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Pre- and post-harvest treatments with phytohormones reduce the incidence of *Botrytis cinerea* in strawberries

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Abstract

Botrytis cinerea rot is the main cause of post-harvest losses in strawberries. For this reason, the objective of this study was to evaluate the effect of pre- and post-harvest applications of salicylic acid (SA) and methyl jasmonate (MeJA) on the incidence of *B. cinerea* in strawberry fruit. The experiment was divided into two stages. In the first stage, applications of the fungicide Fontelis®, 4 and 6 mM SA, and water (as the Control), in flowering *cv* '3128' strawberry plants, at 7-day intervals. The fruits were harvested on day 28. In the second stage, fruits were treated post-harvest with 4 and 6 mM SA, 0.05 and 0.10 mM MeJA, and their respective Control. In both stages, the incidence of *B. cinerea* and quality parameters were measured. After 12 days of storage, the pre-harvest application at 4 and 6 mM SA reduced the incidence of *B. cinerea* by up to 11.4 % compared to control fruit. Meanwhile, the post-harvest application of 0.10 mM MeJA and 4 and 6 mM SA reduced the incidence of the disease by 12.76 %. Additionally, pre- and post-harvest applications of SA and MeJA delayed signs of senescence and maintained quality parameters for up to 12 days. In conclusion, phytohormone treatments are a sustainable alternative to fungicides for controlling the development of *Botrytis cinerea*, extending shelf life, and maintaining the quality of strawberry fruit.

Keywords: *B. cinerea*, salicylic acid, strawberry, incidence, methyl jasmonate.

Introduction

Mexico is one of the world's leading strawberry producers, with an annual output of 641,552 tons, of which 86, 489 tons were exported to the United States, generating revenue of 3,258,924.83 million pesos (FAOSTAT, 2025; Sistema de Información de Producción Agrícola y Pecuaria de México, 2024). Strawberry production and exports can be affected by various pre- and post-harvest factors. Among the main causes of strawberry fruit loss in both stages is the presence of *Botrytis cinerea*. This fungus is considered the second most important phytopathogen in terms of agroeconomic significance, due to its wide range of hosts, causing damage and negatively impacting shelf life and quality (Youssef et al., 2019).

To control the incidence of *B. cinerea*, conventional synthetic fungicides such as Captan® and Fontelis®, among others, are commonly used to help control the infection in the crop. However, some of these fungicides are no longer effective because *B. cinerea has developed resistance* (Hahn, 2014). To achieve effective and safe control of *B. cinerea*, alternative measures must be taken. In this regard, it has been reported that the application of treatments based on phytohormones such as salicylic acid (SA) and methyl jasmonate (MeJA) has shown positive results in plants and their organs since they induce fungistatic activity against *Botrytis* (Dieryckx et al., 2015; Jeyasri et al., 2023).

Salicylic acid (SA) is a simple phenolic compound that activates plant defense systems, particularly the Systemic Acquired Resistance (SAR) (Kumar, 2014). The defense provided by SA acts mainly against biotrophs. Furthermore, it has been observed that spraying with this phytohormone induces increased expression of genes related to flavonoid synthesis and proanthocyanidin accumulation, as well as expression of genes related to pathogenesis (Feng et al., 2020). On the other

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hand, exogenous application of MeJA regulates defense responses, enhancing the production of secondary metabolites, increasing the activity of antioxidant enzymes, and upregulating the expression of genes associated with plant defense (Jeyasri et al., 2023). In this context, the study focused on evaluating the effect of phytohormones (salicylic acid and methyl jasmonate) applied pre- and post-harvest to reduce the incidence of the *Botrytis cinerea* fungus and preserve fruit quality, with the advantage that these treatments can replace the use of fungicides, thereby generating effective and sustainable control strategies for strawberries.

Materials and Methods

General research design

The study was conducted in two stages. In the first stage, applications of the Fontelis® (Corteva Agriscience) fungicide, SA at 4 and 6 mM, and water as control were applied to flowering *cv* '3128' strawberry plants at 7 day intervals. In the second stage, post-harvest fruits were treated with SA at 4 and 6 mM, MeJA at 0.05 and 0.10 mM, and water as Control.

The field treatments were applied during the first stage in a commercial strawberry farm under open-field cultivation technology, located in Camalú, Baja California (30°50'16" N and 116°03'26" W, elevation 21 m above sea level). During the crop's flowering stage, the four treatments were applied to the *cv*. '3128' strawberry plants: SA at two different concentrations (4 and 6 mM), Fontelis® commercial fungicide (200 $g \cdot L^{-1}$), and the control (water) treatment. These treatments were applied in triplicate to 225 plants over 21 days. Each treatment was applied at 7 day intervals (0, 7, 14, and 21 days). The fruits were harvested at commercial maturity 28 days after the first application, and were subsequently placed in 170 g clamshell containers for refrigerated air transport to the Laboratory of Post-Harvest Physiology and Biochemistry of Fruits and Vegetables in the Graduate Program in Food Science at the Autonomous University of Querétaro (UAQ), Mexico, under refrigerated conditions.

For the second stage, involving post-harvest treatments, fruits were harvested from the same commercial orchard at commercial maturity and treated only with the Fontelis® fungicide. The fruits were packaged in 170 g clamshells and transported by air to the Laboratory of Post-Harvest Physiology and Biochemistry of Fruits and Vegetables at the UAQ under refrigerated conditions. In the laboratory, using a spray bottle, SA solutions at 4 and 6 mM and MeJA solutions at 0.05 and 0.10 mM were applied, as well as the control treatment (water).

Preparation of SA and MeJA solutions

The SA solutions were prepared using a modified version of the method described by Haider et al. (2020); salicylic acid (2- hydroxybenzoic acid, molecular weight 138.125 $g \cdot mol^{-1}$, and purity 99 %, Baker Analyzed), needed to prepare final solutions of 4 and 6 mM was dissolved in 3 % ethanol, distilled water was then added (3 L of ethanol in 7 L of distilled water). MeJA solutions at concentrations of 0.05 and 0.10 mM were prepared using the methodology suggested by Saavedra et al. (2017) with modifications; methyl jasmonate (molecular weight 224.30 $g \cdot mol^{-1}$ and 95 % purity, Sigma-Aldrich®) was dissolved in distilled water with 0.05 % (v/v) Tween-20 as a surfactant agent. The Fontelis® fungicide (a.i. pentiopirad 200 $g \cdot L^{-1}$) was prepared according to the technical data sheet and dissolved in water (1.5 $L \cdot ha^{-1}$ of Fontelis® in 500 L of water $\cdot ha^{-1}$). Field applications of SA and Fontelis® were performed using a backpack sprayer, and post-harvest applications of MeJA and SA were performed by atomization.

Inoculation of *Botrytis cinerea* in strawberry fruits

Strawberry fruit inoculation was performed using the methodology described by Saavedra et al. (2017), with slight modifications. The fruits were superficially disinfected with a 1.5 % sodium hypochlorite (NaClO) solution for 1 min and then washed with sterile distilled water. Excess water was then removed with absorbent paper, and inoculation was conducted at the equator of each fruit using a sterile syringe to apply a 20 µL aliquot of suspension containing 1×10^5 spores $\cdot mL^{-1}$.

Measurement of *Botrytis cinerea* incidence

The presence of *B. cinerea* was evaluated at 0, 4, 8, and 12 days on strawberry fruits treated during storage (1 °C; 90 % relative humidity). The fruit surface was examined to determine the presence (decayed area) or absence of infection. Fruit showing gray mold (*B. cinerea*) was considered damaged, and the incidence of the disease was calculated using the Equation (1) (Haider et al., 2020).

$$Incidence\ (\%) = \frac{Number\ of\ damaged\ fruits}{Total\ number\ of\ fruits} \times 100 \quad (1)$$

Fruit quality

Weight loss. This was determined using the methodology described by Muncan et al. (2022). The fruits were weighed at 0, 4, 8, and 12 days on an analytical balance. The rate of weight loss was calculated based on the difference in weight between the first measurement (day 0) and the day of sampling using Equation (2).

$$Weight\ loss\ (\%) = \frac{(Initial\ weight - Final\ weight)}{Initial\ weight} \times 100 \quad (2)$$

Firmness. This was determined using a CT3 texture analyzer (Brookfield, Canada). A cylindrical probe with a diameter of 25.4 mm was used, which compressed 10 % of the strawberry's maximum diameter at a speed of 1 $mm \cdot s^{-1}$ and an activation load of 0.10 N (Hernández-Muñoz et al., 2008). The results were expressed as the force required (N) to compress 10 % of the fruit's maximum diameter.

Titratable acidity and total soluble solids. An aqueous extract was prepared using 3 g of strawberries and 35 mL of distilled water; it was then homogenized using an Ultraturrax T-25 (IKA, Staufen, Germany) at 10,000 rpm for 1 min. The homogenized sample was centrifuged for 15 min at 10,000 rpm and 4 °C. The supernatant was filtered through a filter cloth. Ten mL of the aqueous extract was taken and titrated with NaOH 0.01 N until a pH of 8.2 ± 0.2 (Association of Official Analytical Chemists [AOAC], 1990).

The titratable acidity was expressed as the percentage of citric acid in 100 g of sample using Equation (3).

$$\%\ Acidity = \frac{\text{Volume of NaOH consumed} * \text{N(NaOH)} * Titrated\ volume * meq\ of\ citric\ acid * 100}{\text{Sample volume} * \text{Sample weight} * 1000} \quad (3)$$

To determine total soluble solids (TSS, °Brix), a sample of the aqueous extract was taken and placed in a digital refractometer (A. Krüss Optronic GmbH, Germany). The TSS result was expressed in degrees Brix.

Experimental design and statistical analysis

For the first stage (pre-harvest), a completely randomized experimental design with three replicates was established, in which the treatments were: SA, at concentrations of 4 and 6 mM, Fontelis® fungicide (200 $g \cdot L^{-1}$), and the Control (water). For the second stage, a completely randomized experimental design with three replicates was conducted, evaluating the following treatments: SA at 4 and 6 mM, MeJA at 0, 0.05 and 0.10 mM, and a Control treatment (water). In both stages, the fruits were evaluated at 0, 4, 8, and 12 days of post-harvest storage. Six clamshells of strawberries were used as the experimental unit during post-harvest. The response variables were statistically analyzed using the JMP statistical package via a one-way analysis of variance (ANOVA), and for the data showing differences, a comparison of means was carried out using Tukey's test ($p < 0.05$). To statistically evaluate the incidence variable, the mixed generalized linear model (MGMM) was applied, which allows for the use of a logistic regression model that considers treatment, days of storage, and treatment*day interaction as fixed factors and the fruits as random factors (observations of infected or uninfected fruits are random).

Results and discussion

Effect of pre-harvest application of salicylic acid (SA) on strawberry fruit

The pre-harvest application of salicylic acid (SA) reduced the incidence of *B. cinerea* on strawberries; field application reduced fruit rot during storage; fruits treated with SA and commercial fungicide (Fontelis®) showed the same percentage of gray mold (*B. cinerea*) incidence, which was lower compared to fruits in the Control treatment. After 4 days of storage, strawberries treated with 4 mM of SA showed a 12.1 % reduction in rot compared to the Control. On the other hand, fruits sprayed with the 6 mM SA solution showed an 8.3 % decrease compared to the Control treatment, suggesting that the 4 mM SA concentration was the most effective at inhibiting the development of *B. cinerea*.

By the 8th day of storage, the fruits in all treatment groups showed an increase in the incidence of *B. cinerea*. However, the treatments with 4 mM SA and the commercial fungicide reduced rot by 4.1 % compared to the Control. On the other hand, the application of 6 mM SA did not reduce the presence of gray mold on the strawberries, which showed a higher incidence compared to the Control treatment. At the end of storage on day 12, the Control fruit showed the highest incidence of *B. cinerea* (28 %), which was 1.7 times higher than the fruit treated with commercial fungicide and salicylic acid at 4 and 6 *m*M (Table 1). These results indicate that treatment with 4 mM SA is an alternative just as effective as the commercial fungicide for reducing rot caused by *B. cinerea*.

The overall analysis using the generalized mixed linear model (MGMM) (Table 2), indicated that the treatment factor was significant ($p < 0.05$). The non-significance of

Table 1. Effect of pre-harvest application of salicylic acid (SA) on the incidence of *Botrytis cinerea* in *n* '3128' strawberries during storage at 1 °C and 90 % relative humidity.

Storage time	Control	Fungicide (Fontelis® 1.5 L/ha)	4 mM SA	6 mM SA
Day 0	0.0 %	0.0 %	0.0 %	0.0 %
Day 4	4/25=16.6 %	1/25=4.5 %	1/25=4.5%	2/25=8.3 %
Day 8	4/25=16.6 %	3/25=12.5 %	3/25=12. 5%	5/25=20.0 %
Day 12	7/25=28.0 %	4/25=16.6 %	4/25=16.6 %	5/25=20.0%

Table 2. Statistical significance of the fixed experimental factors on the incidence of *Botrytis cinerea* in strawberry fruits.

Fixed factors	Probability (p-value)	Significance (α=0.05)
Treatment	0.015	**Significant**
Day	0.098	Not significant
Treatment*day	0.380	Not significant

the day factor suggests that there was no significant overall increase in the incidence of infection as storage progressed, while the non-significance of the treatment*day interaction suggested that the progression of infection did not differ significantly among treatments. However, the significant effect of the treatment factor indicated that, although there was no difference due to the effect of time, there was a significant effect of the treatment applied.

These findings are consistent with those reported by other authors, who demonstrated that SA at 1 mM exhibited an inhibitory effect against gray mold in *cv* Festival strawberry fruit, comparable to that of the fungicide fenhexamid (Sekina et al., 2022). The reduction in fruit rot is attributed to increased disease resistance within the fruit (Haider et al., 2020). Furthermore, as shown in Figure 1, SA applied in the field did not affect the visual quality of the fruit, which was preserved for at least 12 days of storage.

The pre-harvest application of SA delays senescence in strawberries. Weight loss and firmness are variables closely related to the senescence of strawberry fruits, with fruits exhibiting high weight loss and reduced firmness having a shorter shelf life. Weight loss increased as storage progressed. However, the comparison of means for each day of storage showed no significant differences in weight loss between treatments on days 4 and 12 of storage at 1°C. Meanwhile, on day 8, significant differences were observed between the applied treatments (Figure 2A). Fruits from the Control treatment showed greater weight loss (5.9 %), while fruits treated with 4 mM SA showed the lowest values (3.5%).

Regarding firmness, the fruits on day 0 did not differ statistically among the studied treatments, with values ranging from 20.1 to 22.6 N. The overall variance analysis indicated that neither the treatment nor the treatment*day interaction was significant (p-values > 0.05), and only the storage day factor was significant ($p < 0.05$). In this regard, days 4 and 8 showed the highest firmness values, and day 12 the lowest (Figure 2B).

The decrease in firmness across all treatments was as expected, due to the natural aging process of the fruit. Nonetheless, although no significant differences were observed, the fruits from the SA treatments showed a tendency toward higher firmness.

To assess whether SA applications affect fruit flavor, analyses of acidity and TSS were conducted. From day 0 through day 12 of storage, fruits treated with SA had a TSS content ranging from 8.9 to 13.8 % (Figure 2D), which is higher than the minimum 7 % TSS that strawberries should have (Mitcham, 2023). At the end of the

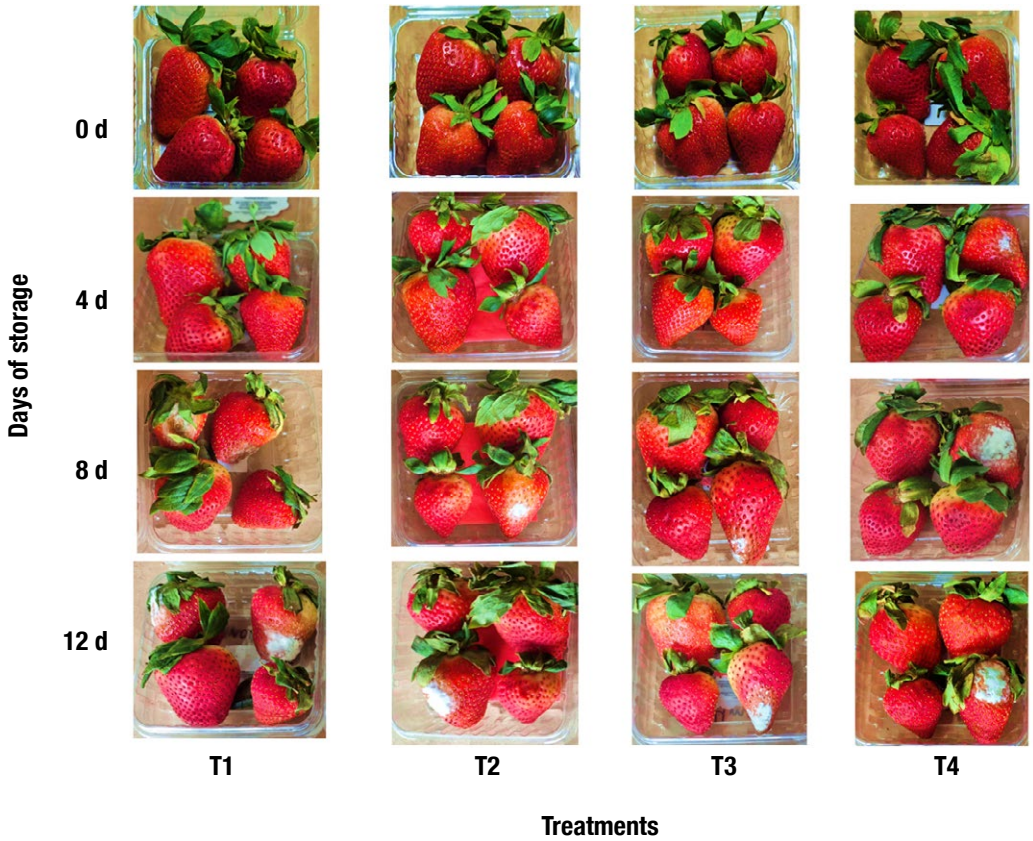


Figure 1. Changes in the incidence of *Botrytis cinerea* on *cv* '3128' strawberry fruits treated pre-harvest with Fontelis® and SA. T1 (control), T2 (Fontelis fungicide), T3 (4 mM SA), and T4 (6 mM SA), on days 0, 4, 8, and 12 of storage at 1 °C and 90 % RH.

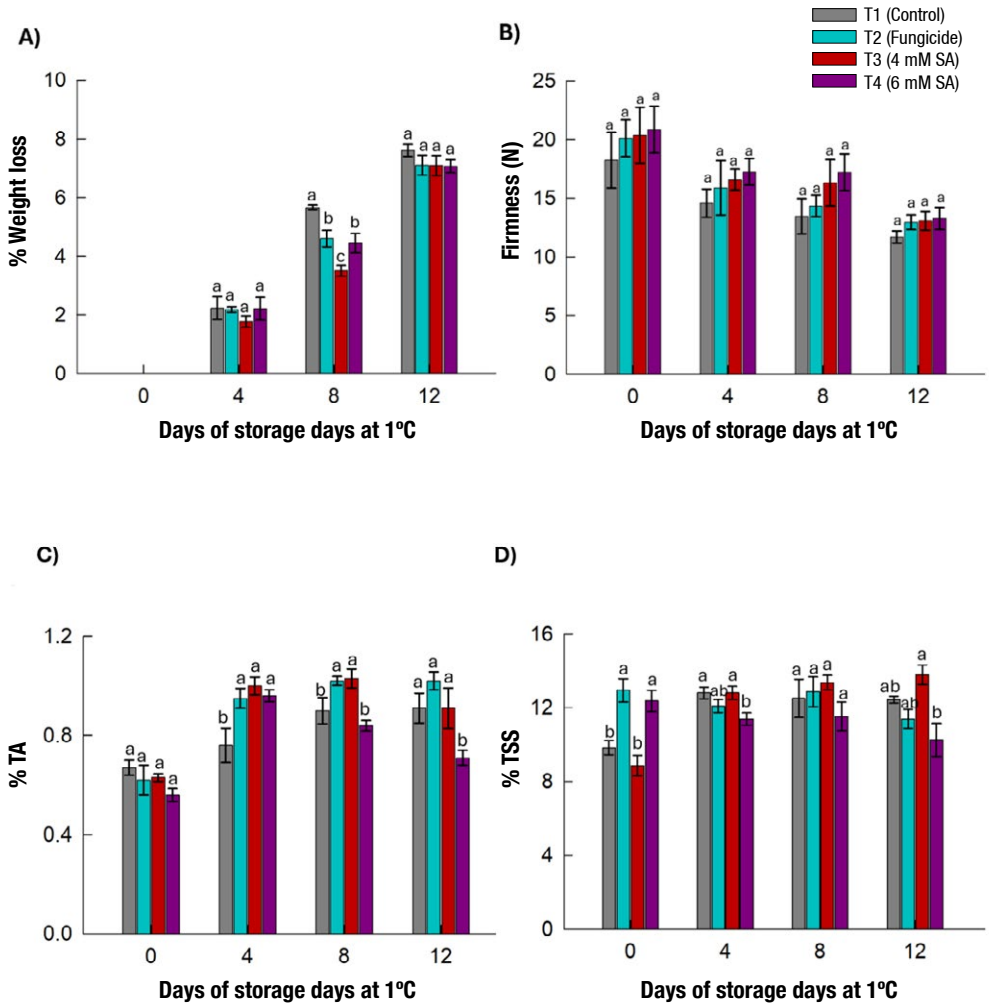


Figure 2. Pre-harvest applications of salicylic acid delay senescence in strawberries and maintain acceptable flavor in the fruit. A) % Weight loss B) Firmness (N), C) % TA, and D) % TSS.

12-day storage period, SA-treated fruits showed higher TSS content (13.78 %) compared to untreated fruits. On the other hand, regarding acidity, at the start of the storage period (day 0), no significant differences were found among all treatments (0.57-0.67). Starting on day 8, the treatment with the fungicide and 4 mM SA recorded the highest acidity values, while the Control treatment and those treated with 6 mM SA recorded the lowest values (Figure 2C). The high acidity percentage obtained may be due to the variety used and cannot necessarily be attributed to the treatments, as the untreated fruits exhibited similar behavior. These results suggest that fruits treated with SA may have a flavor acceptable for consumers, being slightly acidic and sweet, in addition to delaying senescence.

Effect of post-harvest application of SA and MeJA on strawberry fruit

Post-harvest applications of SA and MeJA reduced the incidence of *B. cinerea* in inoculated strawberry fruits (Table 3). The treatments were observed to reduce the presence of rot; the incidence of *B. cinerea* in fruits treated with MeJA and SA was lower compared to the incidence observed in untreated fruits. On day 4 of storage, fruits treated with 4 mM SA and 0.05 mM MeJA showed no symptoms of *B. cinerea*, suggesting that these concentrations are optimal for inhibiting the development of gray mold during short storage periods.

Starting on the 8th day of storage, strawberries treated with 6 mM SA and 0.05 and 0.10 mM MeJA showed the lowest incidence of rot, at 4.5 %, a level that remained stable through the 12th day; this is significantly lower than the 16.6 % (Figure 3). These results suggest that the post-harvest application of SA and MeJA is an effective method that significantly reduces rot caused by *B. cinerea*, thereby extending the shelf life of strawberries.

Statistical analysis using a generalized linear mixed model on the data regarding the incidence of *B. cinerea* indicated significant effects of treatment and the treatment*day storage interaction, as well as a highly significant effect

Table 3. Effect of post-harvest application of salicylic acid (SA) and methyl jasmonate (MeJA) on the incidence of *Botrytis cinerea* in *cv* '3128' strawberry fruit during storage at 1 °C and 90 % RH.

Storage time	Control	0.05 mM MeJA	0.10 mM MeJA	4 mM SA	6 mM SA
Day 0	0.0 %	0.0 %	0.0 %	0.0 %	0.0 %
Day 4	1/25 = 4.5 %	0.0 %	1/25 = 4.5 %	0.0 %	1/25 =4.5 %
Day 8	3/25 = 12.5 %	1/25 = 4.5 %	1/25 = 4.5 %	2/25 = 8.3 %	1/25 = 4.5 %
Day 12	4/25 = 16.6 %	1/25 = 4.5 %	1/25 = 4.5 %	2/25 = 8.3 %	1/25 = 4.5 %

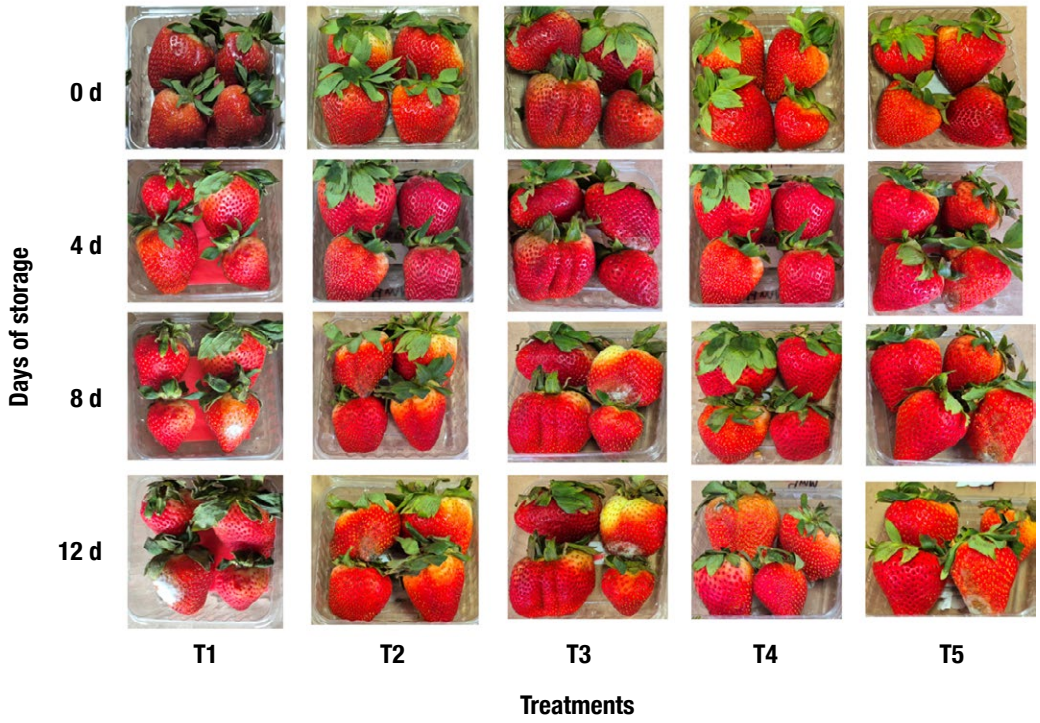


Figure 3. Changes in the incidence of *Botrytis cinerea* in cv '3128' strawberry fruits treated post-harvest with SA and MeJA. T1 (untreated control), T2 (0.05 mM MeJA), T3 (0.10 mM MeJA), T4 (4 mM SA), and T5 (6 mM SA), on days 0, 4, 8, and 12 of storage at 1 °C and 90 % RH.

of storage days at 1 °C (Table 4). Comparable observations have been reported for different fruits. Yu et al. (2009) reported that MeJA applied to harvested tomatoes delayed the appearance of *B. cinerea* during the first 6 days of storage. Similarly, Vaezi et al. (2022) reported that MeJA at 0.01 and 0.10 mM significantly reduced gray mold rot in *cv* 'Sabrosa' strawberries, with 2.66 % decay observed after 12 days of storage.

Quality of post-harvest treated fruits

The MeJA and SA treatments yielded positive results in maintaining quality parameters. After 4 days of storage, fruits treated post-harvest with 4 mM SA lost less weight than the rest of the fruits. At 8 days of storage, fruits treated with 4 mM SA maintained the lowest water loss. Nonetheless, fruits treated with 0.10 mM MeJA significantly reduced their water loss, decreasing weight loss by 1.0 and 2.2 times, respectively, compared to fruits in the control treatment (Figure 4A). Likewise, after 12 days of storage, regardless of concentration, all fruits treated with SA and MeJA exhibited lower weight loss compared to those in the Control treatment, suggesting that the post-harvest application of SA and MeJA helps reduce water loss in the fruits. Similar observations have been previously reported in different fruits. Haider et al. (2020) reported that mandarin fruits treated post-harvest with 4 mM SA lost 11.97 % less weight than control fruits.

On the other hand, fruits treated with SA and MeJA, regardless of concentration, showed no significant changes in firmness during storage. However, fruits treated with MeJA at both concentrations and SA at 4 mM remained firmer on day 12 of storage (Figure 4B). These results indicate that the application of SA at concentrations of 4 and 6 mM and MeJA at 0.05 and 0.10 mM reduces weight loss and main-

Table 4. Statistical significance values for the fixed experimental factors affecting the incidence of *Botrytis cinerea* on strawberry fruits treated with 4 and 6 mM SA and with MeJA (0.05 and 0.10 mM).

Fixed factors	Probability (*p*-value)	Significance α=0.05
Treatment	0.013	Significant
Day	<0.0001	Highly significant
Treatment*day	0.021	Significant

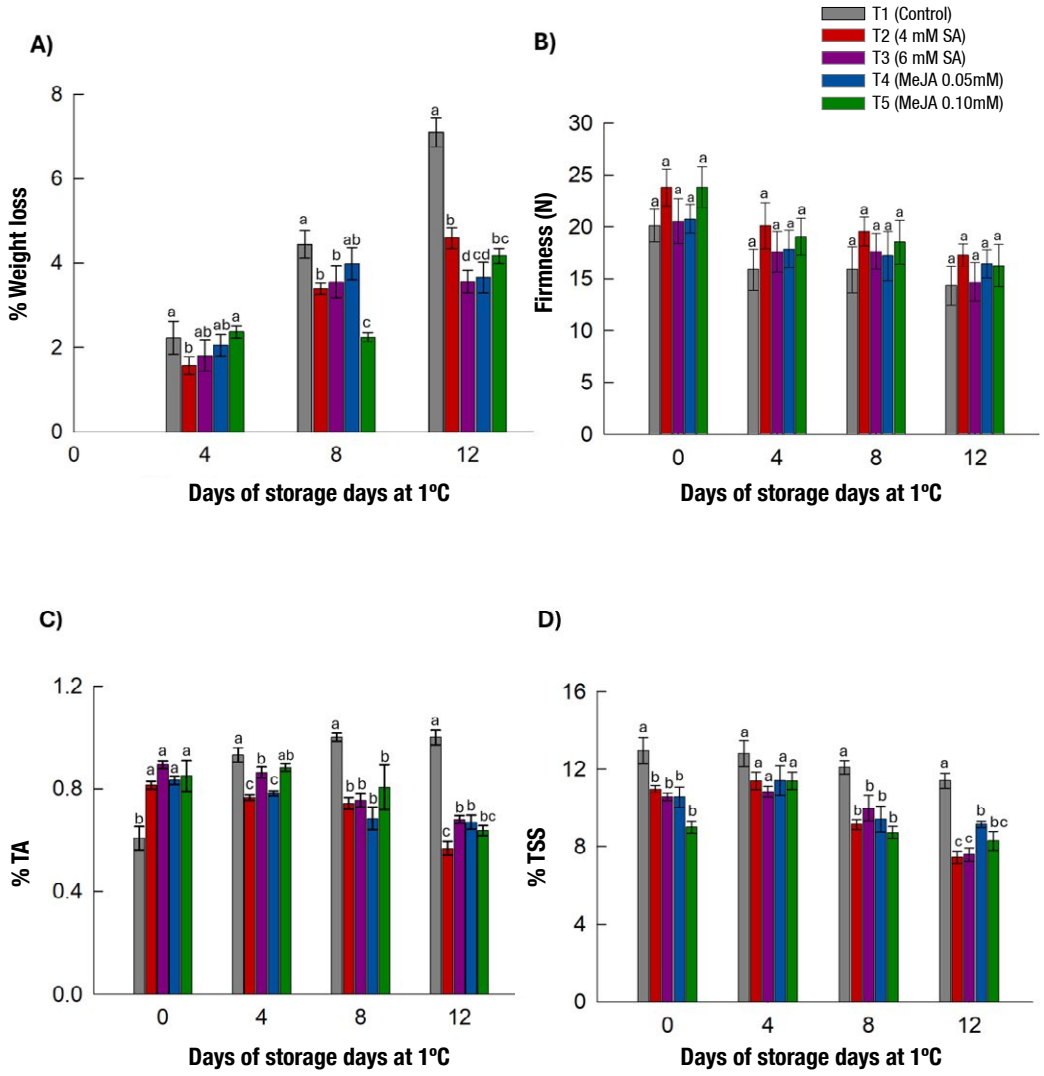


Figure 4. Post-harvest applications of salicylic acid (SA) and methyl jasmonate (MeJA) to strawberries and their effect on quality. A) % Weight loss, B) Firmness (N), C) % TSS, and D) % TA (total acidity).

tains firmness for more than 12 days, which translates into an increase in the product's shelf life, allowing producers to market the strawberries for a longer period.

With regard to the quality parameters of acidity and TSS, acidity levels showed significant differences throughout storage, with fruits from the Control treatment being slightly more acidic than those treated with SA and MeJA after the fourth day of storage (Figure 4C). Regarding TSS content, it was observed that from day 0 through day 12 of storage, the TSS content of fruits treated with SA and MeJA post-harvest remained within a range of 7.5 – 11.4 % and 8.3 – 11.4 %, respectively, suggesting that these results are above the minimum quality threshold; however, SA-treated fruits had 3.87 % lower TSS content compared to control fruits at the end of the 12-day storage period

(Figure 4D). These results were similar to those reported by Haider et al. (2020), who found higher TSS content in the control treatment compared to SA-treated fruit.

The highest values for acidity and total soluble solids were recorded in the fruits from the Control treatment (1.0 and 12.9 % respectively), while the lowest values for this variable were obtained with the 4 mM SA treatment (0.69 %); regarding TSS, no significant differences were found, with values ranging from 9.3 and 10.0 %. In all treatments, a trend toward a reduction in acidity and total soluble solids content was observed, both in the control treatments and in the fruits treated with SA and MeJA (Figures 4C and 4D). Although these parameters varied during storage, the obtained values indicate that the fruits met the quality standard for strawberries; this acidity range falls within the limits established to meet the maximum quality factor (0.80 % maximum) specified by Mitcham (2023). These results indicated that the fruits treated with SA and MeJA maintained a balance between acidity and TSS, so consumer acceptance should not be affected.

Conclusions

Applications of SA (4 and 6 mM) in pre-harvest and post-harvest and MeJA (0.05 and 0.10 mM) in post-harvest are effective alternative treatments for reducing fruit rot caused by *Botrytis cinerea* and extending the shelf life of the fruit. This indicates that the plants' defense system can be activated to generate resistance against pathogen attacks, without the need to resort to fungicides to control fungal damage to the crop and fruit. In addition, the most important quality parameters for fruit marketing are preserved.

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