Annals of Tropical Research 47 (2):334-353(2025)
https://doi.org/10.32945/atr4721.2025

Review Article

Biochemical approaches to prevent pericarp browning in Lychee fruit (*Litchi chinensis*) during storage: A review

David Chandra[1*]

ABSTRACT

Lychee fruit (*Litchi chinensis*) is widely known for its bright red pericarp and delicious flesh. However, during post-harvest storage, the commercial value of this fruit decreases due to pericarp browning. This browning phenomenon is mainly caused by the enzymatic browning process, which involves the activity of enzymes such as polyphenol oxidase and peroxidase. These enzymes catalyze the oxidation of phenolic compounds to brown pigments, which causes discoloration of the pericarp. In addition, the degradation of anthocyanins, the pigments that give the pericarp its red color, also contributes to the browning. These changes are often associated with cell membrane damage, which allows interactions between enzymes and phenolic substrates. Several post-harvest management measures that can be implemented to delay lychee pericarp browning include storing the fruit at an optimum low temperature (3–5°C) with a relative humidity (RH) above 90–95%. Controlled atmosphere storage, typically using low oxygen concentrations and high carbon dioxide levels, is also quite effective. In addition to optimizing the storage temperature of lychees, several postharvest treatments have been shown to delay pericarp browning. These include the application of natural bioactive compounds, ethylene inhibitors, hormonal and signaling regulators, structural integrity enhancers, edible coatings, and organic acid or antioxidant dips.

Keywords: biochemistry, browning, lychee, phenol, storage

Received: 1 June 2025
Revised: 14 September 2025
Accepted: 14 September 2025
Published: 12 December 2025

[1]Department of Agronomy and Horticulture, Faculty of Agriculture, University of Lampung, Bandar Lampung, Lampung, 35141, Indonesia

*Corresponding Author. Address: Department of Agronomy and Horticulture, Faculty of Agriculture, University of Lampung, Bandar Lampung, Lampung, 35141, Indonesia; Email: davidchandra.unila@gmail.com

INTRODUCTION

Lychee (*Litchi chinensis*) is a highly valued tropical fruit, characterized by its bright red pericarp and sweet, transparent white flesh. However, this fruit is susceptible to post-harvest physiological and biochemical changes, especially pericarp browning that occurs within a few days after harvest (Zhang et al., 2001). This phenomenon significantly reduces the commercial value and competitiveness of lychee in the global market.

Pericarp browning in lychee is mainly caused by the oxidation of phenolic compounds, such as anthocyanins, which is catalyzed by oxidative enzymes such as polyphenol oxidase (PPO) and peroxidase (POD). This process is exacerbated by the loss of cell membrane integrity due to aging and environmental stress, which causes cell decompartmentalization and allows interactions between enzymes and their substrates (Jing et al., 2013). In addition, the accumulation of reactive oxygen species (ROS) such as superoxide and hydrogen peroxide during storage accelerates lipid peroxidation, membrane damage, and pigment degradation (Zhang et al., 2018).

Efforts to inhibit postharvest browning of lychee have focused on biochemical approaches that target oxidative pathways and maintain redox balance. Various compounds have been studied, including natural antioxidants such as pyrogallol and melatonin, which have been shown to inhibit PPO and POD activities, and enhance the activities of antioxidant enzymes such as superoxide dismutase (SOD) and catalase (CAT) (Zhang et al., 2018). In addition, the use of surface coatings such as chitosan and treatment with organic acids has been shown to be effective in reducing water loss, maintaining anthocyanin content, and slowing the browning process (Nanglia et al., 2022; Yang et al., 2023).

Given the importance of understanding the biochemical mechanisms underlying postharvest pericarp browning of lychee and the effectiveness of various interventions. This review article aims to summarize recent findings on the mechanisms and biochemical approaches to inhibit postharvest pericarp browning of lychee fruit. The main focus will be on the physiological mechanisms, treatment effectiveness, and potential practical applications in the horticultural industry.

MAIN CAUSES OF LYCHEE PERICARP BROWNING

Enzymatic Oxidation

During postharvest storage, tropical fruits such as lychee often experience pericarp browning, which reduces their visual appeal and commercial value (Deng et al., 2018). This phenomenon is mainly caused by increased enzymatic activities, especially PPO and POD, triggered by physiological stresses such as water loss, temperature fluctuations, and tissue damage during storage (Huang et al., 2024; Wang et al., 2010; Yun et al., 2021).

PPO catalyzes the oxidation of phenolic compounds to o-quinones, which then undergo polymerization to form brown pigments (Jiang, 2000). Meanwhile, POD uses hydrogen peroxide (H_2O_2) to oxidize phenolic and anthocyanin substrates, accelerating the degradation of bright red pigments in the fruit pericarp (Zhang et al., 2005). This interaction is the main cause of the loss of pericarp color

brightness and triggers undesirable browning (Fang et al., 2013). The increase in PPO and POD activities is closely related to cell membrane damage during storage (Huang et al., 2022). When the membrane is damaged, direct contact occurs between the enzyme and the phenolic substrate previously localized in different compartments, accelerating the oxidative reaction and the formation of brown pigments. In addition, environmental factors such as high temperature, oxygen exposure, and water loss exacerbate tissue damage and accelerate these enzymatic activities (Fang et al., 2013; Wang et al., 2010).

Various approaches have been developed to suppress PPO and POD activities, including storage at low temperatures, application of antioxidants such as ascorbic acid, use of enzyme inhibitor compounds, and packaging technologies such as modified atmosphere packaging (MAP). These treatments aim to prevent phenol and anthocyanin degradation and maintain fruit color and quality during storage (Ali et al., 2016, 2018; Sivakumar & Korsten, 2010; Somboonkaew & Terry, 2010). The discoloration pathway of lychee pericarp is presented in Figure 1.

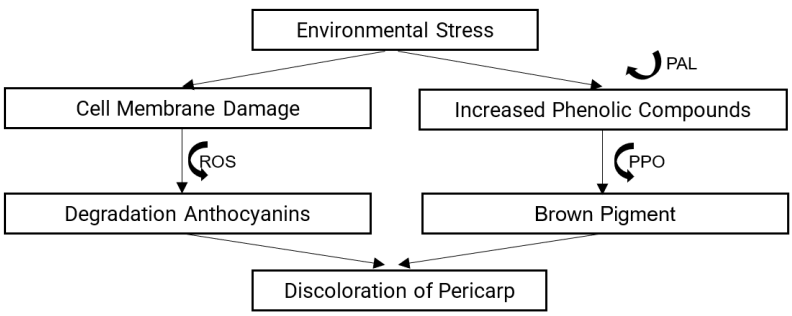

Figure 1. Lychee pericarp discoloration pathway

Oxidative Stress

During post-harvest storage, lychee fruit is susceptible to oxidative stress due to changes in temperature, humidity, and suboptimal atmospheric conditions. This stress triggers disturbances in the redox balance in fruit tissue, which causes increased formation of ROS. ROS such as superoxide radicals (O_2-) and H_2O_2 are formed naturally during normal metabolism, but their excessive accumulation due to environmental stress becomes toxic and damages cellular components. Uncontrolled ROS accumulation will trigger lipid peroxidation, an oxidative reaction that attacks unsaturated fatty acids in cell membranes, resulting in structural damage to the plasma membrane and vacuoles, and increasing cell permeability causing compartment leakage. This condition allows direct contact between enzymes such as PPO and POD with phenolic and anthocyanin substrates, accelerating the browning of the lychee pericarp (Su et al., 2019). In addition, ROS also plays a role in reducing the activity of endogenous antioxidant systems such as ascorbic acid and glutathione, which exacerbates oxidative stress and accelerates fruit quality decline (Jamei et al., 2009; Khan et al., 2021).

Bolaños et al. (2010) found that during storage, PPO activity decreased while POD activity increased, with total phenolic compound content remaining stable, indicating that changes in enzyme activity and ROS contribute to lychee fruit pericarp browning. According to Huang et al. (2023), a study of 50 lychee varieties showed that the average browning index and decay rate increased significantly after nine days of storage at room temperature, with some varieties showing higher resistance to storage. Parameters such as pericarp thickness, relative conductivity value, laccase enzyme activity, and total dissolved solids content have been recognized as crucial indicators in assessing the intensity of browning and the degree of damage in lychee fruit. Increased oxidative stress occurs due to an imbalance between the formation of ROS and the defense capacity of the endogenous antioxidant system, which leads to lipid peroxidation, cell membrane disintegration, and increased membrane permeability. This condition facilitates direct contact of enzymes such as PPO and POD with phenolic and anthocyanin substrates, thereby accelerating the browning of the pericarp.

To reduce the effects of ROS, various strategies have been applied, including storage at low temperatures, the use of modified atmospheres, and the application of exogenous antioxidants such as ascorbic acid and natural phenolic compounds. This approach aims to suppress ROS formation, maintain cell membrane integrity, and slow down the pericarp browning process during storage (Chen et al., 2014; Wang et al., 2025). A study by Sivakumar and Korsten (2010) showed that the combination of MAP and 1-Methylcyclopropene treatment was effective in suppressing PPO and POD activities, as well as maintaining the color and quality of lychee fruit during storage.

In addition, storage in a controlled atmosphere (CA) with a certain combination of O_2 and CO_2 can suppress PPO and POD activities, as well as maintain the quality of lychee fruit during storage. According to Ali et al. (2016), a study of 'Gola' lychee fruit stored in CA at a temperature of 5±1°C and combined CA treatment (1% O_2 + 5% CO_2) showed a delay in pericarp browning, decreased PPO and POD enzyme activity, maintained antioxidant activity and biochemical characteristics and better organoleptic quality of lychee fruit for 35 days compared to without CA combination which only lasted up to 28 days in storage.

During storage, the activity of antioxidant enzymes often decreases, causing an imbalance between ROS production and their detoxification ability. The decrease in the activity of enzymes such as SOD, CAT, and ascorbate peroxidase (APX) accelerates lipid peroxidation, damages cell membranes, and increases cell permeability, which facilitates the interaction between oxidative enzymes such as PPO and phenolic substrates. As a result, browning occurs in the pericarp of lychee fruit (Zhang et al., 2005). Enzymatic antioxidants such as SOD, CAT, and APX play an important role in maintaining the redox balance in lychee fruit tissues during storage. SOD functions to convert O_2- into H_2O_2, which is then detoxified by CAT and APX into water and oxygen. The activity of these enzymes can reduce the accumulation of ROS, thereby inhibiting the oxidation of phenolic compounds which are the main cause of pericarp browning (Ali et al., 2018; Yun et al., 2021; Zhang et al., 2015, 2024).

Several post-harvest treatments have been shown to increase the activity of antioxidant enzymes and slow down browning. For example, treatment with ascorbic acid, low-temperature storage, and the use of MAP have been reported to

increase SOD and CAT activities, reduce ROS, and maintain the pericarp color of lychee fruit (Ali et al., 2016, 2018; Sivakumar & Korsten, 2010; Somboonkaew & Terry, 2010). This suggests that maintaining or increasing enzymatic antioxidant activity is an effective strategy to extend the shelf life of lychee fruit.

Anthocyanin Degradation

Anthocyanins, especially cyanidin-3-rutinoside, are the main flavonoid pigments that give the bright red color to the pericarp of lychee fruit and play an important role in determining the visual appeal and quality of the fruit (Huang et al., 2024). During storage, anthocyanin content tends to decrease due to oxidative degradation triggered by the activity of enzymes such as PPO and POD, as well as by ROS, which causes the color of the fruit pericarp to change from bright red to dull brown, thus reducing the commercial value of the fruit.

In addition to anthocyanins, total phenolic compounds also decreased during storage. Phenols function as natural antioxidants that protect cells from oxidative damage. However, during storage, these compounds undergo oxidation catalyzed by PPO and POD, producing o-quinone compounds that can polymerize into brown pigments, so that this phenolic degradation not only reduces the antioxidant potential of the fruit, but also exacerbates the discoloration of lychee fruit pericarp (Ali et al., 2016; Huang et al., 2024).

Several external factors, such as high temperature, low humidity, and oxygen exposure, can accelerate the degradation of anthocyanins and phenols. Water loss from the pericarp increases the permeability of cell membranes, accelerates the interaction between enzymes and substrates, and exacerbates oxidative damage. In addition, temperature fluctuations during storage can disrupt the enzymatic and non-enzymatic antioxidant defense systems, accelerating the destruction of phenolic compounds and pigments (Deng et al., 2018; Huang et al., 2024).

To maintain total anthocyanin and phenolic levels during storage, various strategies have been developed, such as storage at low temperatures, the use of MAP technology, and the application of exogenous antioxidants such as ascorbic acid and natural phenolic compounds. This strategy aims to suppress the activity of PPO and POD enzymes, slow down the formation of ROS, and maintain the color quality and nutritional value of lychee fruit (Sivakumar & Korsten, 2010; Somboonkaew & Terry, 2010).

ENVIRONMENTAL STRESS FACTORS DURING STORAGE

Storage temperature and relative humidity (RH) are two critical environmental factors that profoundly influence the postharvest quality of lychee fruit. Inappropriate combinations of temperature and RH, particularly high temperatures and low RH can accelerate pericarp browning due to physiological stress and elevated activity of browning-related enzymes. Thus, maintaining optimal storage conditions is essential for preserving the distinctive and appealing color of the lychee pericarp.

However, storing lychee fruit at excessively low temperatures, such as 0°C, while intended to suppress respiration and enzymatic activity, can induce chilling injury that compromises cellular integrity. Huang et al. (2024) reported that such low temperatures disrupt the lipid bilayer of cell membranes, leading to increased

membrane leakage, as indicated by the accumulation of malondialdehyde (MDA), a primary marker of lipid peroxidation. In addition, enhanced activity of the lipoxygenase (LOX) enzyme exacerbates oxidative damage to pericarp tissues. Paradoxically, cold stress also impairs the antioxidant defense system by reducing the activity of key enzymes such as SOD and CAT, which are responsible for detoxifying ROS. This reduction in antioxidant capacity contributes to the acceleration of pericarp browning, underscoring the importance of maintaining storage temperatures within an optimal range to avoid detrimental physiological stress.

Storing lychees at room temperature (27–32°C) under low relative humidity (65–70%) has been shown to be highly suboptimal for maintaining the physiological and biochemical stability of the fruit pericarp. These conditions rapidly accelerate pericarp browning within 1–2 days, primarily due to oxidative stress and the degradation of phenolic pigments, particularly anthocyanins which may decline by as much as 73% (Deng et al., 2018). The loss of these phenolic compounds not only leads to the fading of lychee's characteristic red color but also significantly reduces its antioxidant capacity, as evidenced by decreased oxygen radical absorbance capacity (ORAC) and cellular antioxidant activity (CAA) values (Ali et al., 2016; Sultan, 2014). This deterioration is further aggravated by the low endogenous antioxidant capacity of the tissue, which triggers increased activity of pro-browning enzymes such as PPO and POD (Huang et al., 2024; Xiao et al., 2019). These enzymes catalyze the oxidation of phenolic substrates into melanin-like compounds responsible for browning. Thus, storage at room temperature not only causes rapid visual deterioration but also reflects a redox imbalance in the pericarp tissue, ultimately resulting in significant loss of fruit quality and marketability.

Relative humidity (RH) also plays a crucial role in modulating the browning process of lychee pericarp during storage. Low RH conditions (50%) accelerate pericarp dehydration, inducing physiological stress and damaging cellular structures. Under such conditions, membrane permeability increases, allowing browning enzymes such as PPO to come into direct contact with phenolic substrates, thereby initiating oxidative reactions that form brown pigments (Kaewchana et al., 2006; Silvia et al., 2012). Concurrently, water loss promotes the degradation of phenolic compounds and anthocyanins, both of which are highly sensitive to shifts in internal moisture and pH. In particular, low RH causes the pericarp pH to rise from approximately 4.5 to 5.3, an unfavorable condition for anthocyanin stability thus accelerating pigment destabilization and exacerbating browning (Huang et al., 2024; Silvia et al., 2012). In contrast, storage under high RH (around 90%) helps maintain membrane integrity and biochemical stability, extending the shelf life of the fruit up to approximately 10 days. Overall, low RH systematically induces browning through a network of interrelated physiological, biochemical, and physical pathways.

The combination of high ambient temperature (27°C) and low RH creates highly unfavorable environmental conditions for maintaining the postharvest stability of lychee fruit. Elevated temperatures accelerate fruit respiration and metabolic rates, while low RH enhances transpiration and water loss, leading to rapid dehydration of the pericarp. These stress conditions increase cell membrane permeability and promote the leakage of phenolic compounds, thereby facilitating greater enzyme substrate interaction and initiating oxidative reactions. As a result, the activities of browning-related enzymes such as PPO and POD become more effective in

catalyzing the oxidation of phenolic substrates into melanin pigments responsible for browning (Huang et al., 2024; Jing et al., 2013; Silvia et al., 2012). In parallel, the decline in both enzymatic (e.g., SOD, CAT and non-enzymatic (e.g., phenolics, anthocyanins) antioxidant compounds, exacerbates the redox imbalance within the pericarp tissue (Huang et al., 2024; Xiao et al., 2019). Therefore, the synergistic effect of high temperature and low RH not only accelerates physical deterioration but also intensifies biochemical browning, resulting in a significant reduction in the aesthetic appearance and commercial value of lychee fruit.

STRATEGIES TO DELAY PERICARP BROWNING

Natural Bioactive Compounds

Alginate oligosaccharides

The use of alginate oligosaccharides (AOS) as a natural postharvest coating on lychee fruit has shown significant potential in maintaining fruit quality during storage. AOS, derived from the enzymatic degradation of alginate, a polysaccharide extracted from brown algae has been shown to be effective in inhibiting water loss, maintaining fruit firmness, and preventing browning of the lychee pericarp. By forming a physical barrier and modulating biochemical pathways in the fruit, AOS offers an environmentally friendly and sustainable approach to extend the shelf life and maintain lychee quality during distribution and marketing (Pillai et al., 2024).

AOS forms a semipermeable layer on the fruit surface, which acts as a barrier against water and gas loss. This layer reduces the rate of transpiration and respiration, thereby slowing down the process of fruit dehydration during storage. A study by Pillai et al. (2024) showed that lychees coated with AOS showed a significant decrease in water loss compared to uncoated fruits, which contributed to the extension of shelf life and reduction of drought damage. The firmness of lychee fruit tends to decrease during storage due to cell wall degradation and turgor loss. AOS helps maintain firmness by inhibiting the activity of enzymes involved in fruit softening, such as polygalacturonase and cellulase. AOS-coated lychees also showed higher firmness compared to the control during the storage period, indicating the effectiveness of AOS in maintaining fruit texture. Browning of lychee pericarp is caused by phenolic oxidation catalyzed by enzymes such as PPO and POD. In addition, AOS has antioxidant properties that can inhibit the activity of these enzymes, thereby reducing the rate of browning.

In addition to physical effects, AOS also affect molecular pathways in fruit. Studies on strawberries showed that postharvest treatment with AOS delayed the accumulation of abscisic acid (ABA) and suppressed the expression of ABA signaling-related genes, which contributed to the extension of shelf life and fruit quality (Bose et al., 2019). Although this study was conducted on strawberries, similar mechanisms may apply to lychees, given the similarities in the aging and browning processes of non-climacteric fruits. These results are related to other findings, namely that AOS treatment suppressed the degradation and expression of cell wall degradation genes, suppressed the decrease in the number of anthocyanins, total phenols, flavonoids, in addition to delaying the decrease in hardness, total soluble solids (TSS), titratable acidity (TA), and vitamin C.

Pyrogallol

Application of pyrogallol as a post-harvest treatment on lychee fruit has been proven effective in delaying pericarp browning during storage. Pyrogallol works by inhibiting the activity of oxidative enzymes such as PPO and POD, which play a role in the oxidation of phenolic compounds and the degradation of anthocyanins, the main pigments that give the red color to lychee fruit pericarp. By reducing the activity of these enzymes, pyrogallol helps maintain anthocyanin and phenolic content, and increases the activity of phenylalanine ammonia-lyase (PAL), a key enzyme in the biosynthesis of phenolic compounds. In addition, pyrogallol also maintains cell membrane integrity, reduces membrane permeability, and reduces the accumulation of MDA, an indicator of membrane oxidative damage, thereby slowing pericarp browning and extending the shelf life of lychee fruit.

Research by Jing et al. (2013) showed that 1mM pyrogallol treatment of lychee fruit significantly reduced pericarp browning and delayed decay at both 4°C and 25°C storage temperatures. This treatment also reduced the respiration rate and the activities of PPO and POD enzymes, and delayed the loss of membrane permeability. Pyrogallol increased PAL activity, delayed the decline in anthocyanin and phenolic contents, and maintained high 2,2-diphenyl-1-picrylhydrazyl (DPPH) radical scavenging activity and reducing power. Pyrogallol-treated fruit also showed higher concentrations of four phenolic compounds: procyanidin B1, (+)-catechin, (−)-epicatechin, and (−)-epicatechin-3-gallate, all of which are antioxidants and act as free radical scavengers. Anthocyanins are responsible for the red color of lychee fruit pericarp and are susceptible to degradation during storage, leading to browning (Zhang et al., 2018). PAL is an important enzyme in the biosynthesis of phenolic compounds, including anthocyanins. Increased PAL activity may lead to higher synthesis of these compounds, which contributes to the antioxidant capacity of the fruit.

Melatonin

Melatonin, as an endogenous molecule with antioxidant properties, has been shown to be effective in extending the shelf life and maintaining the postharvest quality of lychee fruit by reducing pericarp browning. This effect is mainly mediated through increasing the activities of antioxidant enzymes such as SOD and CAT, as well as reducing the production of ROS. Exogenous melatonin increases the activities of key antioxidant enzymes, including SOD and CAT. SOD catalyzes the dismutation of superoxide radicals to hydrogen peroxide, which is then decomposed by CAT to water and oxygen, thereby reducing the accumulation of damaging ROS. In a study by Zhang et al. (2018), application of 0.4mM melatonin to 'Ziniangxi' lychee fruit significantly increased the activities of SOD and CAT during storage, which contributed to the delay of pericarp browning.

Exogenous melatonin application to postharvest lychee fruit has been shown to be effective in inhibiting pericarp browning during cold storage through various biochemical and molecular mechanisms. Melatonin plays a role in reducing the accumulation of ROS such as superoxide radicals and hydrogen peroxide, which are the main causes of oxidative stress in fruit tissues. A study by Marak et al. (2024) showed that melatonin treatment with concentrations of 0.1; 0.25; and 0.5mM on lychee fruit stored at cold temperatures significantly reduced the level of membrane

leakage and accumulation of MDA, an indicator of membrane lipid damage due to oxidative stress. Exogenous application of melatonin contributes to maintaining the integrity of cell membranes and suppressing browning in fruits. Treatment with a concentration of 0.5mM melatonin has been shown to be effective in minimizing weight loss, hazard levels, and pericarp color changes. In addition, this treatment is able to maintain the stability of total soluble solids (TSS), acidity, total sugar, ascorbic acid, anthocyanins, antioxidant compounds, and phenolics during cold storage. Melatonin also suppresses the activity of PPO and POD enzymes in the pericarp tissue which are responsible for the oxidation of phenolic compounds, the main trigger for browning. In addition, this compound affects gene expression by decreasing the expression of LcPPO and LcPOD, and increasing the expression of LcDFR and LcUFGT genes involved in anthocyanin biosynthesis, thus maintaining the bright red color of the pericarp. Thanks to its antioxidant activity, melatonin application is able to maintain the taste, nutritional value, and color of lychee pericarp during cold storage for up to 30 days.

Ethylene Inhibitor with 1-Methylcyclopropene

1-Methylcyclopropene (1-MCP) is a synthetic compound that functions as an ethylene inhibitor through a competitive binding mechanism to the ethylene receptor, thereby inhibiting ethylene signal transduction that plays a role in the aging and senescence process in fruit. In lychee fruit, the application of 1-MCP has been shown to be effective in slowing the aging process, maintaining color stability, and preventing browning in the pericarp during storage. By inhibiting ethylene biosynthesis and action, 1-MCP prevents the activation of enzymes associated with tissue degradation. Sivakumar and Korsten (2010) reported that 1-MCP treatment of lychee fruit cultivar 'McLean's Red' significantly reduced the activity of PPO and POD enzymes, maintained cell membrane integrity, and maintained anthocyanin content and bright red color of the pericarp.

A study by Hossain et al. (2021) showed that 1-MCP treatment combined with high-density plastic (HDPE) packaging was able to maintain higher anthocyanin, total phenol, and flavonoid content compared to other treatments for 30 days of storage. This shows that 1-MCP is effective in slowing down the degradation of phenolic compounds that act as natural antioxidants.

In addition, 1-MCP increases the activity of antioxidant enzymes such as SOD and CAT, which function to eliminate ROS. ROS can damage cell membranes and cause ion leakage that triggers the activity of enzymes that cause browning. By suppressing the accumulation of ROS, 1-MCP plays a role in maintaining the stability of cell membranes and suppressing browning reactions. Qu et al. (2006) also showed that the application of 1-MCP significantly reduced the browning index and decreased the activities of PPO and POD, all of which contributed to the prevention of pericarp browning during lychee fruit storage.

Hormonal and Signaling Molecules

Abscisic acid

Exogenous application of abscisic acid (ABA) to lychee fruit has been shown to be effective in reducing pericarp browning symptoms during storage through

various biochemical and molecular mechanisms that affect enzyme activity, pigment stability, and cell membrane integrity. One way that ABA works is by reducing the activity of oxidative enzymes such as PPO and POD, which are known to play a role in phenol oxidation and anthocyanin degradation, thereby suppressing the formation of brown color in the pericarp. In addition, ABA also increases the activity of antioxidant enzymes such as SOD and CAT, which function to eliminate ROS and protect membrane structures from oxidative damage. This mechanism also maintains the integrity of cell membranes against lipid peroxidation and reduces the triggers for browning enzyme activation.

Specifically, the role of ABA in inhibiting browning is also associated with its effects on LOX and anthocyanase (ANT) enzymes, which are involved in lipid peroxidation and anthocyanin degradation, respectively. The activities of these two enzymes usually increase during storage and contribute to accelerated color changes and fruit quality decline (Wang et al., 2010). ABA, both endogenous and exogenous, has been shown to slow down the decline in anthocyanin content during storage by increasing the expression of anthocyanin biosynthesis genes such as LcCHS, LcDFR, and LcUFGT, and activating the transcription factor LcMYB1, which directly increases the accumulation and stability of anthocyanins in lychee pericarp (Hu et al., 2019).

Although specific studies on the effect of ABA on LOX and ANT activities in lychee fruit are still limited, several studies on other horticultural commodities support the potential regulation of ABA on enzymes related to oxidative stress and pigment degradation. For example, Jiang and Joyce (2003) reported that ABA application to strawberries can reduce the activity of PAL, an enzyme involved in the biosynthesis of phenolic compounds, which can also affect pigment stability and oxidative enzyme activity. Further support comes from studies on pineapple fruit, where ABA application and ABA indigenous have been shown to reduce internal browning symptoms during cold storage and reduce the content of phenolic compounds which are the main substrates for PPO and POD enzymatic reactions (Chandra et al., 2023a, 2023b, 2023c; Liu et al., 2017; Zhang et al., 2015, 2016). These findings reinforce the relevance of further studies on the correlation between exogenous ABA application and inhibition of lychee fruit pericarp browning, especially through modulation of PAL activity and availability of phenolic compounds during storage.

Methyl jasmonate

One compound that shows strong potential for maintaining postharvest quality is methyl jasmonate (MeJA), especially when applied through vacuum infiltration to ensure effective penetration into fruit tissues. The use of MeJA via vacuum infiltration has emerged as a promising innovative approach. Deshi et al. (2021) demonstrated that applying 2mM MeJA at 0°C and at room temperature significantly reduced the browning index, extended shelf life by up to 16 days, and preserved fruit weight, antioxidant capacity, total phenolic content, and anthocyanin levels.

The efficacy of MeJA in suppressing browning is attributed to its ability to regulate the fruit's physiological and biochemical defense systems. MeJA functions as a jasmonate signaling molecule that activates antioxidant responses

and reinforces cell structure. Its application has been shown to suppress the production of reactive oxygen species (ROS), which typically increase under cold stress and prolonged storage. MeJA also reduces cell membrane permeability and MDA accumulation, a key marker of lipid peroxidation (Deshi et al., 2021). Moreover, it decreases the activity of browning enzymes such as PPO and POD, which catalyze the oxidation of phenolic compounds to melanin in the pericarp. Conversely, MeJA enhances the activity of phenylalanine ammonia-lyase (PAL), a crucial enzyme in the biosynthesis of phenolics and anthocyanins, thereby supporting the maintenance of lychee's natural red pericarp color.

Further research by Deshi et al. (2022) reinforced these findings, revealing that the effects of MeJA are both systemic and synergistic strengthening cellular defense mechanisms and effectively delaying browning without leaving toxic residues. However, the effectiveness of MeJA is highly dependent on dosage, storage temperature, and the lychee cultivar used. Excessive concentrations may induce oxidative stress, while suboptimal doses may not provide adequate protection. Therefore, the application of MeJA in supply chain systems must be specifically tailored to avoid undesirable effects and should involve standardized protocols based on cultivar characteristics and environmental conditions.

Salicylic acid

Salicylic acid (SA) shows potential in maintaining the quality of lychee fruit. Kaur et al. (2014) reported that the combination of 0.5% salicylic acid treatment with sulfur dioxide (SO_2) fumigation and modified atmosphere (MAP) packaging was able to reduce weight loss, maintain firmness, reduce browning index, and maintain total soluble solids (TSS), acidity, ascorbic acid, color, and anthocyanin content of lychee fruit cv. 'Culcuttia'. This treatment also effectively regulates the atmosphere in the packaging by reducing oxygen levels and increasing carbon dioxide levels, thereby extending the shelf life up to 21 days compared to the control of only 7 days.

Calcium-Induced Structural Integrity

An important strategy for inhibiting postharvest browning of lychee pericarp involves the use of calcium, particularly in the form of calcium chloride ($CaCl_2$), which has been shown to enhance tissue firmness and stabilize cell membrane integrity. Numerous international studies have investigated the efficacy of $CaCl_2$ in preserving the physical and biochemical quality of fruits during storage, with particular emphasis on its ability to reduce the activity of browning-associated enzymes. For example, Guo et al. (2023) evaluated the effect of vacuum infiltration treatment using $CaCl_2$ (5g L^{-1} for 5mins) on the postharvest quality of lychee stored at ambient temperature. The treatment significantly increased the levels of Ca^{2+} ions and cellulose, while decreasing soluble pectin content and the activities of cell wall-degrading enzymes, including polygalacturonase, β-galactosidase, and cellulase.

As a result, pericarp browning, pulp softening, and disease incidence were markedly delayed, confirming the effectiveness of $CaCl_2$ in maintaining tissue integrity and mitigating browning. Supporting this finding, (Fahima et al., 2019) analyzed lychee pericarps from cytokinin-treated cultivars and observed that

higher endogenous Ca^{2+} concentrations were associated with denser cell structures and delayed browning, although $CaCl_2$ was not directly applied. This reinforces the hypothesis that intrinsic calcium plays a mechanical role in maintaining cellular structure and suppressing damage-induced browning during storage. Furthermore, studies by (Ali et al., 2018, 2021) on various fruits, including lychee and pear, demonstrated that increasing internal Ca^{2+} levels either through endogenous accumulation or exogenous application strengthens cell walls, preserves membrane integrity, and reduces the browning index during storage. Although not all studies specifically addressed $CaCl_2$ application to lychee, their consistent correlation between calcium levels, cellular structure, and browning supports the broader relevance of this approach.

Chitosan-Based Edible Coating

Chitosan coating has been shown to be effective in inhibiting pericarp browning of lychee fruit during storage with a working mechanism involving inhibition of oxidative enzyme activity, protection of anthocyanin pigments, and maintenance of cell integrity. Chitosan forms a semipermeable layer on the fruit surface that can reduce oxygen permeability, thereby inhibiting oxidative reactions catalyzed by PPO and POD enzymes. Inhibition of the activity of these two enzymes directly contributes to preventing pericarp browning. A study by Petriccione et al. (2015) on strawberries showed that chitosan coating significantly reduced PPO and POD activity during cold storage, while a study by Adiletta et al. (2018) on loquats supported similar findings by showing decreased PPO and POD activity and decreased MDA levels, an indicator compound of membrane damage due to lipid peroxidation.

In addition to inhibiting oxidative enzyme activity, chitosan coating also plays a role in maintaining anthocyanin content. Chitosan coating can slow down the decline in anthocyanin content by inhibiting the activity of enzymes involved in the degradation of these pigments (Adiletta et al., 2021). According to Romanazzi et al. (2018) in their study stated that chitosan coating on various fruits, including lychees, consistently showed a decrease in anthocyanin degradation during storage, which helped maintain the quality and color of the fruit. Additional support comes from research by Yang et al. (2023), which showed that chitosan coating formulated with citric acid and pomelo extract not only reduced pericarp browning and fungal decay in lychees stored in the cold, but also extended their shelf life. These findings were confirmed by Chandra et al. (2023b), who reported that chitosan coating was also able to reduce internal browning symptoms in pineapple flesh, indicating the broad effectiveness of chitosan as a protective agent in maintaining fruit quality during storage.

Organic Acids and Antioxidant Dips

Various types of organic acids have been studied to inhibit lychee pericarp browning during cold storage, with results showing different effectiveness depending on the type and concentration of acid used and the method of application. Nanglia et al. (2022) evaluated the use of hydrochloric acid (Hcl), citric acid, and ascorbic acid in combination with shellac wax coating on lychee fruit

stored at 2–3°C with 90–95% relative humidity. Among the various treatments, the combination of 0.5 MHCl and shellac proved to be the most effective in extending the shelf life up to 14 days, with minimal physiological weight loss, highest firmness, and lowest decay. This treatment also showed the lowest browning index and the lowest PPO, POD, and PAL enzyme activities, while maintaining maximum bioactive compounds, thus overall showing the best ability to maintain the quality of lychee pericarp and flesh during storage.

Another study by Shafique et al. (2016) highlighted the effectiveness of 2mM oxalic acid in inhibiting pericarp browning of lychee cv. "Gola" during 28 days of cold storage. This treatment not only reduced weight loss and delayed browning, but also maintained anthocyanin content and increased the activity of antioxidant enzymes such as SOD and CAT. In addition, the total phenolic content and antioxidant capacity in the pericarp and fruit flesh were also higher than the control, while PPO and POD activities decreased significantly. The effectiveness of oxalic acid in maintaining fruit quality has also been proven in pomegranate by Sayyari et al. (2010), which showed that oxalic acid treatment, especially at a concentration of 6mM, was able to reduce chilling injury symptoms, maintain phenolic and ascorbic acid content, and increase antioxidant activity during storage. These findings indicate that oxalic acid has the potential as a postharvest treatment that is not only effective for lychee, but also relevant for other horticultural commodities that are sensitive to chilling.

Overall, the use of organic acids such as HCl, ascorbic acid, and oxalic acid, either singly or in combination with storage technologies such as coating or MAP, showed significant effectiveness in suppressing lychee pericarp browning. This effectiveness is generally achieved through decreasing the activity of oxidative enzymes (PPO, POD, and PAL), increasing antioxidants, and stabilizing pigments such as anthocyanins which are the main indicators of visual quality of the fruit during storage.

Modified/Controlled Atmospheres, Temperature, and Moisture Management

Managing the storage environment is a critical factor in preserving the postharvest quality of lychee fruit, particularly in preventing pericarp browning, which is a primary indicator of visual deterioration. Key environmental parameters, such as storage temperature, RH, and atmospheric composition, play a crucial role in influencing the stability of phenolic compounds, the integrity of cellular structures, and the activity of browning related enzymes. Therefore, the optimal regulation of these factors is essential for extending shelf life and maintaining the commercial quality of lychee fruit.

Huang et al. (2024) demonstrated that storage at optimal low temperatures (3–5°C) effectively delays pericarp browning by maintaining membrane integrity and reducing respiration rates, allowing the fruit to remain visually acceptable for up to 10–20 days. However, a significant limitation of this approach arises when the fruit is transferred back to room temperature; a rapid increase in the activities of LOX and phospholipase D, along with elevated membrane leakage, leads to an accelerated browning process. These findings indicate that low temperature storage alone is insufficient without careful management of temperature transitions and continuous protection of membrane structure.

Storage at low temperatures combined with high relative humidity has

consistently been shown to suppress pericarp browning and extend the visual shelf life of lychee fruit. Several studies have reported that storage at approximately 4°C with RH levels above 90% significantly delays pigment degradation, preserves phenolic compound stability, and inhibits the activity of browning enzymes such as PPO and POD. For example, Wang et al. (2014) observed that lychees stored at 4°C maintained a low browning index even after 20 days, whereas fruit stored at room temperature exhibited complete browning within just five days. Similarly, Xiao et al. (2019) reported that cold storage combined with a humidification system (RH~95%) preserved pericarp color and prevented visible browning for over 25 days.

In addition to temperature, maintaining high RH in the storage environment plays a vital role in minimizing water loss from pericarp tissues, which is directly associated with the preservation of cell membrane stability. Kaewchana et al. (2006) observed that lychee fruit stored at 90%RH exhibited minimal browning for up to 10 days, whereas fruit stored at 50%RH showed significant browning within just three days. Supporting these findings, Jiang et al. (1999) reported that high RH helps maintain anthocyanin content and reduces the activity of PPO, thereby slowing enzymatic browning. Consequently, cold storage at approximately 4°C in combination with high RH (>90%) is strongly recommended to preserve the visual quality and marketability of lychee fruit for at least 7–10 days postharvest.

The combined use of low temperature and high RH has been widely demonstrated to be effective in suppressing pericarp browning and extending the visual shelf life of lychee fruit. Multiple studies have confirmed that storage at approximately 4°C with RH levels above 90% significantly delays pigment degradation, maintains the stability of phenolic compounds, and inhibits the activity of browning-related enzymes such as PPO and POD. For instance, Wang et al. (2014) reported that lychees stored at 4°C had a very low browning index even after 20 days, whereas fruit stored at room temperature became fully browned within five days. Similarly, Xiao et al. (2019) found that lychees stored in a cold chamber equipped with a humidification system (RH~95%) retained pericarp color and exhibited minimal browning for more than 25 days.

To overcome the limitations of conventional cold storage, controlled atmosphere storage (CAS), typically employing low oxygen concentrations (1% O_2) and elevated carbon dioxide levels (5% CO_2), offers a more stable and effective alternative. This method not only suppresses the activities of browning enzymes such as PPO and POD, but also reduces the accumulation of MDA, a key indicator of membrane lipid peroxidation. Furthermore, CAS has been shown to preserve anthocyanin content, total phenolic compounds, ascorbic acid levels, and the activity of essential antioxidant enzymes, including SOD and CAT (Ali et al., 2016). The principal advantage of CAS lies in its ability to slow oxidative metabolism without inducing anaerobic stress, thereby creating optimal physiological conditions for maintaining lychee fruit quality during storage.

In addition, modified atmosphere packaging (MAP) with a gas composition of 20% O_2, 20% CO_2, and 60% N_2, as examined by Passafiume et al. (2023), has also proven effective in minimizing water loss and preserving tissue firmness by maintaining high internal humidity within the packaging environment. Unlike CAS, which requires specialized storage infrastructure, MAP presents a more practical solution that still effectively inhibits pericarp browning. Its protective effect results

from a combination of reduced browning enzyme activity and delayed dehydration, which together preserve pericarp structural integrity and limit enzyme substrate interactions responsible for phenolic oxidation.

CONCLUSION

The acceleration of discoloration in the lychee pericarp is induced by storage-related environmental stress, particularly when the temperature deviates from the optimal range of 3–5°C and relative humidity (RH) falls below 90%. Such stress leads to damage of cell membranes, resulting in the generation of reactive oxygen species (ROS) and the subsequent signaling of secondary metabolite (phenolic) synthesis. Pericarp browning occurs as ROS degrade anthocyanin pigments (the red color of the pericarp) and promote the oxidation of phenolic compounds, catalyzed by polyphenol oxidase (PPO), producing brown pigments. Several strategies have been proposed to delay lychee pericarp browning during the postharvest period, including the application of natural bioactive compounds (e.g., alginate oligosaccharides, pyrogallol, melatonin), ethylene inhibition using 1-methylcyclopropene, hormonal and signaling regulators such as abscisic acid (ABA), methyl jasmonate (MeJA), and salicylic acid (SA), calcium-mediated enhancement of structural integrity, chitosan-based edible coatings, and organic acid or antioxidant dips (e.g., HCl, ascorbic acid, oxalic acid). In addition, storage under controlled environmental conditions, specifically at 3–5°C with 90–95% RH, is critical to maintain pericarp color and delay browning.

Acknowledgment

Many thanks are expressed to the University of Lampung and especially to Prof. Dr. Ir. Soesiladi Esti Widodo, M.Sc. for sharing his knowledge and guidance.

Author Contributions

DC carries out all processes starting from creating a framework, collecting literature materials, to writing the manuscript.

Funding Source

This study was financed by an Australian Development Scholarship to PSM.

Availability of Data and Materials

Data and materials generated in this article and its supplementary files, and/or available from the corresponding author upon request.

Ethical Considerations

This study did not involve human participants or animals. Therefore, ethical approval was not required.

Competing Interest

I declare no conflict of interest.

References

Adiletta, G., Di Matteo, M., & Petriccione, M. (2021). Multifunctional role of chitosan edible coatings on antioxidant systems in fruit crops: A review. *International Journal of Molecular Sciences, 22*(5), 2633. https://doi.org/10.3390/ijms22052633

Adiletta, G., Pasquariello, M. S., Zampella, L., Mastrobuoni, F., Scortichini, M., & Petriccione, M. (2018). Chitosan coating: A postharvest treatment to delay oxidative stress in loquat fruits during cold storage. *Agronomy, 8*(4), 54. https://doi.org/10.3390/agronomy8040054

Ali, I., Abbasi, N. A., & Hafiz, I. (2021). Application of calcium chloride at different phenological stages alleviates chilling injury and delays climacteric ripening in peach fruit during low-temperature storage. *International Journal of Fruit Science, 21*(1), 1040–1058. https://doi.org/10.1080/15538362.2021.1975607

Ali, S., Khan, A. S., Malik, A. U., Nawaz, A., & Shahid, M. (2018). Postharvest application of antibrowning chemicals modulates oxidative stress and delays pericarp browning of controlled atmosphere–stored litchi fruit. *Journal of Food Biochemistry, 43*(3), e12746. https://doi.org/10.1111/jfbc.12746

Ali, S., Khan, A. S., Malik, A. U., & Shahid, M. (2016). Effect of controlled atmosphere storage on pericarp browning, bioactive compounds, and antioxidant enzymes of litchi fruits. *Food Chemistry, 206*, 18–29. https://doi.org/10.1016/j.foodchecm.2016.03.021

Bolaños, E. N. A., Velázquez, R. C., Cárdenaz, A. V., Santamaría, I. R., Vera, N. G., Fuentes, A. D. H., & Silva, E. M. (2010). Effect of storage temperature and time on quality in minimally processed litchi fruit (*Litchi chinensis* Sonn.). *Journal of Food Quality, 33*(3), 269–403. https://doi.org/10.1111/j.1745-4557.2010.00324x

Bose, S. K., Howlader, P., Jia, X., Wang, W., & Yin, H. (2019). Alginate oligosaccharide postharvest treatment preserves fruit quality and increases storage life via abscisic acid signaling in strawberry. *Food Chemistry, 283*, 665–674. https://doi.org/10.1016/j.foodchem.2019.01.060

Chandra, D., Widodo, S. E., Kamal, M., & Waluyo, S. (2023a). Effect of storage temperature transfer on the internal browning and other fruit qualities of GP3 and MD2 pineapple clones after postharvest applications of ABA, chitosan, and decrowning. *IOP Conference Series: Earth and Environmental Science, 1230*(1), 012065. https://doi.org/10.1088/1755-1315/1230/1/012065

Chandra, D., Widodo, S. E., Kamal, M., & Waluyo, S. (2023b). Pineapple responses to postharvest applications of ABA, chitosan, and decrowning on the severity of internal browning and other fruit qualities. *Acta Innovations, 47*, 64–72. https://doi.org/10.32933/ActaInnovations.47.6

Chandra, D., Widodo, S. E., Kamal, M., & Waluyo, S. (2023c). Postharvest treatments influenced the incidence of internal browning, phenol, ABA, and GA contents of two pineapple clones. *Acta Innovations, 50* (Special Issue). https://doi.org/10.32933/ActaInnovations.50.7

Chen, W., Zhang, Z., Shen, Y., Duan, X., & Jiang, Y. (2014). Effect of tea polyphenols on lipid peroxidation and antioxidant activity of litchi (*Litchi chinensis* Sonn.) fruit during cold storage. *Molecules, 19*(10), 16837–16850. https://doi.org/10.

.3390/molecules191016837
Deng, M., Deng, Y., Dong, L., Ma, Y., Liu, L., Huang, F., Wei, Z., Zhang, Y., Zhang, M., & Zhang, R. (2018). Effect of storage conditions on phenolic profiles and antioxidant activity of *litchi* pericarp. *Molecules, 23*(9), 2276. https://doi.org/10.3390/molecules23092276
Deshi, V., Homa, F., Ghatak, A., Aftab, M. A., Mir, H., Ozturk, B., & Siddiqui, M. W. (2022). Exogenous methyl jasmonate modulates antioxidant activities and delays pericarp browning in litchi. *Physiology and Molecular Biology of Plants, 28*(8), 1561–1569. https://doi.org/10.1007/s12298-022-01230-3
Deshi, V., Homa, F., Tokala, V. Y., Mir, H., Aftab, M. A., & Siddiqui, M. W. (2021). Regulation of pericarp browning in cold-stored litchi fruit using methyl jasmonate. *Journal of King Saud University – Science, 33*(5), 101445. https://doi.org/10.1016/j.jksus.2021.101445
Fahima, A., Levinkron, S., Maytal, Y., Hugger, A., Lax, I., Huang, X., Eyal, Y., Lichter, A., Goren, M., Stern, R. A., & Harpaz-Saad, S. (2019). Cytokinin treatment modifies litchi fruit pericarp anatomy leading to reduced susceptibility to postharvest pericarp browning. *Plant Science, 283*, 41–50. https://doi.org/10.1016/j.plantsci.2019.02.006
Fang, F., Zhang, Z.-Q., Zhang, X.-L., Wu, Z.-X., Yin, H.-F., & Pang, X.-Q. (2013). Reduction in activity/gene expression of anthocyanin degradation enzymes in lychee pericarp is responsible for the color protection of the fruit by heat and acid treatment. *Journal of Integrative Agriculture, 12*(9), 1694–1702. https://doi.org/10.1016/S2095-3119(13)60410-4
Guo, X., Li, Q., Luo, T., Han, D., Zhu, D., & Wu, Z. (2023). Postharvest calcium chloride treatment strengthens cell wall structure to maintain litchi fruit quality. *Foods, 12*(13), 2478. https://doi.org/10.3390/foods12132478
Hossain, M. S., Ramachandraiah, K., Hasan, R., Chowdhury, R. I., Kanan, K. A., Ahmed, S., Ali, M. A., Islam, M.T., & Ahmed, M. (2021). Application of oxalic acid and 1-methylcyclopropane (1-MCP) with low- and high-density polyethylene on postharvest storage of litchi fruit. *Sustainability, 13*(7), 3703. https://doi.org/10.3390/su13073703
Hu, B., Lai, B., Wang, D., Li, J., Chen, L., Qin, Y., Wang, H., Qin, Y., Hu, G., & Zhao, J. (2019). Three LcABFs are involved in the regulation of chlorophyll degradation and anthocyanin biosynthesis during fruit ripening in *Litchi chinensis*. *Plant and Cell Physiology, 60*(2), 448–461. https://doi.org/10.1093.pcp/pcy219
Huang, C. C., Paull, R. E., & Wang, T. T. (2024). Litchi postharvest physiology and handling. *Crop Science, 64*(4), 2014–2063. John Wiley & Sons, Inc. https://doi.org/10.1002/csc2.21274
Huang, H., Wang, L., Bi, F., & Xiang, X. (2022). Combined application of malic acid and lycopene maintains content of phenols, antioxidant activity, and membrane integrity to delay the pericarp browning of litchi fruit during storage. *Frontiers in Nutrition, 9*, 849385. https://doi.org/10.3389/fnut.2022.849385
Huang, K., Fu, D., Jiang, Y., Liu, H., Shi, F., Wen, Y., Cai, C., Chen, J., Ou, L., & Yan, Q. (2023). Storability and linear regression models of pericarp browning and decay in fifty *litchi* (*Litchi chinensis* Sonn.) cultivars at room temperature storage. *Foods, 12*(8), 1725. https://doi.org/10.3390/foods12081725
Jamei, R., Heidari, R., Khara, J., & Zare, S. (2009). Hypoxia-induced changes in lipid peroxidation, membrane permeability, reactive oxygen species generation, and antioxidative response systems in *Zea mays* leaves. *Turkish Journal of*

Biology, 33(1), 45–52. https://doi.org/10.3906/biy-0807-14

Jiang, Y. (2000). Role of anthocyanins, polyphenol oxidase, and phenols in lychee pericarp browning. *Journal of the Science of Food and Agriculture, 80*(3), 305–310. https://doi.org10.1002/(SICI)1097-0010(200002)80:3<305::AID-JSFA518>3.0.CO;2-H

Jiang, Y., & Joyce, D. C. (2003). ABA effects on ethylene production, PAL activity, anthocyanin and phenolic contents of strawberry fruit. *Plant Growth Regulation, 39*(2), 171–174. https://doi.org/10.1023/A:1022539901044

Jiang, Y. M., & Fu, J. R. (1999). Postharvest browning of litchi fruit by water loss and its prevention by controlled atmosphere storage at high relative humidity. *LWT – Food Science and Technology, 32*(5), 278–283. https://doi.org/10.1006/fstl.1999.0546

Jing, G., Huang, H., Yang, B., Li, J., Zheng, X., & Jiang, Y. (2013). Effect of pyrogallol on the physiology and biochemistry of litchi fruit during storage. *Chemistry Central Journal, 7*(1), 19. https://doi.org/10.1186/1752-153X-7-19

Kaewchana, R., Nivomlao, W., & Kanlavanarat, S. (2006). Relative humidity influences pericarp browning of litchi cv. 'Hong Huay.' In A. C. Purvis *et al.* (Eds.), *Proceedings of the IVth International Conference on Managing Quality in Chains* (pp. 823–827). *Acta Horticulturae, 712.* International Society for Horticultural Science. https://doi.org/10.17660/ActaHortic.2006.712.97

Kaur, R., Kumar, A., Mahajan, B., & Javed, M. (2014). Control of pericarp browning and quality retention of litchi fruit by post-harvest treatments and modified atmosphere packaging. *International Journal of Agricultural Science and Research (IJASR), 4*(2), 38-50.

Khan, M. R., Huang, C., Durrani, Y., & Muhammad, A. (2021). Chemistry of enzymatic browning in longan fruit as a function of pericarp pH and dehydration, and its prevention by essential oil: An alternative approach to So_2 fumigation. *PeerJ, 9*, e11539. https://doi.org/10.7717/peerj.11539

Liu, J., He, C., Shen, F., Zhang, K., & Zhu, S. (2017). The crown plays an important role in maintaining quality of harvested pineapple. *Postharvest Biology and Technology, 124*, 18–24. https://doi.org/10.1016/j.postharvbio.2016.09.007

Marak, K. A., Mir, H., Siddiqui, M. W., Singh, P., Homa, F., & Alamri, S. (2024). Exogenous melatonin delays oxidative browning in litchi during cold storage by regulating biochemical attributes and gene expression. *Frontiers in Plant Science, 15*, 1402607. https://doi.org/10.3389/fpls.2024.1402607

Nanglia, S., Mahajan, B. V. C., Singh, N., Kapoor, S., Bhullar, K. S., Kaur, S., & Kumar, V. (2022). Combined effect of acids and shellac coating on pericarp browning, enzymatic activities, and biochemical attributes of litchi fruit during storage. *Journal of Food Processing and Preservation, 46*(5), e16535. https://doi.org/10.1111/jfpp.16535

Passafiume, R., Roppolo, P., Tinebra, I., Pirrone, A., Gaglio, R., Palazzolo, E., & Farina, V. (2023). Reduction of pericarp browning and microbial spoilage on litchi fruits in modified atmosphere packaging. *Horticulturae, 9*(6), 651. https://doi.org/10.3390/horticulturea9060651

Petriccione, M., Mastrobuoni, F., Pasquariello, M. S., Zampella, L., Nobis, E., Capriolo, G., & Scortichini, M. (2015). Effect of chitosan coating on the postharvest quality and antioxidant enzyme system response of strawberry fruit during cold storage. *Foods, 4*(4), 501–523. https://doi.org/10.3390/foods4040501

Pillai, A. R. S., Eapen, A. S., Zhang, W., & Roy, S. (2024). Polysaccharide-based edible biopolymer-based coatings for fruit preservation: A review. *Foods, 13*(10), 1529. https://doi.org/10.3390/foods13101529

Qu, H., Duan, X., Su, X., Liu, H., & Jiang, Y. (2006). Effects of anti-ethylene treatments on browning and energy metabolism of harvested litchi fruit. *Australian Journal of Experimental Agriculture, 46*(8), 1085–1090. https://doi.org/10.1071/EA04238

Romanazzi, G., Feliziani, E., & Sivakumar, D. (2018). Chitosan, a biopolymer with triple action on postharvest decay of fruit and vegetables: Eliciting, antimicrobial, and film-forming properties. *Frontiers in Microbiology, 9*, 2745. https://doi.org/10.3389/fmicb.2018.02745

Sayyari, M., Valero, D., Babalar, M., Kalantari, S., Zapata, P. J., & Serrano, M. (2010). Prestorage oxalic acid treatment maintained visual quality, bioactive compounds, and antioxidant potential of pomegranate after long-term storage at 2°C. *Journal of Agricultural and Food Chemistry. 58*(11), 6804–6808. https://doi.org/10.1021/jf100196h

Shafique, M., Khan, A. S., Malik, A. U., & Shahid, M. (2016). Exogenous application of oxalic acid delays pericarp browning and maintains fruit quality of litchi cv. "Gola." *Journal of Food Biochemistry, 40*(2), 170–179. https://doi.org/10.1111/jfbc.12207

Silvia, D. F. P., Lins, L. C. R., Cabrini, E. C., Brasileiro, B. G., & Salomão, L. C. C. (2012). Influence of the use of acids and films in post-harvest lychee conservation. *Revista Ceres, 59*(6), 745–750. https://doi.org/10.1590/s0034-737X2012000600002

Sivakumar, D., & Korsten, L. (2010). Fruit quality and physiological responses of litchi cultivar McLean's Red to 1-methylcyclopropene pre-treatment and controlled atmosphere storage conditions. *LWT – Food Science and Technology, 43*(6), 942–948. https://doi.org/10.1016/j.lwt.2010.02.001

Somboonkaew, N., & Terry, L. A. (2010). Effect of packaging films on individual anthocyanins in pericarp of imported non-acid treated litchi. *Acta Horticulturae, 876*, 193–200. https://doi.org/10.17660/ActaHortic.2010.876.21

Su, L. J., Zhang, J. H., Gomez, H., Murugan, R., Hong, X., Xu, D., Jiang, F., & Peng, Z. Y. (2019). Reactive oxygen species-induced lipid peroxidation in apoptosis, autophagy, and ferroptosis. *Oxidative Medicine and Cellular Longevity, 2019*, Article 5080843. https://doi.org/10.1155/2019/5080843

Sultan, M. Z. (2014). Effect of postharvest coating with gum arabic on pericarp browning and desiccation of litchi fruit (*Litchi chinensis* Sonn.) during storage. In R. Cronje (Ed.), *Proceedings of the Fourth IS on Lychee, Longan and Other Sapindaceae Fruits* (pp. 345–351). *Acta Horticulturae, 1029*. International Society for Horticultural Science (ISHS). https://doi.org/10.17660/ActaHortic.2014.1029.43

Wang, C., Zhang, S., Zhang, D., Li, F., Xie, L., Dai, T., & Jiang, Y. (2025). Gallic acid reduces pericarp browning of litchi fruit during storage. *Postharvest Biology and Technology, 219*, 113248. https://doi.org/10.1016/j.postharvbio.2024.113248

Wang, J. B., Wang, X. S., & Jin, Z. Q. (2010). Enzymatic browning of postharvest litchi: A review. *Acta Horticulturae, 863*, 613–618. https://doi.org/10.17660/ActaHortic.2010.863.86

Wang, J., Liu, B., Xiao, Q., Li, H., & Sun, J. (2014). Cloning and expression analysis of litchi (*Litchi chinensis* Sonn.) polyphenol oxidase gene and relationship with postharvest pericarp browning. *PLoS ONE, 9*(4),e93982. https://doi.org/10.1371/journal.pone.0093982

Xiao, L., Li, T., Jiang, G., John, A., Zhang, D., Jin, W., Duan, X., & Jiang, Y. (2019). Effects of dry fog humidification on pericarp browning and quality of litchi fruit stored at low temperature. *International Journal of Agricultural and Biological Engineering, 12*(4), 192–196. https://doi.org/10.25165/j.ijabe.20191204.4420

Yang, C., Lee, F.-W., Cheng, Y.-J., Chu, Y.-Y., Chen, C.-N., & Kuan, Y.-C. (2023). Chitosan coating formulated with citric acid and pomelo extract retards pericarp browning and fungal decay to extend shelf life of cold-stored lychee. *Scientia Horticulturae, 310*, 111735. https://doi.org/10.1016/j.scienta.2022.111735

Yun, Z., Gao, H., Chen, X., Chen, Z., Zhang, Z., Li, T., Qu, H., & Jiang, Y. (2021). Effects of hydrogen water treatment on antioxidant system of litchi fruit during the pericarp browning. *Food Chemistry, 336*, 127618. https://doi.org/10.1016/j.foodchem.2020.127618

Zhang, H. N., Li, W. C., Wang, H. C., Shi, S. Y., Shu, B., Liu, L. Q., Wei, Y. Z., & Xie, J. H. (2016). Transcriptome profiling of light-regulated anthocyanin biosynthesis in the pericarp of litchi. *Frontiers in Plant Science, 7*, 963. https://doi.org/10.3389/fpls.2016.00963

Zhang, J., Chen, X., Liu, Q., Li, M., Feng, S., Lin, M., Chen, Y., & Lin, H. (2024). Slightly acidic electrolyzed water treatment enhances the quality attributes and the storability of postharvest litchis through regulating the metabolism of reactive oxygen species. *Food Chemistry: X, 23*, 101644. https://doi.org/10.1016/j.fochx.2024.101644

Zhang, Y., Huber, D. J., Hu, M., Jiang, G., Gao, Z., Xu, X., Jiang, Y., & Zhang, Z. (2018). Delay of postharvest browning in litchi fruit by melatonin via the enhancing of antioxidative processes and oxidation repair. *Journal of Agricultural and Food Chemistry, 66*(28), 7475–7484. https://doi.org/10.1021/acs.jafc.8b01922

Zhang, Z., Huber, D. J., Qu, H., Yun, Z., Wang, H., Huang, Z., Huang, H., & Jiang, Y. (2015). Enzymatic browning and antioxidant activities in harvested litchi fruit as influenced by apple polyphenols. *Food Chemistry, 171*, 191–199. https://doi.org/10.1016/j.foodchem.2014.09.001

Zhang, Z., Pang, X., Ji, Z., & Jiang, Y. (2001). Role of anthocyanin degradation in litchi pericarp browning. *Food Chemistry, 75*(2), 217–221. https://doi.org/10.1016/S0308-8146(01)00202-3

Zhang, Z., Pang, X., Xuewu, D., Ji, Z., & Jiang, Y. (2005). Role of peroxidase in anthocyanin degradation in litchi fruit pericarp. *Food Chemistry, 90*(1–2), 47–52. https://doi.org/10.1016/j.foodchem.2004.03.023