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Original article

Regulation of pericarp browning in cold-stored litchi fruit using methyl jasmonate

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ABSTRACT

Postharvest litchi fruit is highly perishable and vulnerable to pericarp browning (PB), which affects marketability. In this study, the effect of vacuum infiltrated methyl jasmonate (0, 1, or 2 mM) on the quality of fresh cold stored (7 ± 1 °C and RH 85–90%) litchi. The MeJA effectively reduced PB and increased storage life up to 16 d by retaining higher fruit weight, soluble solids, acidity, and anthocyanin contents. MeJA (2 mM) treated fruits maintained higher levels of phenols, ascorbic acid and antioxidant activity. Moreover, the accumulation of reactive oxygen species (superoxide anion and hydrogen peroxide), membrane permeability, lipid peroxidation, and quinone was downregulated. The MeJA treatment also reduced the activity of PPO and POD as well as maintained higher PAL activity with delayed PB in litchi. Therefore, the MeJA infiltration (2 mM) could be suggested to enhance the storability of litchi fruits during cold storage.

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1. Introduction

Litchi (*Litchi chinensis* Sonn.) is a globally relished subtropical summer fruit crop, known for its refreshing pleasant flavour, rich succulent juicy arils, and numerous nutritional values (Deshi et al., 2020). Because of their non-climacteric behaviour, litchi fruit is picked at the fully ripe stage, immediately after attaining full bright red pericarp colour. In India, fruit comes to the market during the hot humid season (May - June), for a short period (4–6 weeks). This is the period when the market remains full of litchi fruit. However, these fruits are highly perishable and have a shelf life of 2–3 d at ambient condition. Fruits are vulnerable to desiccation and lose the red pericarp colour, drastically affecting cosmetic appeal, consumer acceptability and market value (Ali et al., 2016).

The browning of pericarp tissue is considered as one of the important postharvest hindrances for the full commercial exploitation of litchi fruit in different regions of the country. In case of any market delay, fruit can be stored for a relatively extended period, using cold storage at 7 °C and 90–95% RH, accompanied by different chemical treatments, packaging materials, and modified storage environments. However, there are limited cold storage infrastructure in developing countries like India and existing cold storage are mostly occupied by other fruit and vegetables. Currently, sulphur treatment is widely used to maintain fruit quality during long-distance transportation. Though sulphur treatment is readily available and relatively economical, it has several health concerns. Moreover, it is not permissible for export, if the residue of the sulphur exceeds 10 mg kg^{-1} (Ali et al., 2016).

Presently, food safety is globally considered as the most important aspect, right from the production to processing of products. Chemical measures are strictly prohibited in the postharvest handling system of fresh commodities, which warrants investigation of novel eco-safe, easy to apply, and effective technologies. Different non-sulphur-based approaches have been reported to maintain postharvest quality of litchi with delayed pericarp browning (PB) and decay incidence. Promising results have been observed using signalling molecules such as hydrogen sulphide (Deshi et al.,

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2020), melatonin (Zhang et al., 2018), methionine (Ali et al., 2018), polyamines (Jiang and Chen, 1995), nitric oxide (Barman et al., 2014) and oxalic acid (Shafique et al., 2016). Application of methyl jasmonate (MeJA) was also found to efficiently maintain the postharvest quality and extend shelf life of sweet orange (Rehman et al. 2018), apricot (Ezzat et al. 2017), cherry tomato (Liu et al. 2018), medlar (Ozturk et al., 2019), plum (Karaman et al., 2013; Kucuker and Ozturk, 2014) and apple (Aglar and Ozturk, 2018).

MeJA is a naturally occurring low molecular elicitor compound known to regulate many plants' developmental activities as well as response to different stresses. Pre-storage application of MeJA regulates different biochemical and physiological processes in the fruit, for instance, enhance antioxidant activity in blueberry (Wang et al., 2019); induce chilling tolerance in blood orange (Habibi et al., 2019); regulate ripening in strawberry fruit (Han et al., 2019) as well as alleviate browning in pineapple (Sangprayoon et al., 2019). Yang et al. (2011) reported that application of $1 \mu\text{g L}^{-1}$ MeJA extended cold storage life and reduced PB in litchi by effectively maintaining anthocyanin and (–)-epicatechin, delaying accumulation of substances similar to lipofuscin. These findings suggest that MeJA has the potential to be an eco-safe and natural option to positively modulate physiological processes in harvested products. Moreover, MeJA is considered to be safe for human health (Han et al., 2019). To date, studies on the effect of MeJA on litchi shelf-life extension have focused on anthocyanin degradation and enzymatic changes. Its ability to modulate the physiological processes linked to reactive oxygen species (ROS) production, antioxidative capacity, and shelf life of litchi during cold storage, has not been fully explored. Moreover, the majority of the studies involved MeJA treatment as dip, spray or fumigation, but there is no work reported on the effects of MeJA applied through vacuum filtration. The vacuum infiltration methods require relatively lesser time for application and are several folds efficient, compared to other methods of application (Wang et al., 2006; Tavallali and Zareiyani, 2018). The vacuum generated negative atmospheric pressure could decrease air spaces between the cells in the plant tissue and could ensure prompt absorption of treated compounds. Therefore, in the present study, the effects of vacuum infiltrated MeJA on minimizing PB, regulating metabolic qualitative changes and increasing shelf life of the cold stored litchi fruit were investigated.

2. Materials and methods

Commercially ripe (fully red, flattened smooth tubercles, TSS > 18%) litchi (cv. Purbi) fruits were hand-harvested from the orchard of Bihar Agricultural University Sabour ($25^{\circ} 14' \text{ N}$, $87^{\circ} 03' \text{ E}$) and brought to the laboratory within an hour. Blemished or diseased fruits were discarded, and good quality healthy fruits were washed thoroughly in running water and allowed to dry in the air. Each treatment was replicated thrice with 100 fruits per replication. The MeJA treatment was applied through the vacuum infiltration (0.01 MPa) method at concentrations 1 and 2 mM for 15 min following an additional 5 min in ambient condition (Deshi et al., 2020). Control fruits were treated with distilled water under the same conditions. Immediately after the treatment, the fruits were packed in corrugated cardboard boxes and stored in cold storage (at $7 \pm 1^{\circ} \text{ C}$ and RH 85–90%) until the appearance of mould growth or decay incidence or browning symptoms (>75%) on the fruit pericarp. Fruits were randomly sampled for different analyses at 2 d intervals during storage. Samples intended for enzymatic analyses were preserved in liquid nitrogen and kept at -40° C until analysis. All results were presented on a fresh weight basis.

2.1. Weight loss, pericarp browning (PB) and fruit decay

Fruits were weighed daily during storage and subsequently, the weight loss was calculated considering initial and final weight on each sampling day. PB was calculated using the browning intensity score explained by Kumar (2000). The number of fruit in each category was multiplied with the respective browning score and expressed in per cent (%). Decay loss was computed according to Ali et al. (2016) and expressed as a per cent (%).

2.2. Total soluble solids (TSS), titratable acidity (TA), and ascorbic acid (AA) content

The TSS (%) of juice extracted from litchi aril was estimated using a digital refractometer (Make-Hanna, Germany). To analyse TA, a diluted juice sample was titrated against NaOH solution (0.1 N) in the presence of phenolphthalein indicator. The recorded titre value was used for calculating TA and expressed as per cent (%) of citric acid (AOAC, 2000). For the determination of AA content, the fresh juice sample was diluted with 3% metaphosphoric acid (1:10) and 10 mL aliquot was titrated against the 2, 6-dichlorophenol indophenol dye till the appearance of pink colour. The results were expressed as mg L^{-1} (Jones and Hughes, 1983).

2.3. Anthocyanin content

For the extraction of anthocyanin, 1 g of pericarp was taken in 9 mL methanol-HCL solution (85:15 v/v), then homogenised and kept overnight. The extract was centrifuged at $6000 \times g$ and the optical density (OD) of the supernatant was recorded at 535 nm in a UV-Vis spectrophotometer (Dynamica HALO DB-20S, Australia). The total anthocyanin contents were calculated in terms of cyanidin 3- glucoside and expressed in mg kg^{-1} .

2.4. Total phenolics

Phenolic contents of pericarp were extracted in ethanol (80%) on a 1: 10 (w/v) ratio. The homogenised extract was centrifuged at $10000 \times g$ for 20 min at 20° C and the collected supernatant was used in total phenolics assay. The reagent mixture containing 100 μL pericarp extract, 2.9 mL deionized water, 0.5 mL Folin-Ciocalteu reagent, and 2.0 mL Na_2CO_3 (20%) was left for one hour at ambient conditions (Singleton et al., 1999). During incubation colourless mixture was turned to blue, after which the absorbance was recorded at 765 nm against a reagent blank using UV-Vis spectrophotometer (Dynamica HALO DB-20S, Australia). The readings were compared with the standard gallic acid calibration curve ($100\text{--}500 \text{ mg L}^{-1}$) and given as mg kg^{-1} GAE.

2.5. Quinone content

For the estimation of quinone content, 1 g of pericarp tissue was taken in 4 mL (70%) methanol and left overnight. Then, the extract was subjected to centrifugation at $12000 \times g$ for 20 min and optical density (OD) of supernatant was measured at 437 nm in a UV-vis spectrophotometer. The soluble quinone content was expressed as the absorbance per g (Degl'Innocenti et al., 2007).

2.6. Total antioxidant capacity

Total antioxidant capacity (TAC) was determined using the CUPRAC assay (Apak et al., 2008). 100 μL of the extracted sample (discussed in total phenol assay) and 1 mL each solution of copper (II) chloride, neocuproine, ammonium acetate buffer and distilled water were mixed and vortexed in a test tube. After 1 h, the absorption was recorded at 450 nm in a UV-vis spectrophotome-

ter, against a blank reagent. The results were expressed as mmol kg^{-1} Trolox.

2.7. Superoxide (O_2^-) production rate

To determine O_2^- production rate, 1 g pericarp tissue and 4 mL of potassium phosphate buffer (65 mM; pH 7.8) was homogenised and centrifuged at $5000 \times g$ for 10 min. 1 mL of supernatant was then mixed with 0.9 mL of potassium phosphate buffer (65 mM; pH 7.8), 0.1 mL hydroxylammonium chloride (10 mM) and the mixture was incubated for 20 min at 25 °C. Afterwards, sulphanic acid (17 mM) and α -naphthylamine (7 mM) were added and OD was read at 530 nm. The O_2^- production rate was calculated through a NaNO_2 standard curve and expressed as $\text{mmol kg}^{-1} \text{min}^{-1}$ (Zhao et al., 2008).

2.8. Hydrogen peroxide (H_2O_2) production rate

To determine H_2O_2 production rate, 1 g of pericarp tissue was taken in 10 mL trichloroacetic acid (0.1%; w/v) and centrifuged at $12000 \times g$ for 15 min. 1 mL of the supernatant was then added to 1 mL of potassium phosphate buffer (10 mM; pH 7.0) and 2 mL of potassium iodide (1 M). The OD of the mixture was observed at 390 nm. Readings were compared with the freshly prepared H_2O_2 standard curve to obtain the H_2O_2 concentration (Velikova et al., 2000).

2.9. Membrane leakage

For the estimation of membrane permeability, pericarp pieces were incubated in distilled water for 30 min at 25 °C and the initial conductivity of the solution was recorded using a digital conductivity meter. The same solution was then boiled for 15 min and after cooling another reading of conductivity was taken. The membrane leakage was expressed as a percentage (Ali et al., 2016).

2.10. Malondialdehyde (MDA) content

To assay the malondialdehyde (MDA) content, litchi pericarp (1 g) was homogenized in 15 mL of trichloroacetic acid (10%) and then centrifuged at $10,000 \times g$ for 20 min. Afterwards, 2 mL of each supernatant and 2-thiobarbituric acid (0.6%) was mixed, of which OD was observed at 600, 532, and 450 nm. The MDA contents were calculated and presented as $\mu\text{mol kg}^{-1}$ (Li, 2000).

2.11. Extraction of crude enzyme and determination of phenylalanine ammonia lyase (PAL), polyphenol oxidase (PPO), and peroxidase (POD) activities

To determine the activity of polyphenol oxidase (PPO) and peroxidase (POD), 1 g of pericarp tissues was mixed and homogenized with 20 mL of potassium phosphate buffer (50 mM; pH 7.0). The potassium phosphate buffer contained 1% (w/v) polyvinylpyrrolidone (insoluble). The extract was centrifuged at $17,000 \times g$ for 20 min at 4 °C. The supernatant was used as the crude enzyme (Chongchatuporn et al., 2013). For phenylalanine ammonia lyase (PAL) assay, 1 g of pericarp tissues was mixed and homogenized with 20 mL of sodium borate buffer (100 mM; pH 8.0). The sodium borate buffer contained 10% (w/v) polyvinyl poly-pyrrolidone (PVPP), 1 mM EDTA, and 50 mM β -mercaptoethanol. The extract was centrifuged at $17,000 \times g$ for 20 min at 4 °C and the supernatant was collected for PAL assay.

To determine the phenylalanine ammonia lyase (PAL) activity, 0.1 mL of enzyme extract was added in 2.9 mL of sodium borate buffer (0.1 M; pH 8.0) containing L-phenylalanine (3 mM). The mixture was then incubated at 37 °C for 60 min. The increasing

absorbance due to the formation of *trans*-cinnamate was recorded at 290 nm in a UV-vis spectrophotometer. One unit of enzyme activity was defined as the amount that caused an increase of 0.01 in the absorbance per hour. The enzyme activity was expressed as U g^{-1} protein (Duan et al., 2011).

Catechol (20 mM), prepared in sodium phosphate buffer (0.01 M; pH 6.8), was used as a substrate in PPO assay, while the peroxidase (POD) activity was recorded using guaiacol (4%) as substrate. The methods followed for the determination of PPO and POD were given elsewhere (Jiang et al., 2004; Jiang and Fu, 1999). One unit of enzyme activity is defined as the amount of enzyme causing a 0.1 (PPO) and 0.01 (POD) change in absorbance per min under standard assay conditions. The enzyme activity was expressed as U g^{-1} protein for both enzymes.

2.12. Statistical analysis

Factorial Completely Randomized Design (FCRD) was used to conduct the experiment. There were three treatments and each treatment was replicated thrice. The statistical significance ($p \leq 0.05$) of the difference between means was obtained using Duncan's Multiple Range Test (DMRT).

3. Results and discussion

3.1. Pericarp browning

The pericarp browning (PB) was 37.5 and 27.5% lower in the litchi fruit treated with 2 and 1 mM MeJA, respectively when compared to control on the final day of storage (Table 1). Reduction in PB primarily occurs with the maintenance of high antioxidant activity and reduced successive disintegration in the pericarp membrane (Jiang et al., 2004). Upon the harvest, the fruit pericarp is gradually desiccated and form micro-cracks on it. The membrane disintegration also occurs with the accumulation of phospholipase-D and ROS (Deshi et al., 2020). Similarly, the lipid peroxidation leads to de-compartmentation resulting in the interaction of oxidative enzymes (PPO and POD present in the cytosol) and substrates (epicatechin and anthocyanin in vacuole). All these changes thereby initiate enzymatic browning reactions and retard red colour in the pericarp (Yang et al., 2011; Barman et al., 2014). Therefore, lower PB in the litchi fruit treated with MeJA could be attributed to reduced moisture losses and enhanced total phenolic and anthocyanin levels in the pericarp (Table 2 and 3).

3.2. Decay incidence

Litchi is vulnerable to many fungal and bacterial diseases during storage, which commonly occurs through cracks or injury in the pericarp (Jiang et al., 2003). An early decay incidence was observed in the control fruit and it increased until the last day of storage (Table 1). The fruit treated with MeJA showed lower decay incidence and on the final day of storage, fruit treated with 2 and 1 mM MeJA, exhibited 76.3 and 65.78% lower decay incidence, respectively, than control fruit (Table 1). PB in litchi fruit has a strong correlation with decay incidence during storage (Deshi et al., 2020). The reduced incidence of decay in the fruit treated with MeJA could be related to the reduced levels of PB as well as enhanced levels of antioxidants and phenolics (Asghari and Aghdam, 2010).

3.3 wt. loss

Water loss, due to postharvest physiological activities such as respiration and transpiration, is the primary reason for the loss

Table 1
Effect of treatments on browning and decay incidence of litchi fruit during refrigerated storage.

Treatments	Browning (score)			Decay incidence (%)		
	Days in storage					
	12	14	16	12	14	16
MeJA (1 mM)	1.85 ^b	3.45 ^b	3.85 ^b	—	9.33 ^b	21.67 ^b
MeJA (2 mM)	1.5 ^b	2.75 ^c	3.25 ^b	—	9.33 ^b	15.00 ^c
Control	4.0 ^a	4.40 ^a	4.8 ^a	15.00	35.00 ^a	63.33 ^a

The value indicates the mean of three replicates. Different letters in the same column indicate significant differences at $p \leq 0.05$ (Duncan's Multiple Range Test).

Table 2
Effect of treatments on weight loss, total soluble solids, titratable acidity, and ascorbic acid contents of litchi fruit during refrigerated storage.

Treatments	Days in storage									
	0	2	4	6	8	10	12	14	16	
	Weight loss (%)									
MeJA (1 mM)	0.00	0.08 ^a	0.12 ^b	0.20 ^b	0.32 ^b	0.48 ^b	0.69 ^{ab}	0.88 ^b	1.13 ^b	
MeJA (2 mM)	0.00	0.09 ^a	0.12 ^b	0.19 ^b	0.31 ^b	0.43 ^b	0.58 ^b	0.85 ^b	1.09 ^b	
Control	0.00	0.10 ^a	0.20 ^a	0.24 ^a	0.51 ^a	0.79 ^a	0.98 ^a	1.22 ^a	1.53 ^a	
	Total soluble solids (%)									
MeJA (1 mM)	20.0	17.8 ^a	18.2 ^{ab}	15.8 ^b	21.0 ^a	17.9 ^a	17.1 ^a	19.0 ^a	17.1 ^{ab}	
MeJA (2 mM)	20.0	18.9 ^a	17.6 ^{ab}	17.0 ^{ab}	18.8 ^b	18.0 ^a	17.2 ^a	17.8 ^b	18.3 ^a	
Control	20.0	17.4 ^a	18.9 ^a	19.2 ^a	20.0 ^{ab}	19.3 ^a	17.8 ^a	17.7 ^b	16.8 ^b	
	Titratable acidity (%)									
MeJA (1 mM)	0.68	0.63 ^a	0.52 ^a	0.47 ^b	0.41 ^a	0.37 ^a	0.30 ^a	0.26 ^a	0.19 ^a	
MeJA (2 mM)	0.68	0.61 ^a	0.56 ^a	0.53 ^a	0.47 ^a	0.38 ^a	0.33 ^a	0.27 ^a	0.20 ^a	
Control	0.68	0.59 ^a	0.47 ^b	0.41 ^c	0.32 ^b	0.27 ^b	0.23 ^b	0.18 ^b	0.12 ^b	
	Ascorbic acid (mg L⁻¹)									
MeJA (1 mM)	312.5	280.0 ^a	254.2 ^b	226.8 ^a	194.5 ^a	160.0 ^a	128.9 ^a	99.2 ^{ab}	69.5 ^b	
MeJA (2 mM)	312.5	281.2 ^a	267.8 ^a	230.1 ^a	202.5 ^a	156.2 ^a	133.4 ^a	102.3 ^a	74.9 ^a	
Control	312.5	280.9 ^a	252.4 ^b	202.6 ^b	162.7 ^b	135.0 ^b	104.5 ^b	80.9 ^b	60.2 ^c	

The value indicates the mean of three replicates. Different letters in the same column indicate significant differences at $p \leq 0.05$ (Duncan's Multiple Range Test).

Table 3
Effect of treatments on total phenol, anthocyanin, quinone contents, and antioxidant capacity of litchi fruit during refrigerated storage.

Treatments	Days in storage									
	0	2	4	6	8	10	12	14	16	
	Total phenolics (mg kg⁻¹ GAE)									
MeJA (1 mM)	2.68	2.56 ^a	2.29 ^b	2.12 ^b	2.02 ^b	1.81 ^b	1.49 ^b	1.38 ^b	1.06 ^b	
MeJA (2 mM)	2.68	2.57 ^a	2.45 ^a	2.29 ^a	2.14 ^a	1.99 ^a	1.75 ^a	1.53 ^a	1.21 ^a	
Control	2.68	2.58 ^a	2.39 ^a	2.10 ^b	1.97 ^b	1.78 ^b	1.45 ^b	1.32 ^b	0.88 ^c	
	Anthocyanin content (mg kg⁻¹)									
MeJA (1 mM)	4.06	3.77 ^a	3.78 ^a	3.38 ^b	3.22 ^a	2.91 ^{ab}	2.67 ^b	2.65 ^a	2.22 ^b	
MeJA (2 mM)	4.06	3.79 ^a	3.66 ^a	3.54 ^a	3.24 ^a	3.13 ^a	2.97 ^a	2.72 ^a	2.58 ^a	
Control	4.06	3.79 ^a	3.70 ^a	3.29 ^b	3.04 ^b	2.72 ^b	2.57 ^b	2.43 ^b	2.20 ^b	
	Quinone content (OD₄₁₀ g⁻¹)									
MeJA (1 mM)	0.12	0.24 ^c	0.60 ^a	0.64 ^a	0.73 ^b	0.75 ^b	0.85 ^b	0.93 ^b	1.24 ^b	
MeJA (2 mM)	0.12	0.27 ^b	0.46 ^c	0.54 ^b	0.62 ^c	0.67 ^b	0.77 ^b	0.88 ^b	1.33 ^b	
Control	0.12	0.39 ^a	0.55 ^b	0.67 ^a	0.87 ^a	1.03 ^a	1.30 ^a	1.58 ^a	1.84 ^a	
	Total Antioxidant Capacity (mmol kg⁻¹ Trolox)									
MeJA (1 mM)	6.31	6.19 ^a	6.02 ^a	5.79 ^a	5.60 ^a	5.38 ^a	5.16 ^a	4.64 ^{ab}	4.00 ^{ab}	
MeJA (2 mM)	6.31	6.17 ^a	6.07 ^a	5.86 ^a	5.64 ^a	5.48 ^a	5.21 ^a	4.94 ^a	4.17 ^a	
Control	6.31	6.09 ^a	5.86 ^b	5.60 ^a	5.26 ^b	4.92 ^b	4.69 ^b	4.23 ^b	3.55 ^b	

The value indicates the mean of three replicates. Different letters in the same column indicate significant differences at $p \leq 0.05$ (Duncan's Multiple Range Test).

in fruit weight. These activities are sensitive to changes in relative humidity and prevailing temperature in the storage environment. The browning reactions in the fruit tissue begin with moisture loss and thereby decrease in the fruit weight (Jiang and Fu, 1999). On the final day of refrigerated storage, the litchi fruit treated with MeJA exhibited reduced weight loss by 28.75 and 26.14% in 2 and 1 mM MeJA treated to fruit, respectively, compared to control fruit (Table 2). The lowest weight loss was recorded in fruit treated with 2 mM MeJA, throughout the storage period. Application of MeJA was reported to maintain relatively higher cellular integrity, which further leads to reduced dehydration during storage (Rehman et al., 2018; Habibi et al., 2019). García-Pastor et al.

(2020) also reported that the application of MeJA retards the respiration rate in fruit during cold storage and hence delays weight loss.

3.4. Total soluble solids (TSS) and titratable acidity (TA)

Levels of TSS and titratable acidity (TA) are essential factors, which determine the taste and consumer acceptability of litchi fruit. In this study, the litchi fruit treated with MeJA kept under refrigerated storage condition showed inconsistent TSS levels, while titratable acidity declined continuously with increasing storage period. However, when compared to control, the fruit treated

with MeJA showed a relatively lower decline in the TA levels (Table 2). On the last day of storage, fruit treated with 2 and 1 mM MeJA retained 66.0 and 58.33% higher titratable acid content, respectively, compared to control fruit. The decline in TA levels is generally associated with fruit senescence processes. Postharvest application of MeJA was reported to retard ripening associated changes and respiration rates in the fruit (García-Pastor et al., 2020).

3.5. Ascorbic acid (AA)

Similarly, the ascorbic acid (AA) content gradually declined with progress in the storage period, irrespective of treatments. Whilst, on the last day of storage, fruit infiltrated with 2 and 1 mM MeJA exhibited 24.0 and 15.44% higher AA content than control ones, respectively (Table 2). Liu et al. (2018) also observed that postharvest MeJA application improves ascorbic acid content in cherry tomato during storage at ambient conditions. The improved AA is regarded as the main bioactive compound in non-enzymatic antioxidant reactions and scavenges reactive oxygen species (ROS), accumulated during stress and different physiological activities (Deshi et al., 2020). The senescence process involves several oxidative reactions and the levels of bioactive compounds such as AA are significantly reduced with progress in senescence. The postharvest application of MeJA retarded such fruit ripening associated changes (García-Pastor et al., 2020).

3.6. Total phenolics

Phenols are another major class of bioactive compounds found abundantly in litchi fruit (Jiang et al., 2003). Even though phenols have many health benefits and exhibit strong natural antioxidant property, they are predominant substrates for oxidative reactions, which ultimately hold responsible for the browning of red pericarp tissue of litchi fruit (Deshi et al., 2020). The total phenolic content (TPC) in litchi pericarp was declined gradually with advancing storage duration, irrespective of the applied treatments (Table 3). However, MeJA treated fruit showed significantly ($p < 0.05$) higher TPC than control fruit throughout the storage period. On the final day of storage, 2 and 1 mM MeJA treated fruit retained 37.19 and 20.63% higher phenolics as compared to control fruit (Table 3). The decrease in TPC with the extension of the storage period is due to the oxidative reactions associated with fruit senescence processes (Duan et al., 2011). The retention of higher TPC levels in the MeJA treated fruit might be attributed to delayed senescence-associated changes and suppressed PPO and POD activities in the fruit (Barman et al., 2014).

3.7. Anthocyanin and quinone contents

The anthocyanin content in the pericarp was gradually declined, while quinone content was increased, with the extension of the storage duration, irrespective of the treatments (Table 3). At the end of the storage period, fruit treated with 2 mM MeJA exhibited the highest levels of total anthocyanins (2.58 mg kg^{-1}). Fruit that underwent MeJA infiltration retained comparatively higher anthocyanin content than the control fruit. Quinones (*ortho*-quinones) are the oxidative by-products of phenols and anthocyanins. Yang et al. (2011) reported that MeJA dipping treatment in combination with Sportak fungicide delayed the loss of anthocyanin and (-)-epicatechin during 6 d storage at 25 °C. However, the effect of vacuum infiltrated MeJA alone on anthocyanin content is not reported yet. Accumulation of quinones is one of the prime causes of PB in harvested litchi fruit. The delayed degradation of anthocyanin content and lower levels of quinone accumulation in the litchi fruit treated with MeJA could be correlated with higher total phenol

content and retarded activity of oxidative enzymes (Zhang et al., 2018). The levels of quinones accumulated in the MeJA treated fruit was found to be lower, unlike the levels of total anthocyanin content and total phenols, which were higher in MeJA treated fruit. However, there is no clear evidence available on the effect of vacuum infiltrated MeJA on the regulation of quinone contents, which warrants the mode of action that should be investigated.

3.8. Total antioxidant capacity

The antioxidant system in the plants regulates ROS production by continuously scavenging them through antioxidant enzyme activities like SOD, CAT peroxidases as well low molecular non-enzymatic antioxidant compounds such as phenolics, ascorbate and flavonoids (Duan et al., 2011). In this study, there was a gradual decline in total antioxidant capacity (TAC) with increasing storage period, irrespective of the treatments (Table 3). However, MeJA treated fruit maintained significantly ($p < 0.05$) higher TAC, when compared to control fruit. The fruit treated with 2 and 1 mM MeJA maintained 15.67 and 12.67% higher antioxidant activity, respectively compared to control. Rehman et al. (2018) have opined that MeJA improves the functional quality of harvested fruit by enhancing antioxidant potential. Similarly, Cao et al. (2009) while observing the effect of MeJA on loquat fruit, reported higher levels of bioactive compounds such as phenol MeJA treated fruit and in turn higher antioxidant potential. Therefore, higher TAC values in the litchi fruit treated with MeJA could be associated with the enhanced levels of antioxidant compounds like AA, TPC and total anthocyanins.

3.9. Superoxide anion (O_2^-) and hydrogen peroxide rate (H_2O_2)

Superoxide anion (O_2^-) and hydrogen peroxide (H_2O_2) is the most prevalent reactive oxygen species (ROS) in the plant cell and their production and activity lead to a browning reaction. Irrespective of the treatments applied, ROS concentration increased with an increase in refrigerated storage days (Table 4). However, MeJA-treated fruit exhibited significantly ($p < 0.05$) lower levels of O_2^- and H_2O_2 , throughout the storage period. On the final day of storage, fruit treated with 2 and 1 mM MeJA, exhibited 23.83 and 22.34% lower O_2^- concentration and 32.41 and 21.23% lower H_2O_2 concentration, respectively, when compared to control fruit. The fruit ripening involves the accumulation of ROS due to numerous oxidative reactions as well as catabolic reactions, which give out free radicals as by-products. In postharvest litchi, accumulation of H_2O_2 during storage was also reported by Zhang et al. (2018). They opined that postharvest treatments that delay ROS accumulation could increase the shelf life of litchi. García-Pastor et al. (2020) reported that MeJA application has significantly retarded respiration and ripening associated processes and in turn reduce the accumulation of ROS in the pomegranate fruit. The MeJA also possess the capacity to detoxify ROS by enhancing the activity of antioxidant enzymes under stressful conditions (Mustafa et al., 2016). Phenolics and anthocyanin are considered non-enzymatic antioxidants and have the capability either to scavenge or neutralise free radicals by donating electron (Habibi et al., 2019). In agreement with these findings, MeJA treated fruit exhibited increased levels of AA content, TAC, Anthocyanin, and TPC, which might have actively scavenged ROS in our study.

3.10. Membrane leakage and malondialdehyde (MDA)

Membrane leakage is used to evaluate the permeability and integrity of the cell membrane. During the fruit senescence process, the membrane integrity is degenerated in the litchi pericarp due to the activity of cell wall disintegrating enzymes (Habibi

Table 4

Effect of treatments on superoxide anion production rate, hydrogen peroxide production rate, and membrane permeability of litchi fruit during refrigerated storage.

Treatments	Days in storage									
	0	2	4	6	8	10	12	14	16	
	Superoxide anion production rate ($\mu\text{mol kg}^{-1} \text{min}^{-1}$)									
MeJA (1 mM)	0.13	0.21 ^b	0.51 ^b	0.75 ^b	0.88 ^b	1.71 ^b	2.20 ^b	3.06 ^c	4.17 ^b	
MeJA (2 mM)	0.13	0.20 ^b	0.49 ^b	0.68 ^b	0.83 ^b	1.66 ^b	2.04 ^c	3.30 ^b	4.09 ^b	
Control	0.13	0.27 ^a	0.58 ^a	0.95 ^a	1.79 ^a	2.47 ^a	3.15 ^a	4.72 ^a	5.37 ^a	
	Hydrogen peroxide production rate ($\text{mmol kg}^{-1} \text{min}^{-1}$)									
MeJA (1 mM)	2.33	2.33 ^b	4.67 ^b	9.00 ^b	16.00 ^b	21.33 ^b	29.67 ^b	40.67 ^b	47.00 ^b	
MeJA (2 mM)	2.33	1.00 ^c	4.00 ^b	8.00 ^b	12.67 ^b	20.00 ^b	28.67 ^b	38.67 ^b	40.33 ^c	
Control	2.33	3.67 ^a	7.00 ^a	16.33 ^a	25.67 ^a	37.33 ^a	43.00 ^a	55.00 ^a	59.67 ^a	
	Membrane permeability (%)									
MeJA (1 mM)	13.26	14.85 ^b	16.9 ^b	19.32 ^b	22.16 ^b	25.0 ^b	29.0 ^b	32.0 ^b	38.0 ^b	
MeJA (2 mM)	13.26	15.16 ^a	16.54 ^c	18.97 ^b	21.33 ^c	23.8 ^c	26.0 ^c	31.0 ^b	34.0 ^c	
Control	13.26	15.32 ^a	17.31 ^a	20.02 ^a	23.45 ^a	27.0 ^a	32.67 ^a	38.0 ^a	43.24 ^a	
	Malondialdehyde content (nmol kg^{-1})									
MeJA (1 mM)	2.88	3.40 ^b	4.29 ^b	5.45 ^b	7.97 ^b	10.18 ^b	12.89 ^b	14.32 ^b	16.21 ^b	
MeJA (2 mM)	2.88	3.30 ^b	4.26 ^b	5.31 ^b	7.70 ^b	9.82 ^c	12.33 ^c	14.25 ^b	16.12 ^b	
Control	2.88	4.22 ^a	6.01 ^a	7.01 ^a	8.90 ^a	11.11 ^a	13.61 ^a	15.74 ^a	17.42 ^a	

The value indicates the mean of three replicates. Different letters in the same column indicate significant differences at $p \leq 0.05$ (Duncan's Multiple Range Test).

et al., 2019). Whilst MDA is a by-product of membrane disintegration and peroxidation processes (Duan et al., 2011). Irrespective of all treatments, membrane leakage and MDA in litchi pericarp increased with the advancement in storage duration (Table 4). However, fruit subjected to MeJA treatment exhibited a significantly lower leakage rate than control fruit. On the final day of storage, fruit treated with 2 and 1 mM MeJA, exhibited 21.36 and 16.74% lower leakage rate compared to control fruit, respectively. Similarly, on the final day of storage, fruit treated with 2 and 1 mM MeJA showed 7.46 and 6.94% lower MDA content than control fruit, respectively. The results are in agreement with Venkatachalam and Meenune (2015), who reported that MeJA treatment inhibits the activity of cell membrane degrading enzymes in long kong (*Lansium parasiticum*) fruit under cold storage. The lower levels of membrane leakage and MDA in the fruit treated with MeJA, suggests that the treatment could successfully maintain membrane integrity and limit ROS production in the cells during cold storage (García-Pastor et al., 2020).

3.11. Phenylalanine ammonia lyase (PAL), polyphenol oxidase (PPO), and peroxidase (POD) activity

PAL actively involves in the biosynthesis of phenolic compounds in the plant cell. In litchi fruit treated with MeJA, the PAL activity initially increased up to 6 d of storage and then gradually decreased till the end (Table 5). In the case of control fruit, PAL activity decreased continuously with storage duration. On the final

day of storage, fruit treated with 2 and 1 mM MeJA, exhibited 56 and 45% higher PAL activity compared to control fruit, respectively. PPO and POD are the key enzymes responsible for senescence-associated oxidative reactions as well as PB in the litchi fruit. PPO and POD levels gradually increased with an increase in the storage duration in the litchi pericarp, irrespective of treatments. However, the MeJA treated fruit exhibited significantly lower levels of the enzymes, when compared to the control fruit (Table 5).

The results also indicated that lower activity of PPO and POD and higher activity of PAL could be attributed to delayed PB in litchi. MeJA application has been reported to delay senescence-associated changes in the fruit thorough decreased activity of oxidizing enzymes during storage (Habibi et al., 2019). The higher levels of total phenols, AA, anthocyanins and total antioxidant capacity could be associated with decreased activity of PPO and POD in the litchi fruit treated with MeJA. The exact mode of action of vacuum infiltrated MeJA on regulating activities of different enzymes in cold-stored litchi fruit is yet to be investigated.

4. Conclusion

Postharvest application of MeJA through vacuum infiltration significantly reduced the incidence of PB in cold-stored litchi fruit, by suppressing the activity of oxidative enzymes. Furthermore, the treatment also maintained high levels of TSS, TA, TAC, anthocyanins as well as increased non-enzymatic bioactive compounds

Table 5

Effect of treatments on different enzyme (PAL, PPO and POD) activities of litchi fruit during refrigerated storage.

Treatments	Days in storage									
	0	2	4	6	8	10	12	14	16	
	PAL activity ($\text{U g}^{-1} \text{protein}$)									
MeJA (1 mM)	0.16	0.17 ^b	0.17 ^b	0.18 ^b	0.17 ^b	0.16 ^a	0.15 ^a	0.13 ^b	0.09 ^a	
MeJA (2 mM)	0.16	0.18 ^a	0.19 ^a	0.19 ^a	0.18 ^a	0.17 ^a	0.16 ^a	0.14 ^a	0.11 ^a	
Control	0.16	0.15 ^c	0.14 ^c	0.13 ^c	0.11 ^c	0.10 ^b	0.09 ^b	0.07 ^c	0.06 ^b	
	PPO activity ($\text{U g}^{-1} \text{protein}$)									
MeJA (1 mM)	2.22	2.28 ^{ab}	2.29 ^b	2.33 ^b	2.35 ^b	2.36 ^b	2.37 ^b	2.33 ^a	2.24 ^a	
MeJA (2 mM)	2.22	2.25 ^b	2.27 ^b	2.29 ^b	2.31 ^b	2.34 ^b	2.36 ^b	2.31 ^a	2.19 ^a	
Control	2.22	2.36 ^a	2.43 ^a	2.53 ^a	2.68 ^a	2.64 ^a	2.51 ^a	2.31 ^a	1.84 ^b	
	POD activity ($\text{U g}^{-1} \text{protein}$)									
MeJA (1 mM)	1.87	2.00 ^b	2.29 ^b	2.43 ^b	2.47 ^c	2.78 ^a	2.94 ^a	2.67 ^a	2.16 ^a	
MeJA (2 mM)	1.87	1.89 ^c	2.27 ^b	2.35 ^b	2.60 ^b	2.74 ^a	2.74 ^b	2.64 ^a	2.15 ^a	
Control	1.87	2.21 ^a	2.43 ^a	2.63 ^a	2.97 ^a	2.79 ^a	2.50 ^c	1.79 ^b	1.24 ^b	

The value indicates the mean of three replicates. Different letters in the same column indicate significant differences at $p \leq 0.05$ (Duncan's Multiple Range Test)

like ascorbic acid and TPC, during 16 d cold storage. Hence, it can be concluded that MeJA plays a positive regulatory role in extending the storage life of litchi fruit while maintaining optimum fruit quality. The MeJA (2 mM) treatment was found relatively most effective in regulating biochemical parameters associated with PB of litchi fruit. There is no information regarding the activity mechanism of preharvest or postharvest MeJA application at the molecular or on its effect on the flavour of the fruit, which needs to be explored.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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