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Influence of pre-harvest methyl jasmonate application on the fruit quality of strawberry cv. Paros at harvest and during cold storage

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ABSTRACT

Purpose: Strawberry fruits are perishable with a short shelf life. Methyl jasmonate (MJ) is a well-known signaling molecule involved in the regulation of many processes in plants. Previous studies have addressed the effectiveness of pre- and postharvest MJ treatments on the quality of fruits. Therefore, in this study, the effect of pre-harvest MJ on the quality and physio-chemical traits of strawberry at harvest and during cold storage were investigated. **Research Method:** The effect of pre-harvest foliar spraying of MJ (0, 50, 100, and 200 µM) at three times (full flowering, production of green fruits, and the beginning of the pink stage) on quality and bioactive compounds of strawberry fruit (cv. Paros) stored at 4 °C for 12 d was studied. **Findings:** Our results showed that fruit obtained from MJ-treated plants had significantly higher firmness and APX enzyme activity than fruit from control plants. However, no significant differences in other traits were observed between control and MJ-treated fruits at this stage. During cold storage, MJ treatment significantly reduced firmness loss, physiological loss in weight, and ascorbic acid content compared to control fruits. In cold storage, MJ treatment reduced firmness loss and weight loss, while maintaining higher levels of titratable acidity, antioxidant compounds (ascorbic acid, anthocyanins, and phenolics), and total antioxidant activity. Furthermore, MJ treatment resulted in increased catalase and ascorbate peroxidase enzyme activity, as well as lowered guaiacol-peroxidase, total soluble solids/ titratable acidity ratio. Total soluble solids were not affected by MJ treatment at harvest and during cold storage. **Research limitations:** No limitations were found. **Originality/Value:** Pre-harvest application of MJ, especially 200 µM, can increase the shelf life of strawberry fruits by increasing or maintaining higher levels of bioactive compounds and antioxidant enzyme activity.

INTRODUCTION

Strawberry (*Fragaria* × *ananassa* Duch.) is one of the most popular fruits belonging to the Rosaceae family. It is cultivated and consumed worldwide due to its special taste, attractive color, distinctive sweetness, and nutritional value, including minerals, vitamins, phenolics, anthocyanins, amino acids, and antioxidant properties (Nguyen & Nguyen, 2021; Asgari et al., 2024; Xu et al., 2024). These bioactive compounds can reduce the risk of chronic diseases such as heart disease, type II diabetes, obesity, cancer, and neurodegenerative diseases (Darwish et al., 2021). However, strawberry is classified as a non-climacteric fruit, so they do not ripen after harvest and should be harvested at the nearly full maturity stage (Nguyen & Nguyen, 2021; Meighani & Roozkhosh, 2024). In addition, the shelf life of strawberry fruit is very limited due to its susceptibility to mechanical injury, physiological deterioration, water loss, and microbial decay (Saavedra et al., 2017, Adl et al., 2024). The shelf life of strawberry fruit is affected by various factors, such as growing conditions, harvest stage, pre- and postharvest treatments, transportation method, storage conditions, and others (Xu et al., 2024). Quality losses after harvest can be reduced by the pre and post-harvest treatments. Pre-harvest treatments not only improve fruit quality but also have positive effects on extending shelf life and preserving bioactive compounds of fruits and vegetables (Ağlar & Öztürk, 2018; Darwish et al., 2021). Many efforts have been made to improve the quality and extend the shelf life of fruits using natural compounds. One of them is the application of plant growth regulators before and after harvest.

Methyl jasmonate (MJ), as an endogenous plant hormone from the jasmonate family, plays an important role in various biological processes in plants, including growth and development, fruit growth and ripening, pigment accumulation, ethylene synthesis, disease resistance, and environmental stress (Han et al., 2019; Zuñiga et al., 2020; Asgari et al., 2024). Recent studies have shown the positive effect of pre-harvest application of MJ on the postharvest behavior of fruit, including raspberry (Shah et al., 2025), strawberry (Darwish et al., 2021), and pomegranate (García-Pastor et al., 2019). Based on previous reports, Pre-harvest application of MJ increased the biosynthesis of phytochemicals such as phenolics, flavonoids, anthocyanins, carotenoids, enzymatic and non-enzymatic antioxidants, as well as essential nutrients (Hasan et al., 2025) and activities of key enzymes involved in flavonoid biosynthesis (Zheng et al., 2024; Shah et al., 2025). Also, MJ can enhance the ripening of non-climacteric fruits by participating in anthocyanin accumulation, cell wall modification, and the biosynthesis of ethylene and jasmonates (Concha et al., 2013). In addition, García-Pastor et al. (2020) observed that pre-harvest MJ treatments increased crop yield, fruit quality, and its content of bioactive compounds at harvest and during storage. Furthermore, it has been reported that pre-harvest application of MeJA significantly preserved the volatile aroma and improved the activities of disease-resistant enzymes in kiwifruit (Yang et al., 2025).

Our idea is that the pre-harvest spraying of MJ can promote the quality of strawberry fruits at harvest and during refrigerated storage. Therefore, this study aimed to assess the effectiveness of MJ pre-harvest spraying on fruit quality attributes, bioactive compounds, decay incidence, and antioxidant enzyme activities of strawberry fruits (cv. Paros) during refrigerated storage.

MATERIALS AND METHODS

Plant material and treatment

Strawberry (*Fragaria*× *ananassa*, cv. 'Paros') transplants were cultivated in October 2023 in a plastic greenhouse located in Jiroft, southern Kerman Province, Iran. The equal-sized, healthy,

and disease-free transplants were planted over cultivation beds covered with black plastic mulch at 25 × 25 cm space between plants in a triangular planting pattern. The experimental soil was sandy-loam and irrigation was done through a drip tape system under plastic mulch. The experiment was conducted as a randomized complete block design, with four treatments and three independent replicates. About 150 strawberry plants of the 'Paros' cultivar was considered for each block.

Treatments included different concentrations of MJ (0, 50, 100, and 200 µM, Sigma–Aldrich, Germany). Distilled water was used as a control. In all treatments, 0.05% (w/v) Tween-20 was used as a surfactant. Strawberry plants were fully sprayed three times (10-day intervals) at different developmental stages: full flowering, production of green fruits, and the beginning of the pink stage (Darwish et al., 2021).

Strawberry fruits in each treatment were harvested at the 80% red color stage and immediately transported to the postharvest laboratory. Then, 40 fruits with uniform color and size, without any visual defect were randomly separated from each block and treatment, packed in polystyrene boxes with lids (750 ml, 10 fruits per box in one row), and stored at 4˚C and 90% relative humidity for 12 days. One box containing ten fruits for each block and treatment was randomly sampled after 0 (at harvest), 4, 8, and 12 days of cold storage for measurement of physio-chemical attributes and antioxidant enzyme activity.

Fruit firmness and physiological loss in weight

Fruit firmness was determined using a texture analyzer (Santam, STM-5, Iran) equipped with a flat probe (8 mm) at a constant speed of 20 mm $min^{-1}$and a penetration depth of 10 mm. The results were expressed in Newton (N) units.

For physiological loss in weight (PLW), strawberry fruits were weighed at the beginning of the experiment, after treatment, and at the end of each sampling time. The percentage of PLW was calculated using the following equation (1):

$$PLW\ (\%) = (Wi - Wf) \times 100/\ Wi \qquad (1)$$

Where Wi is the initial weight and Wf is the weight at each sampling time.

Total soluble solids (TSS), titratable acidity, and TSS/TA

Analysis of TSS, TA, and TSS/TA ratio were performed according to Saavedra et al. (2016). TSS of strawberry juice was measured at 25˚C with a hand-held digital refractometer (PDR-108-1, Taiwan) and the results were expressed as Brix degrees (˚Brix). To determine the TA, strawberry juice was diluted with distilled water (1:10 v/v), and then titrated with 0.1 N NaOH to pH 8.2. Results were calculated and expressed as the percentage of citric acid per 100 g of fresh weight (AOAC, 2000). The TSS/TA ratio was calculated by dividing the TSS value by the TA value.

Ascorbic acid content

Ascorbic acid content was determined based on the 2, 6- dichloroindophenol titration method. The amount of ascorbic acid in the strawberry fruits was expressed as mg per 100 g FW (AOAC, 2000).

Total phenolic content and total antioxidant activity

For the determination of total phenolic content (TPC) and total antioxidant activity (TAA), 2 g strawberry fruit tissue without achene was well homogenized with 10 mL of methanol (80%)

and centrifuged at 14000 rpm at 4°C for 10 min. The supernatant was used for TPC and TAA analysis.

TPC was measured using the Folin–Ciocalteau reagent according to the method of Singleton & Rossi (1965). About 250 µL of the extract was mixed with 1250 µL of 10% Folin-Ciocalteau reagent and 1000 µL of 7.5% Na_2CO_3. The samples were incubated at room temperature in darkness for 60 min, and then the absorbance of the reaction mixture was measured at 765 nm using a UV/VIS spectrometer (Lambda 25, PerkinElmer, USA). Gallic acid was used as an external standard and the results were expressed as mg gallic acid equivalents per 100 g fresh weight (mg GAE 100 g^{-1} FW).

Total antioxidant activity (TAA) was determined using the 2, 2-diphenyl-1-picrylhydrazyl (DPPH) method as outlined in Brand-Williams et al. (1995). DPPH methanolic solution (950 µL) was mixed with 50 µL of extract and kept in the dark at ambient temperature for 30 min. The solution absorbance was measured at 517 nm, and the TAA was calculated as the following equation (2):

$$TAA\ (\%) = [(Ac - As)/Ac] \times 100 \qquad (2)$$

Where 'Ac' is the absorbance of the DPPH and 'As' is the absorbance of the sample.

Total anthocyanin content

Total anthocyanin content (TAC) was determined using the pH differential method described by Darwish et al. (2021) with some modifications. Fruit puree without achenes (2 g) was homogenized in 10 mL of methanol/HCl (85/15%, v/v) and centrifuged at 14000 rpm at 4°C for 10 min. The extract was diluted in pH_1 and pH_7 solution buffers and after 30 min incubation in ambient temperature, the absorbance was measured at 510 and 700 nm. TAC was calculated as mg cyanidin 3-glucoside equivalent per kg of fresh fruit.

Antioxidant enzymes

Preparation of enzyme extract

Strawberry tissue (1 g) was homogenized in 2 mL potassium phosphate buffer (50 mM, pH, 7.0, containing 0.5 mM EDTA and 60 g/L PVPP). The homogenate was centrifuged at 14000 rpm for 15 min, and the supernatant was used as the crude extract to measure the activity of CAT and SOD enzymes (Li et al., 2023).

Catalase (CAT, EC 1.11.1.6)

CAT activity was assayed using the protocol of Li et al. (2023). Briefly, 100 µL enzyme extract was reacted with 100 µL H_2O_2 (20 mM). The absorbance of the reaction mixture was determined at 240 nm and expressed as U/mg protein. One unit of CAT activity was defined as an absorbance change of 0.01 U/min, and the CAT activity was expressed as U/mg protein.

Guaiacol peroxidase (GPX, EC 1.11.1.7)

The reaction mixture for the GPX assay consisted of 0.7 mL of phosphate buffer (50 mM, pH 5.0), 0.1 mL hydrogen peroxide (40 mM), 0.1 mL guaiacol (20 mM), and 0.1 mL enzyme extract. The absorbance of the reaction mixture was measured at 470 nm and expressed as U/mg protein. The change absorbance in 0.01 U/min is defined as one unit of GPX activity (Ali et al., 2021).

Ascorbate peroxidase (APX, EC 1.11.1.11)

APX activity was determined according to Ali et al. (2021). The reaction mixture was prepared by mixing 0.1 mL L-ascorbate (0.5 mM), 0.1 mL hydrogen peroxide (0.1 mM), 0.2 mL

phosphate buffer (50 mM, pH 5.0), and 0.1 mL enzyme extract. The absorbance of the reaction mixture was determined at 290 nm and expressed as U/mg protein. One unit of APX is defined as the amount of enzyme that can oxidize 1 µmol of ascorbate per minute.

Statistical design

The postharvest study was performed using a factorial experiment with a randomized block design, with the main factors being the MJ treatment (control, 50, 100. and 200 mM) and storage time (0, 4, 8, and 12 days). The data were analyzed with two-way analysis of variance (ANOVA) using the methods of Statistical Analysis System (SAS, version 9.1). Least significance difference (LSD) was used to compare means between applied treatments at a 5% level of probability. The values of the results were presented as means (n=3) ± SE. The graphs were prepared with the Microsoft Excel program.

RESULTS AND DISCUSSION

Firmness and physiological loss in weight (PLW)

The effect of MJ foliar spraying on the firmness and PLW of strawberry fruits are represented in Table 1. The pre-harvest treatments significantly affected firmness values ($p<0.05$). At harvest (0 d), fruits treated with MJ obtained significantly higher firmness than the untreated fruits (control). Throughout the storage, strawberry fruits regardless of treatment showed continuous declines in firmness, with a slower softening in MJ-treated fruits. At the end of the storage, the lowest and highest firmness as obtained from control (4.84 N) and 100 µM MJ treatment (5.71 N), respectively. Although, no significant difference in firmness was found between 100 and 200 µM MJ treatment throughout the study (Fig. 1A). Firmness is an important quality parameter for fresh produce. Fruit softening is a crucial characteristic of ripening in many fleshy fruits. The main factors contributing to fruit softening are cell wall disassembly and reduced cell-to-cell adhesion, primarily due to the degradation of the middle lamella. In strawberry fruit, cell wall disassembly involves solubilization of pectins, slight depolymerization of bound pectins, loss of galactose and arabinose, and reduced hemicellulosic content, which contributes to the fruit softening (Moya-León et al., 2019). Pre-harvest MJ application has been reported to increase the firmness of lemon (Serna-Escolano et al., 2019) and Fuji apple (Ağlar & Öztürk, 2018) at harvest and also maintain firmness during storage in raspberries (Shah et al., 2025) and papaya (Li et al., 2023). Several enzymes are involved in the softening of strawberry fruit. Shah et al. (2025) demonstrated that MJ application in raspberry fruit reduces the activity of cell wall-hydrolyzing enzymes, including pectin methylesterase (PME), polygalacturonase (PG), and cellulase (Cx), leading to less cell wall degradation and potentially increased fruit firmness. Furthermore, Wu et al. (2025) reported that MJ treatment can slow down the softening of blackberry fruits by increasing antioxidant contents and antioxidant enzyme activity, which is similar to the results of this study.

As illustrated in Fig. 1B, PLW in control and MJ-treated fruits showed a similar pattern of changes that involved its gradual increase with storage time. Up to 4 days of storage, no significant difference in PLW was observed between control and MJ-treated fruits, later on, MJ-treated fruits were observed significantly lower PLW compared to control fruits. At the end of storage, strawberry fruits treated with 100 µM MJ exhibited the lowest PLW (1.30%), which was significantly lower than that of the control but not that of the 50 and 200 µM MJ-treated fruits. In general, PLW during the storage of fruits is a result of increased transpiration and respiration rates (Ilea et al., 2025). The large cells and thin cell walls in the epidermis of strawberry fruits make it susceptible to moisture loss. García-Pastor et al. (2019) reported that pre-harvest application of MJ significantly reduced respiration rate in pomegranate fruits at

harvest and during postharvest storage. Also, a previous study indicated that MJ (methyl jasmonate) can delay decay and PLW in raspberry fruits by activating an antioxidant defense mechanism against free radicals and retarding membrane peroxidation (Shah et al., 2025). Therefore, the positive effect observed in MJ-treated strawberry fruit could be attributed to a combination of factors including a slower rate of respiration and transpiration, as well as its ability to enhance antioxidant levels and protect cell membranes from oxidative damage.

Table 1. Effect of methyl jasmonate pre-harvest application on some characteristics of strawberry fruit cv. Paros during 12 days of storage at 4°C.

Source of variation	Firmness (N)	Physiological loss in weight (%)	TSS (˚Brix)	TA (mg 100 g^{-1}FW)	TSS/TA	AsA (mg 100 g^{-1}FW)
Methyl Jasmonate (T)	**	**	ns	**	**	**
Storage time (ST)	**	**	**	**	**	**
T×ST	**	**	ns	ns	**	**
Storage Time (day)						
0 (harvest)	7.51±0.13 a	0.00±0.00 d	6.93±0.06 c	1.18±0.05 a	5.88±0.24 d	69.83±1.60 a
4	7.09±0.13 b	0.74±0.05 c	7.00±0.08 bc	1.11±0.05 b	6.37±0.31 c	64.30±1.25 b
8	6.55±0.26 c	0.92±0.10 b	7.06±0.06 b	0.95±0.06 c	7.53±0.52 b	58.49±2.47 c
12	5.43±0.22 d	1.72±0.37 a	7.21±0.14 a	0.81±0.06 d	9.08±0.82 a	50.50±2.89 d

Source of variation	TAC (mg 100 g^{-1}FW)	TPC (mg GAE 100 g^{-1}FW)	TAA (%DPPHsc)	CAT (U g^{-1} FW min^{-1})	GPX (U g^{-1} FW min^{-1})	APX (U g^{-1} FW min^{-1})
Methyl Jasmonate (T)	**	**	**	**	*	**
Storage time (ST)	**	**	**	**	ns	**
T×ST	ns	ns	*	*	ns	**
Storage Time (day)						
0 (harvest)	11.31±0.35 d	221.11±7.01 c	74.41±1.91 b	13.02±0.47 c	13.84±0.77 ab	41.57±1.15 b
4	12.14±0.31 c	241.50±5.12 bc	78.74±3.04 a	15.20±0.42 a	13.98±1.06 ab	50.14±2.96 a
8	12.75±0.46 b	248.79±7.67 a	80.55±2.88 a	13.91±0.59 b	14.47±1.04 a	39.12±3.22 c
12	13.14±0.50 a	238.78±9.9 b	71.79±3.35 c	13.42±0.65 c	14.09±0.72 ab	29.72±2.69 d

**, * and ns indicate significant at $P \leq 0.01$, $P \leq 0.05$ and non-significant.

Means±SE (n = 3) covered by the same letter are not significantly different ($P<0.05$).

TSS: total soluble solids, TA: titratable acidity, AsA: ascorbic acid, TAC: total anthocyanin content, TPC: total phenolic content, TAA: total antioxidant activity, CAT: catalase, GPX: guaiacol peroxidase, APX: ascorbate peroxidase.

Table 2. Effect of methyl jasmonate pre-harvest concentration on the titratable acidity, TAC, TPC, guaiacol peroxidase activity in strawberry fruit cv. Paros.

MJ concentration (µM)	Titratable acidity (mg 100 g^{-1}FW)	TAC (mg 100 g^{-1}FW)	TPC (mg GAE 100 g^{-1}FW)	GPX (U min^{-1} g^{-1} FW)
0	0.89±0.05 a	11.41±0.35 c	226.81±7.01 b	15.83±0.77 a
50	1.06±0.05 b	12.32±0.31 b	238.41±5.12 a	14.93±1.06 b
100	1.05±0.06 c	12.72±0.46 a	239.87±7.67 a	13.26±1.04 c
200	1.04±0.06 d	12.87±0.50 a	245.09±9.91 a	12.36±0.72 d

Means±SE (n = 3) within each column covered by the same letter are not significantly different ($P<0.05$). TAC: total anthocyanin content, TPC: total phenolic content, GPX: guaiacol peroxidase.

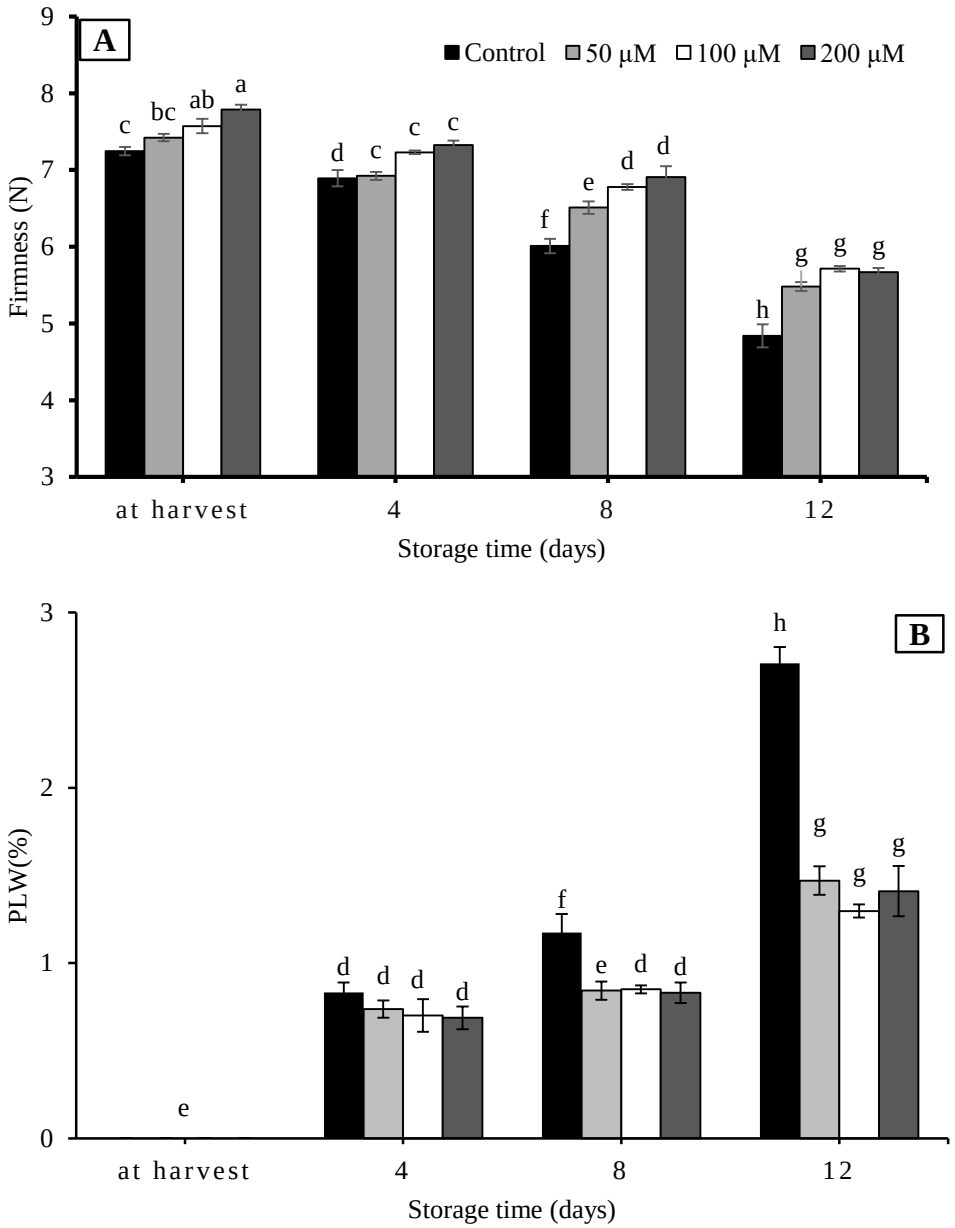

Fig. 1. Effect of methyl jasmonate (MJ) pre-harvest treatment on firmness (A) and physiological loss in weight (B, PLW) of strawberry fruit cv. Paros during 12 days of storage. Mean ± SE (n=3), followed by different letters are significantly different (P<0.05).

Total soluble solids (TSS), titratable acidity (TA), and TSS/TA ratio

The TSS and TSS/TA ratio of all treatments gradually increased throughout the storage time. In contrast, the TA values of control and MJ-treated fruits continuously decreased throughout the storage time. Storage time had a positive influence on the TSS of strawberry fruits. However, the MJ treatment and its interaction with storage time did not significantly affect TSS. The TSS value of strawberry fruit at the end of storage (7.21 ˚Brix) was significantly higher (6.93 ˚Brix) than at harvest (Table 2). The TA content of strawberry fruit was significantly affected by pre-harvest MJ treatment and storage time, but not by their interaction (Table 1). Untreated strawberry (control) exhibited significantly lower TA content (0.89 mg $100g^{-1}$ FW) than those treated with MJ, while no significant differences were observed among different MJ concentrations (Table 2). The TA content indicated a significant decline with

prolonged cold storage. The maximum and minimum TA content of strawberry fruits were recorded at harvest (1.18 mg 100 g^{-1} FW) and the end of storage (0.81 mg 100g^{-1} FW), respectively (Table 1). The TSS/TA ratio significantly increased from 5.88 to 9.08 during 12 days of cold storage (Table 1). However, at harvest and up to 8 days after storage, no significant difference was found in the TSS/TA ratio between different concentrations of MJ and the control samples. At the end of storage, control strawberry fruits showed a significantly higher TSS/TA ratio than MJ treatments, while no significant differences were observed among the different MJ concentrations (Fig. 2).

In this study, pre-harvest MJ treatment had no significant effect on TSS content, which is consistent with previous findings on lemon (Serna-Escolano et al., 2019) and blood orange (Vithana et al., 2024) fruits. On the contrary, MJ-treated raspberry fruits expressed significantly higher TSS than the control sample. TSS content in strawberry fruits increased during cold storage. The increase in TSS with the extension of storage periods has been attributed to the breakdown of complex polysaccharides and other organic acid into simple sugars and moisture loss (Wu et al., 2025). Previous studies on lemon fruits have indicated a positive correlation between PLW and TSS (Liao et al., 2022). In Our study, the TA content of all treatments gradually declined throughout the storage period, although MJ inhibited the decrease of TA in comparison with the control fruit, specifically at the end of storage, which is consistent with those obtained from raspberry (Wu et al., 2025), blueberry (Wang et al., 2019), and lemon fruits (Liao et al., 2022). The reduction in TA during cold storage could be related to a combination of factors, including metabolic changes, respiratory activity, and senescence, which these processes result in the conversion of organic acids into sugars, or the utilization of organic acids as respiratory substrates (Li et al., 2023). García-Pastor et al. (2019) reported that MJ treatment decreased TA losses during storage in pomegranate fruit by reducing respiration rate and the consumption of organic acids as respiratory substrates. In our study, the TSS/TA ratio in strawberry fruit showed an increasing trend with the extension of cold storage periods. Liao et al. (2022) reported that the TSS/TA ratio in lemon fruits increased during cold storage, and this increase was more pronounced when the fruits were treated with MJ pre- and postharvest. In general, the TSS/TA ratio is directly related to TSS and TA, and changes in these two factors affect its value. Therefore, the relative increase in TSS and decrease in TA of strawberry fruits during cold storage led to a change in the TSS/TA ratio.

Total anthocyanin content (TAC) and total phenolic content (TPC)

Significant changes and an increasing trend in the TAC of strawberry fruits were observed during the cold storage, such that the TAC at the end of storage was 16% higher than at harvest (Table 1). TAC at harvest was affected by MJ foliar spraying and was higher in MJ-treated fruits compared to the control sample. As shown in Table 2, TAC in strawberry fruits treated with MJ was higher than in the control sample. The highest TAC was obtained from 200µM MJ treatment (12.87 mg 100 g^{-1} FW) followed by 100 µM (12.72 mg 100 g^{-1} FW) and 500 µM (12.32 mg 100 g^{-1} FW) MJ treatment and the lowest from the control sample (11.41 mg 100 g^{-1} FW). Pre-harvest spraying of MJ increased the TPC of strawberry fruits at harvest. In this stage, the highest level (226.63 mg 100 g^{-1} FW) was recorded in MJ-treated fruits with 200 µM, and the lowest level (218.12 mg 100 g^{-1} FW) was found in the control sample. TPC exhibited an upward trend up to 8 days but then had a downward trend until the end of cold storage (Table 1). Strawberry fruits treated with MJ showed significantly higher TPC than control fruits. However, there was no significant difference between different MJ treatments (Table 2).

Phenolic compounds, plant secondary metabolites, play a crucial role in both enhancing the sensory and nutritional quality of fruits and inducing stress-related defense mechanisms in plants (Shah et al., 2025). Anthocyanins are a group of water-soluble pigments responsible for

the bright red color in strawberry fruits, and the predominant anthocyanins found in strawberries are pelargonidin-3-glucoside and cyanidin-3-glucoside (Wang & Li, 2000). At harvest and during postharvest storage, strawberries treated with MJ showed higher TPC and TAC than control fruits, as previously reported in raspberries (Shah et al., 2025), and 'Sabrosa' strawberry (Asghari & Hasanlooe, 2016). The increase in TPC and TAC can be attributed to the impact of MJ on phenylpropanoid metabolism. Especially, MJ can enhance the activity of key enzymes in this pathway, including phenylalanine-ammonia lyase (PAL) and shikimate dehydrogenase (SKDH), leading to increased production of phenolic compounds (Shah et al., 2025). Several studies support the idea that MJ treatment positively impacts TPC and TAC by enhancing the activity of the PAL enzyme (Cao et al., 2009; Hasan et al., 2024; Zheng et al., 2024). However, in blood orange, postharvest MJ-treated fruit pre-harvest foliar spraying

Ascorbic acid (AsA) and total antioxidant activity (TAA)

At harvest, no significant differences were observed between the control and MJ-treated fruits in AsA content. Significant variations and a downward trend in AsA content were observed in MJ-treated and control strawberry fruits during the cold storage, with this reduction being significantly less in MJ-treated fruits compared to the control. The highest (71.78 mg 100 g^{-1} FW) and lowest (42.63 mg 100 g^{-1} FW) levels of AsA were recorded from 100 mM methyl jasmonate treatment at harvest (day 0) and from the control at the end of storage, respectively (Table 3).

AsA, also known as vitamin C, is a water-soluble vitamin that decreases in levels with moisture loss and postharvest senescence (Shah et al., 2025). AsA is susceptible to oxidative and enzymatic degradation during storage, leading to the formation of dehydroascorbic acid (DHA) and eventually diketogulonic acid (DKG), which have no vitamin C activity (Hasan et al., 2025). In this study, the AsA content in strawberry fruits decreased over time in all treatments, and the MJ treatment slowed this decline compared to the control. These findings are consistent with a previous study on raspberry (Chanjirakul et al., 2006) and pomegranate (García-Pastor et al., 2019) fruits. It has been shown that pre-harvest application of MJ can increase the AsA content at harvest and maintain it during cold storage in raspberries (Shah et al., 2025) and blueberries (Wang et al., 2019) by delaying oxidation reactions and reducing moisture loss. Furthermore, Wolucka et al. (2005) reported that MJ can enhance the transcription of genes involved in the de novo biosynthesis and regeneration of AsA. Conversely, AsA levels in blood orange fruits were not significantly influenced by both pre-harvest foliar spraying and postharvest dipping treatments with MJ (Vithana et al., 2024).

MJ foliar application enhanced the TAA content of strawberry fruits. TAA, at harvest, was the highest in strawberry fruits treated by 200 µM MJ with a significant difference compared to the control. TAA in both control and MJ-treated fruits increased with storage time, reached the maximum after 8 days of storage, and then decreased sharply from days 8 to 12. At the end of storage, the highest TAA (73.33%) was observed in the fruit sprayed pre-harvest with 100 µM MJ, while the lowest TAA (60.04%) was recorded in the control samples (Table 3).

The antioxidant activity of plant tissues is attributed to some phytochemicals, such as AsA, phenolics, anthocyanins, and other flavonoid compounds (Wang & Li, 2000). Tulipani et al. (2008) reported that 55-70% of TAA in strawberry fruits is related to ASA and anthocyanins. Cao et al. (2009) observed a positive relationship between TPC and TAA. Furthermore, Wang & Li (2000), observed a linear correlation between antioxidant activity and TPC for fruits and leaves, as well as with TAC for ripe berries (blackberry, raspberry, and strawberry). Therefore, changes in the TAA of strawberry fruits at harvest and during cold storage could be due to the changes in these compounds. In the present study, a higher TAA content was recorded in MJ-treated fruits. Similarly, Wang et al. (2019) reported that postharvest application of MJ

significantly increased the antioxidant capacity of blueberry fruits by increasing the enzymatic and non-enzymatic antioxidants. Furthermore, García-Pastor et al. (2019) reported that TAA [hydrophilic (H-TAA) and lipophilic (L-TAA) fractions] was higher in arils of pomegranate fruits treated with pre-harvest MJ than in the controls at harvest and during 60 days of cold storage.

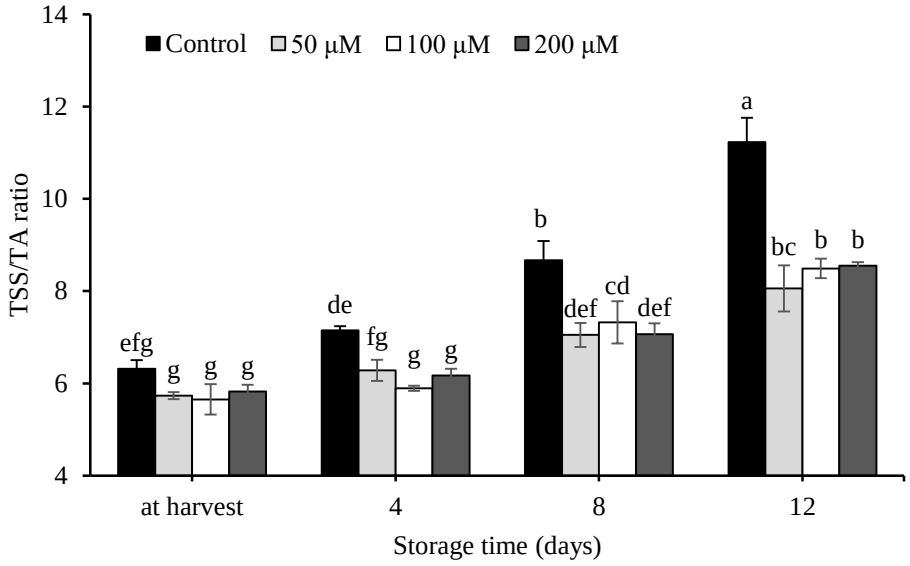

Fig. 2. Effect of methyl jasmonate (MJ) pre-harvest treatment on TSS/TA ratio of strawberry fruit cv. Paros during 12 days of storage. Mean ± SE (n=3), followed by different letters are significantly different (P<0.05).

Table 3. Effect of methyl jasmonate (MJ) pre-harvest treatment on ascorbic acid (AsA), total antioxidant activity (TAA), and antioxidant enzyme of strawberry fruit cv. Paros during 12 days of storage.

Storage time (day)	MJ (µM)	AsA (mg 100 g^{-1}FW)	TAA (%DPPHsc)	Catalase (U min^{-1} g^{-1} FW)	APX (U min^{-1} g^{-1} FW)
0 (at harvest)	0	68.56±2.31 abc	72.56±2.31 ghi	12.64±0.52 ghi	39.23±1.14 e
	50	69.27±1.44 ab	74.83±1.78 efg	12.31±0.31 hi	41.52±0.45 cde
	100	71.78±1.72 a	72.59±1.02 ghi	13.60±0.28 ef	42.91±0.37 c
	200	69.71±0.97 a	77.67±1.29 cdef	13.50±0.38 efg	42.60±1.21 cd
4	0	62.17±1.22 efg	74.08±1.29 efgh	14.25±0.36 de	42.64±0.36 cd
	50	65.37±0.59 cde	75.38±0.45 defg	15.20±0.21 abc	50.27±1.02 b
	100	63.84±0.91 def	85.63±1.28 ab	15.85±0.10 a	55.35±1.44 a
	200	65.83±1.34 bcd	79.89±2.56 cd	15.52±0.25 ab	52.27±0.71 b
8	0	53.09±1.16 h	75.65±1.72 defg	12.90±0.39 fgh	32.81±1.24 fg
	50	60.48±0.76 fg	79.03±2.74 cde	14.25±0.38 de	40.75±0.76 cde
	100	59.09±1.08 f	86.36±1.37 a	13.86±0.25 de	39.77±0.81 de
	200	61.29±1.72 fg	81.14±0.99 bc	14.62±0.33 cd	43.13±1.79 c
12	0	42.63±0.73 i	60.04±1.48 j	11.81±0.26 i	23.42±0.98 i
	50	51.81±1.10 g	68.90±0.95 i	13.44±0.21 efg	31.27±1.05 gh
	100	54.11±1.19 g	73.33±2.40 fgh	14.65±0.23 bcd	35.05±1.29 f
	200	53.46±0.30 g	69.73±2.39 hi	13.80±0.14 de	29.15±0.79 h

Means±SE (n = 3) within each column covered by the same letter are not significantly different (*P<0.05*) APX, ascorbate peroxidase.

Antioxidant enzymes activity

The results indicated that activities of catalase (CAT) and ascorbate peroxidase (APX) enzymes in strawberry fruit were influenced by the storage time, MJ treatment, and their interaction, while guaiacol peroxidase (GPX) activity was only affected by storage time (Table 1). Pre-harvest applications of MJ to strawberry plants increased the antioxidant enzyme activities of CAT and APX compared to the control at harvest, conversely, the activity of GPX enzyme in treated fruits was lower than control. During the cold storage, CAT and APX enzyme activities in control and MJ-treated strawberry fruits initially increased (up to day 4) and then decreased until the end of storage with a slower decrease in treated fruits. At the end of storage, the highest CAT (14.65 U min^{-1} g^{-1} FW) and APX (35.05 U min^{-1} g^{-1} FW) activities were observed in MJ-treated fruit with 100 µM, whereas the lowest CAT (11.81 U min^{-1} g^{-1} FW) and APX (23.42 U min^{-1} g^{-1} FW) activities were found in the control sample (Table 3). GPX enzyme activity was significantly reduced with increasing MJ concentration in strawberry fruits. The minimum GPX activity (12.36 U min^{-1} g^{-1} FW) of strawberry fruit was observed in the 200 µM MJ treatment and the maximum GPX activity (15.83 U min^{-1} g^{-1} FW) was recorded in the control sample (Table 2).

The senescence process in stored fruits is accelerated by reactive oxygen species (ROS) production, which leads to oxidative damage and a decline in fruit quality and bioactive compounds. SOD, APX, and CAT are crucial enzymatic antioxidants that play a key role in the antioxidant system, mainly by scavenging ROS and protecting cells from oxidative damage. SOD converts superoxide radicals into hydrogen peroxide, which is then converted into water by CAT and APX (Wang et al., 2019). Shah et al. (2025) reported that pre-harvest MJ treatment in raspberry fruits suppressed H_2O_2 production during cold storage, potentially due to increased activity of SOD and CAT enzymes. In our study, MJ increased the activity of CAT and APX as antioxidant and defense enzymes, which was associated with better fruit quality attributes compared to the control group. In alignment with our results, Yang et al. (2025) reported that CAT activity in kiwifruit treated with pre- or postharvest MJ was significantly higher compared to the control, while GPX activity was significantly higher in the control sample. Liao et al. (2022) also observed that the activity of APX, SOD, CAT, and POD enzymes increased during cold storage in control and MJ-treated lemon fruits, and this increase was significantly higher in the fruit treated with both pre- and postharvest MJ compared to the control fruits. Furthermore, Li et al. (2018) reported that MJ induced higher gene expression of ROS scavenging enzymes in fresh-cut pitaya fruit, leading to higher enzymatic activity in the treated fruits.

CONCLUSION

Pre-harvest application of MJ treatment showed a beneficial effect on the quality parameters of strawberry fruits. The results of the present study indicate the pre-harvest application of MJ reduces the loss of TA, ASA, firmness, and PLW at cold storage. All pre-harvest MJ concentrations displayed higher TAC, TPC, and TAA content than the control fruit at the end of cold storage. In addition, treated fruits had higher CAT and APX activities and lower GPX compared to control samples. The TSS content of strawberry fruit was not affected by pre-harvest MJ treatment at harvest time and during cold storage. The antioxidant activity of MJ-treated fruits was improved by increasing the activity of antioxidant enzymes and preserving bioactive compounds during cold storage. In conclusion, pre-harvest MJ treatment, especially at 200 µM, can be used to maintain the quality and antioxidant properties of strawberry fruits at harvest and during cold storage.

Conflict of interest

The authors declare that there is no conflict of interest.

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