane system under conventional refrigerated and supercooled storage temperatures. Therefore, SHOP inhibits the browning and texture softening of fresh-cut potatoes by enhancing resistance to membrane lipid damage caused by mechanical cutting and continuous SC stimulation.

Conclusions

This study indicated that the combination of SHOP and SC was more effective in controlling browning and delaying texture decline of fresh-cut potatoes than either treatment alone. The activities of PPO and POD were reduced and the SQC was increased by these three treatments compared with the control. There was no statistical difference in PPO activity between SC and SHOP + SC, but the POD activity and BI of SC were higher than that of SHOP + SC. Moreover, phenolic and ROS metabolism, including PAL and CAT activities, TPC, DPPH, and H_2O_2 content, was affected by SHOP, SC, and SHOP + SC. Moreover, the SHOP + SC had the highest membrane integrity with the lowest LOX activity and MDA content among all the groups. Furthermore, minor changes in EA ratios in the SHOP and SHOP + SC indicated reduced and alleviated biological activities. Overall, SHOP combined with SC has the potential to be an effective and promising method in maintaining texture and controlling the browning of fresh-cut potatoes. Compared with the use of food additives, SHOP + SC treatment as a combined physical preservation method has the advantages of effective, environmentally friendly, ease of operation, which is promising for application in fresh-cut industry.

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Author Contribution Xuejin Li (First Author) and Yuqian Jiang (First Author) wrote the main manuscript text and prepared all figures and table. Yue Liu and Lu Li were responsible for data curation. Fuhao Liang, Xiaodong Wang, Dandan Li, and Na Pan participated in experiment preparation and data determination. Xihong Li, Xiangzheng Yang (Corresponding Author), and Yao Tang (Corresponding Author) provided funders and writing–review and editing. All authors reviewed the manuscript.

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Data Availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Competing Interests The authors declare no competing interests.

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