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Investigating the Enzymatic System of Mexican Lime Fruits in Low-Temperature Storage under Post-Harvest Treatment of Salicylic Acid

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ABSTRACT

Lime (*Citrus aurantifolia* v.) susceptibility to chilling injury and its limited shelf life are common challenges in postharvest management. There has been a growing trend of replacing harmful chemicals with natural substances that pose no harm to plants, the environment, or humans. To address this issue, we conducted a factorial experiment using a randomized complete block design with four replications. Our study aimed to evaluate the impact of different concentrations of salicylic acid (SA) (0, 1, 2, and 3 mM) on the enzymatic activity of limes during storage (0 and 60 d). Experimental conditions maintained a temperature of 4 ± 1 °C and a humidity of 85 ± 2%. Several enzymes were measured, including phenylalanine ammonia-lyase (PAL), peroxidase (POD), superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), antioxidant activity, and chilling injury (CI). Our results indicated that all concentrations of SA led to increased activity of antioxidant and defensive enzymes in the fruits. At 3 mM SA, the activity of antioxidant enzymes increased by 4.06%, and SOD activity increased by 13.2%. The treatment of 2 mM SA increased POD (24.53%) and CAT (86.3%) activities. Also, 1 mM SA enhanced APX enzyme activity by 27.78%, while PAL enzyme activity decreased by 38.35%. In sum, all SA concentrations, particularly 2 and 3 mM, reduced the CI index. Our study demonstrated that increasing the SA concentration significantly extended the shelf life of Mexican lime fruits. This finding is supported by the observed increase in antioxidant enzyme activities.

Introduction

Citrus fruits are vital agricultural commodities in many countries, though overproduction sometimes occurs. These fruits, being non-climacteric, produce low levels of ethylene and have a slow respiration rate, meaning they do not soften or undergo significant compositional changes after harvest. As noted by Kader (2002), this trait allows for the storage of some citrus varieties for up to 6-8 weeks. Lime, a globally significant horticultural crop, is particularly important in Iran. Valued for its high acidity and vitamin C content, lime also serves as a source for lemon juice, a widely used food acidulant. The shelf life of lime is influenced by storage conditions and handling practices, as postharvest injuries can increase respiration rates and reduce storage quality. While refrigeration can extend the

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shelf life by slowing ripening, prolonged storage may lead to chilling injuries.

The quality of citrus fruits is determined by a combination of physical, chemical, and physiological traits, alongside nutrient concentration. High-quality limes are firm, green, and free from defects. Factors such as harvest timing, fruit variety, and environmental conditions also play a critical role in determining fruit quality (Maftoonazad et al., 2019).

Salicylic acid (SA), a naturally occurring phenolic compound, is crucial in plant signal transduction, affecting growth, development, and responses to stress. SA regulates processes such as stomatal closure, transpiration, fruit yield, seed germination, heat production, glycolysis, and flowering (Chen et al., 2023). Because it is non-toxic, SA holds potential for reducing postharvest losses in horticultural crops by inducing various physiological and metabolic responses (Asghari & Soleimaniaghdam, 2010). When plants face stress—whether from biotic or abiotic factors—reactive oxygen species (ROS) such as hydroxyl ions, hydrogen peroxide, and superoxide are generated, which can damage cellular structures (Tan et al., 2023). Plants combat oxidative stress using non-enzymatic antioxidants (like ascorbate and carotenoids) and enzymatic systems, including catalase (CAT) and ascorbate peroxidase (APX). APX, in particular, reduces H_2O_2 levels by utilizing ascorbate as an electron donor (Orabi et al., 2015). Additionally, SA enhances plant antioxidant defenses and plays roles beyond stress resistance. Research links SA to processes such as stomatal regulation, growth, photosynthesis, disease resistance, seed germination, and adaptation to environmental challenges like heavy metals, extreme temperatures, and salinity (Hayat et al., 2010).

SA is instrumental in plant defense, particularly in disease prevention and post-harvest quality management. One of its key functions is inhibiting ethylene biosynthesis, thereby delaying fruit senescence, which is vital for extending the shelf life of harvested produce (Chen et al., 2023). Systemic acquired resistance (SAR), a form of induced resistance, relies on SA-mediated signaling pathways that activate pathogenesis-related proteins, strengthening the plant's defenses (Beckers & Spoel, 2006). Administering safe levels of external SA to vulnerable plants has been shown to bolster their resistance to pathogens. For instance, studies have demonstrated that SA treatment can reduce post-harvest chilling injury in tomatoes (Zhang et al., 2011) and pomegranates (Sayyari et al., 2009). Similarly, SA application—either pre- or post-harvest—has been effective in minimizing fungal decay in peaches by enhancing the activity of antioxidant enzymes (Wang et al., 2006).

SA's role in alleviating chilling injury is linked to several physiological changes, including improved antioxidant system function, enhanced membrane stability, activation of the C-repeat binding factor (CBF) pathway, upregulation of heat shock protein (HSP) and arginine pathway gene expression, and alterations in phenylalanine ammonia-lyase (PAL) and polyphenol oxidase (PPO) enzyme activities. The use of resistance inducers, such as SA, is thus a valuable strategy for preserving post-harvest fruit quality (Zhou et al., 2018).

SA's multifaceted impact on plant health makes it indispensable for both disease prevention and post-harvest management. Resistance inducers or elicitors, like SA, activate chemical defense mechanisms in plants (Rasouli et al., 2019). When applied, these compounds stimulate biosynthetic pathways, leading to the production of protective substances, such as pathogenesis-related proteins and polyphenols (Shi et al., 2018). Recent research underscores SA's efficiency in mitigating chilling damage, enhancing resistance to decay, reducing lipid peroxidation, and slowing down the softening process (Ennab et al., 2020).

Lime storage conditions are crucial for maintaining fruit quality. Typically, limes are stored between 13°C and 14°C. However, at these temperatures, rot can occur severely. Conversely, storing limes below 10°C often results in chilling injury, which disrupts membrane lipids and increases membrane permeability (Nasrin et al., 2020). This damage manifests as various symptoms, including rind staining, pitting, red blotches, scald, and watery breakdown on the flavedo, all of which significantly reduce the fruit's overall quality, shelf life, and marketability (Liao et al., 2022).

Given SA's role as a natural signaling compound that triggers plant defense responses, its application offers a safer alternative to synthetic chemicals for post-harvest management. Considering the risks associated with improper chemical usage and the cold sensitivity of limes, exploring secure post-harvest treatments in conjunction with cold storage is imperative. Limes, due to their susceptibility to chilling injury and limited post-harvest lifespan, serve as an ideal candidate for such studies.

The objective of this research is to evaluate the impact of SA treatment on maintaining the quality of lime fruits during cold storage, thereby extending their shelf life. By understanding the effects of SA, we aim to enhance fruit integrity, reduce post-harvest losses, and ensure consumer satisfaction.

Material and Methods

Plant material and treatments

To investigate the effects of SA immersion on the enzymatic activity of Mexican limes (*Citrus aurantifolia* cv.) during cold storage, a factorial experiment was conducted. The study utilized a complete randomized design with two variables: storage conditions and SA treatment. The research was carried out in 2017 at the Agricultural Faculty of Rafsanjan University, with Mexican limes harvested at peak ripeness from a commercial grove in Jahrom, Iran. The selection criteria for the limes included a 10% color shift from green to yellow, a TSS of 9.8, and a pH value of 7. Uniformity in size and color ensured consistency across the samples.

The experimental treatments involved immersing the limes in SA solutions at concentrations of 0, 1, 2, and 3 mM. Each immersion lasted precisely 5 minutes, following the procedure outlined by Mirdehghan and Ghotbi (2014). After the SA treatment, the limes were air-dried and packed in low-density polyethylene containers, with 10 fruits per group. The limes were then placed in cold storage, maintained at a temperature of 4 ± 1 °C and a relative humidity of 85 ± 2% for either 0 or 60 d.

Assay of enzymatic activities

Frozen tissue samples (weighing 2 g) from 10 different fruits were blended with 10 mL of chilled extraction buffer containing 0.2 g of PVPP, and then processed with a grinder at a temperature of 4 °C. The extraction buffer used for superoxide dismutase (SOD) consisted of 100 mmol L^{-1} sodium phosphate with a pH of 7.8, whereas for ascorbate peroxidase (APX) and catalase (CAT), it was made up of 100 mmol L^{-1} sodium phosphate with a pH of 7.0. Additionally, the APX buffer contained 0.1 mmol L^{-1} EDTA, 1 mmol L^{-1} ascorbic acid, and 1% polyvinyl-pyrrolidone. In the case of the phenylalanine ammonia-lyase (PAL) assay, the extraction buffer used was composed of 50 mmol L^{-1} sodium borate buffer with a pH of 8.8 and containing 5 mol L^{-1} β-mercaptoethanol. For the enzyme assay, the supernatant was obtained by centrifuging the homogenate at 15000×g for 30 min at a temperature of 4 °C. The method of Jin et al. (2009) was used to determine SOD activity, where one unit of SOD activity is equivalent to a change of 1 min^{-1} in OD560. The results were expressed in units g^{-1} of fresh weight (U g^{-1} FW). A reaction mixture consisting of 1 mL sodium phosphate buffer (50 mmol L^{-1}, pH 7.0), 1 mL H_2O_2 (40 mmol L^{-1}), and 1 mL enzyme extract was used to analyze CAT activity, based on the method of Wang and Tian (2005) with certain modifications. A change of 0.01 min^{-1} in OD240 was defined as one unit of CAT activity, and the results were expressed in units g^{-1} of fresh weight (U g^{-1} FW).

The method of Nakano and Asada (1989) was used to determine APX activity, where one unit of APX is equivalent to a change of 0.01 min^{-1} in OD290. The results were expressed in units g^{-1} of fresh weight (U g^{-1} FW). The method of Chance and Maehly (1955) was used to determine POD activity, with the extraction buffer being 50 mL phosphate (pH 5). An absorbance change of 0.01 min^{-1} in OD470 was defined as one unit of POD activity, and the results were expressed in units g^{-1} of fresh weight (U g^{-1} FW). The method of Meng et al. (2008) was used to assay PAL activity, where one unit of PAL is equivalent to a change of 0.01 min^{-1} in OD290. The results were expressed in units g^{-1} of fresh weight (U g^{-1} FW).

Total antioxidant activity (TAA)

TAA was determined by the 2,2-diphenyl-1-picryl-hydrazyl (DPPH) radical-scavenging method. The absorbance was measured at 517 nm using a spectrophotometer (PerkinElmer Lambda, American) and was expressed as the inhibition percentage of the DPPH radical.

Chilling injury (CI) index

The chilling injury (CI) index of fruits was evaluated at 4 °C for 60 d in cold storage. The fruits were returned to ambient temperature (20 °C) for the development of chilling injury symptoms. Symptoms were manifested as surface pitting according to the method of Ding et al. (2002). The severity of the symptoms was assessed visually on a 4-stage scale: 0 = no pitting; 1 = pitting covering <25% of the fruit surface; 2 = pitting covering <50%, but >25% of the surface; 3 = pitting covering <75%, but >50% of the surface; and 4 = pitting covering >75% of the surface. The average extent of cold damage was expressed as a CI index, which was calculated using the following formula:

$$CI\ index\ (\%) = \frac{[(CI\ level) \times (number\ of\ fruits\ at\ the\ CI\ level)]}{(total\ number\ of\ fruits) \times 4} \times 100.$$

Statistical analysis

The statistical analysis of our data was conducted using SAS statistical software (version 9.1; SAS Institute). To compare mean values, we employed Duncan's multiple range test. Significance was determined based on a P-value less than 0.05.

Results

SOD activity

The analysis of variance results indicated significant effects of both SA treatment and storage conditions, as well as their interaction (P≤0.01) (Table 1). Notably, SOD activity increased during cold storage, with SA treatment being a key factor in promoting this enhancement. The most pronounced increase in SOD activity occurred at the 3 mM SA concentration, demonstrating the treatment's effectiveness at this level. In contrast, the 2 mM SA treatment did not result in a significant increase in SOD activity (Fig. 1). This suggests that while SA generally promotes SOD activity, its effectiveness is dose-dependent, with higher concentrations yielding more pronounced effects.

Table 1. Analysis of variance of some traits of Mexican lime under the effects of SA (0, 1, 2 and 3 mM), storage in two durations (0 and 60 d), and their interaction.

Sources of variation	df	Mean squares						
		SOD activity	APX activity	CAT activity	POD activity	PAL activity	TA activity	CI index
Treatment	3	0.59*	0.03**	0.00009**	0.43*	0.001**	2.06*	0.001**
Storage	1	14.21**	1.36**	0.0003**	38.16**	0.01**	16.14**	0.003**
Treatment × Storage	3	0.59*	0.03**	0.00009**	0.43*	0.001**	2.06*	0.001**
Error	8	0.14	0.002	0.000005	0.09	0.00002	0.45	0.0000008
Coefficient of variation		6.63	3.52	8.70	6.81	4.28	0.80	6.28

* and ** show significance at the 5% and 1% levels, and ns means no significant difference.

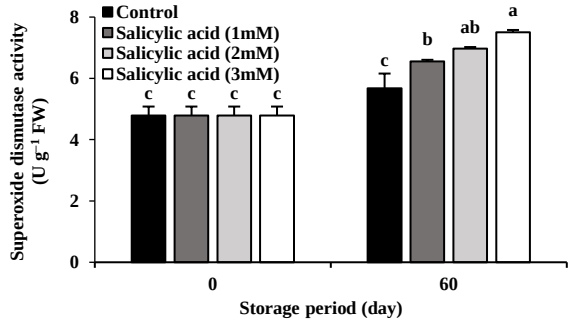

Fig. 1. Superoxide dismutase activities of lime fruits stored at 4 ± 1 °C, 85 ± 2% RH. Vertical bars indicate the standard errors of 4 replicates. Values with similar letters are not significantly different (P ≤ 0.05).

APX activity

The analysis of variance revealed significant effects of both SA and storage time (P≤0.01), along with their interaction (Table 1). During storage, APX activity levels increased in both the control group and the group treated with SA. Notably, the use of SA resulted in a significant increase in APX activity levels. Limes treated with SA exhibited higher APX activity compared to the control group (Fig. 2).

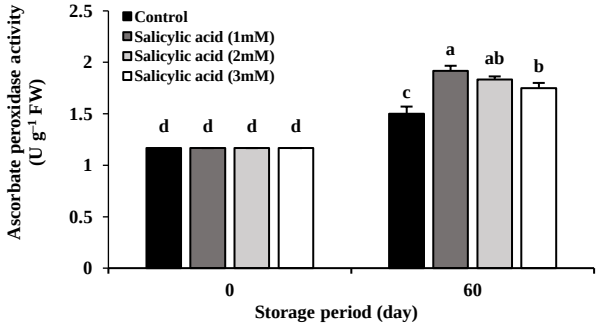

Fig. 2. Ascorbate peroxidase activities of lime fruit stored at 4 ± 1 °C, 85 ± 2% RH. Vertical bars indicate the standard errors of 4 replicates. Values with similar letters are not significantly different (P ≤ 0.05).

CAT activity

The data analysis revealed that both SA and storage time significantly influenced CAT activity (P≤0.01), along with their interaction (Table 1). CAT activity levels increased during storage. The 2 and 3 mM SA treatments exhibited significantly higher peaks compared to the control group. The optimal effective dose was determined to be 2 mM (Fig. 3).

POD activity

According to the analysis of variance, both SA treatment and storage time, as well as their interaction, significantly affected POD activity (Table 1). After the 60 d storage period, there was a sharp increase in POD activity in all samples. Notably, the group treated with SA exhibited significantly higher values than the control group. Among all the treatments, the one with 2 mM SA demonstrated the highest POD activity (Fig. 4).

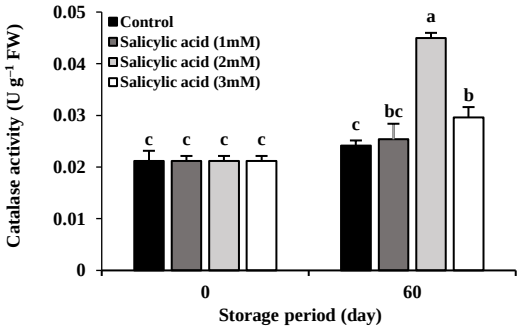

Fig. 3. Catalase activities of lime fruit stored at 4 ± 1 °C, 85 ± 2% RH. Vertical bars indicate the standard errors of 4 replicates. Values with similar letters are not significantly different (P ≤ 0.05).

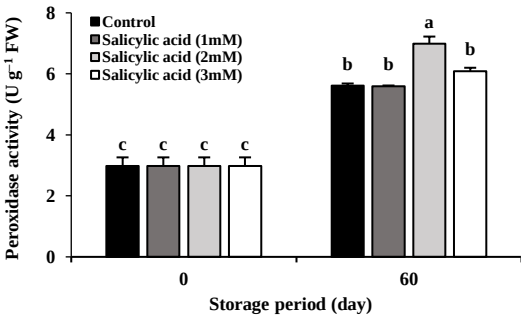

Fig. 4. Peroxidase activities of lime fruit stored at 4 ± 1 °C, 85 ± 2% RH. Vertical bars indicate the standard errors of 4 replicates. Values with similar letters are not significantly different (P ≤ 0.05).

PAL activity

According to the analysis of variance, the effects of both SA treatments and storage time, as well as their interaction, were found to be significant on PAL activity (P≤0.01) (Table 1). During cold storage, the fruits treated with SA exhibited significantly lower PAL activity compared to the control group. Notably, the control group of PAL activity peaked at 60 d, while the group treated with 1 mM SA had the lowest PAL activity (Fig. 5).

TA activity

According to the analysis of variance (Table 1), the effect of SA, storage time, and their interaction on antioxidant activity was significant. As shown in the figure, the level of antioxidant activity in both the control and SA-treated samples decreased throughout the storage period. However, the use of SA significantly inhibited this decrease and resulted in higher values of this parameter in SA-treated limes (Fig. 6).

CI index

The analysis of variance indicated that the effect of SA treatment, storage time, and their interaction were significant (P≤0.01), regarding the chilling injury (CI) index (Table 1). In this study, the severity of chilling symptoms in limes was assessed using the CI index parameter. By day 60, the control samples exhibited severe chilling symptoms. However, SA treatment significantly mitigated the increase in the CI index, with the greatest reduction observed at concentrations of 2 and 3 mM (Fig. 7).

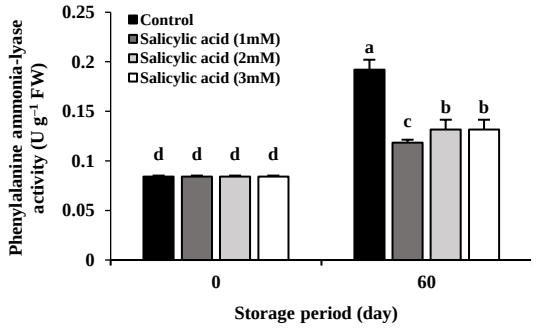

Fig. 5. Phenylalanine ammonia-lyase activities of lime fruits stored at 4 ± 1 °C, 85 ± 2% RH. Vertical bars indicate the standard errors of 4 replicates. Values with similar letters are not significantly different (P≤0.05).

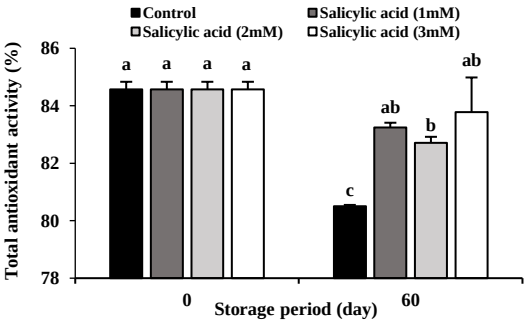

Fig. 6. Total antioxidant activities of lime fruit stored at 4 ± 1 °C, 85 ± 2% RH. Vertical bars indicate the standard errors of 4 replicates. Values with similar letters are not significantly different (P≤0.05).

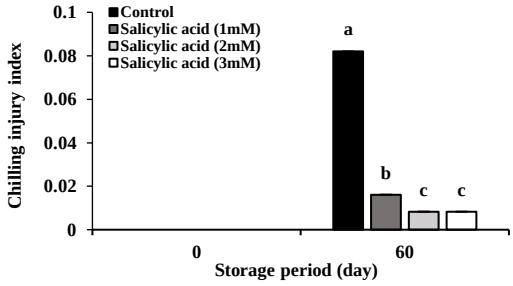

Fig. 7. Chilling injury index of lime fruit stored at 4 ± 1 °C, 85 ± 2% RH. Vertical bars indicate the standard errors of 4 replicates. Values with similar letters are not significantly different (P ≤ 0.05).

Discussion

The levels of vitamin C, phenolic compounds, flavonoids, and anthocyanins are closely linked to antioxidant activity. At the end of storage, blood oranges, rich in anthocyanins, maintained higher antioxidant activity, while other citrus varieties showed a decline (Hamedani et al., 2014). Treatment with antioxidants like SA significantly increased the total content of unsaturated fatty acids and decreased saturated fatty acids. The rise in unsaturated fatty acids, prompted by SA, enhances the fluidity of lipid membranes, which can influence their permeability and stability (Sakineh et al., 2012).

The activation of antioxidant systems, triggered by low temperatures, may explain the initial rise in antioxidant activity. In the early stages of storage, SA promotes the accumulation of H_2O_2 and certain ROS, which are essential for the expression of disease resistance genes. Over time, however, these free radicals must be neutralized. Antioxidants act as electron donors to stabilize free radicals, which may explain the gradual decrease in antioxidant activity (Wang et al., 2006).

In this study, SA had a significant effect on maintaining antioxidant activity, which remained relatively stable throughout storage. Pre-storage application of SA in oranges was found to boost the activity of antioxidant enzymes such as glutathione reductase, SOD, and dehydroascorbate reductase, as well as ascorbate and glutathione levels. This treatment also delayed lipid peroxidation of membrane lipids (Huang et al., 2008). Enzymes such as SOD, CAT, APX, and POD play key roles in metabolizing ROS and scavenging free radicals (Han et al., 2017).

Treating limes with SA has emerged as a safe, natural method for enhancing their storage capabilities. This may be due to the plant defense mechanism, where SA induces SOD activity, detoxifying superoxide ions into H_2O_2. PAL, a crucial enzyme in the biosynthesis of phenolic compounds and responsible for tissue browning in fruits and vegetables, increased in activity during storage in both the control and SA-treated lime samples. However, SA significantly inhibited the rise in PAL activity, resulting in lower levels in SA-treated limes. This finding is consistent with previous studies on pomegranates, where SA was found to suppress tissue browning by inhibiting PAL activity (Sayyari et al., 2009).

The mechanism by which SA inhibits tissue browning may be similar to the one proposed by Peng and Jiang (2006). In sweet cherries, SA has been shown to stimulate the synthesis of antioxidant enzymes, boost cellular antioxidant capacity, and induce the activity of other enzymes such as PPO, PAL, and β-1,3-glucanase (Chen et al., 2023).

In our study, we observed that SA-treated fruits exhibited higher activity levels of antioxidant enzymes, including APX, POD, SOD, and CAT, compared to the control group. Throughout storage, defense-related enzymes such as PAL increased in activity, but this rise was mitigated by SA treatment. Similar observations have been reported in studies on citrus and other fruits (Chen et al., 2023; Ennab et al., 2020). Our findings, together with existing evidence, suggest that SA treatment stimulates antioxidant enzyme activity while inhibiting defense-related enzyme activity, thereby delaying fruit senescence. These results are consistent with the work of Han et al. (2017), who noted that SA's beneficial effects may stem from its ability to suppress enzymes associated with browning. For example, in pineapple, SA treatment significantly suppressed PAL activity, delaying internal browning. Likewise, Sayyari et al. (2009) reported that extended cold storage in pomegranate increased PAL activity, which was subsequently reduced by SA treatment. However, the exact role of PAL in chilling injury remains to be clarified through further biochemical and genetic analyses.

The complexity of these processes arises from overlapping mechanisms, including antioxidant systems, membrane integrity factors, and PAL itself, which may all influence outcomes, as suggested by conflicting reports. During fruit ripening and senescence—oxidative processes—detoxifying enzymes like CAT tend to decrease, while enzymes that generate superoxide or hydrogen peroxide increase, leading to toxic levels (Tan et al., 2023). The balance between CAT and SOD activities determines the steady-state levels of O^{2-} and H_2O_2 in cells. When SA interacts with certain enzymes, it triggers the accumulation of H_2O_2, which activates protective enzymes and PR-proteins, enhancing fruit resistance to pathogens (Chen et al., 2023).

Under biotic and abiotic stress, plants produce ROS, such as superoxide, hydroxyl ions, and hydrogen peroxide. Excessive ROS can damage cellular structures and contribute to chilling injury. If these ROS are not effectively removed, they cause lipid peroxidation (Tan et al., 2023). According to Chen et al. (2023), applying SA exogenously during fruit storage enhances defense mechanisms and antioxidant production, reducing lipid peroxidation and maintaining cell membrane integrity.

Plants have evolved mechanisms to maintain relatively low concentrations of ROS by scavenging these toxic and reactive compounds through antioxidant compounds and enzymatic systems such as SOD, APX, and CAT (Zahedi et al., 2023). SOD serves as the primary enzyme responsible for scavenging O^{2-} radicals, catalyzing their disproportionation into H_2O_2 and O2. APX and CAT then facilitate the degradation of H_2O_2 into H_2O and O^2.

Consistent with previous research on cucumber (Cao et al., 2009) and peach (Wang et al., 2006), treatment with SA led to higher activities of SOD, APX, and CAT in lime fruit compared to the control group. Furthermore, Asghari and Soleimaniaghdam (2010) reported that pre-treating tomatoes and peaches with SA before low-temperature storage could induce the biosynthesis of HSPs, enhancing their tolerance to chilling injury. Thus, applying SA to chilling-sensitive horticultural products enables their storage at low temperatures without incurring chilling injury.

According to Wang et al. (2006), SA effectively reduces postharvest chilling injury in fruits and vegetables by boosting the activity of critical antioxidant enzymes such as GR and APX. The potential of exogenous SA application for quality control is noteworthy (Wang et al., 2022). This

occurs due to its ability to delay fruit ripening, modify pigment composition, minimize browning, reduce the activity of cell wall-degrading enzymes, maintain cell membrane integrity, preserve fruit aroma, enhance flavor, retain nutrient content, and increase antioxidant activity.

The reduction of chilling injury in limes attributed to SA application is linked to its enhancement of antioxidant enzyme activities (Siboza et al., 2017). A significant correlation exists between the antioxidant capacity of plants and the dosage of SA applied. The increase in APX activity observed is a result of SA activating the plant's resistance system, thus enhancing cellular antioxidant defenses (Orabi et al., 2015). Additionally, exogenous application of SA can alleviate stress-induced toxicity, decrease lipid peroxidation rates, and bolster overall antioxidant activity (Asadi et al., 2013).

Conclusion

The current research highlighted the efficacy of SA treatment in preserving the postharvest quality of limes over an extended period. Notably, the 2 mM SA treatment had the most significant impact on enhancing lime quality, as evidenced by increased enzymatic activities of SOD, APX, CAT, and POD. Furthermore, antioxidant activity was enhanced, while PAL activity showed a more pronounced decrease in response to the 2 mM SA-treated group compared to other concentrations and the control group. Given that SA acts as a plant regulator and poses no environmental threat, it can be effectively employed for the storage of lime fruits at 4 °C.

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Conflict of Interest

The authors indicate no conflict of interest in this work.

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