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BIOLOGY

# Methyl jasmonate does improve postharvest conservation of 'Golden' papaya fruit

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**ABSTRACT**: *Methyl jasmonate (MeJA) is recognized as a plant hormone that induces several biochemical changes related to improving fruit quality, but it is evident that the effect of MeJA during postharvest is very variable upon concentration, plant species, and even cultivars. The objective of this research was to relate the application of this regulator at low concentration (10 µmol $L^{-1}$ for 24 h) to changes in postharvest physiology, on the incidence of anthracnose and quality of 'Golden' papaya fruit during storage at 24 ± 1°C. From the seventh day of storage, anthracnose incidence was reduced by more than 50% with MeJA treatment. The lesion area after infection was also reduced. Although, MeJA reduced fruit acidity, the ascorbic acid and soluble solids content were not altered during storage with the hormonal treatment. The skin color and pulp firmness showed slight retention. The reduction in ethylene production was accompanied by a reduction of respiration in treated fruits. MeJa increased CAT activity only in the skin whereas SOD activity was not induced by MeJA in both skin and pulp. Although, the increase of CAT from the third day of storage may have contributed to the reduction of lipid peroxidation in the skin, the MDA reduction in the pulp cannot be explained only by CAT activity. In summary, the application of MeJA in 'Golden' papaya reduced the incidence and severity of anthracnose, decreased respiration, ethylene production and lipid peroxidation. It is concluded that the application of MeJA at a low concentration (10 µmol $L^{-1}$) may contribute to anthracnose control in ´Golden`papaya and slows the ripening of fruits.*
**Key words**: *Carica papaya, Colletotrichum gloeosporioides, lipid peroxidation, respiration, ripening.*

## Metil jasmonato contribui para a conservação de mamão 'Golden'

**RESUMO**: *O metil jasmonato (MeJA) é reconhecido como um hormônio vegetal que induz várias alterações bioquímicas relacionadas à qualidade dos frutos, mas é evidente que o efeito do MeJA durante a pós-colheita é muito variável quanto à concentração, espécies de plantas e até mesmo cultivares. O objetivo deste trabalho foi relacionar a aplicação deste regulador em baixa concentração (10 µmol $L^{-1}$ por 24 h) às mudanças na fisiologia pós-colheita, na incidência de antracnose e na qualidade do mamão 'Golden' durante o armazenamento a 24 ± 1 ° C. A partir do sétimo dia de armazenamento, a incidência de antracnose foi reduzida em mais de 50% com o tratamento com MeJA. Incidência da doença também foi reduzida. Embora o MeJA tenha reduzido a acidez dos frutos, os teores de ácido ascórbico e sólidos solúveis não foram alterados durante o armazenamento com o tratamento hormonal. A cor da casca e a firmeza da polpa apresentaram ligeira retenção. A redução na produção de etileno foi acompanhada pela redução da respiração nos frutos tratados. MeJa aumentou a atividade da CAT apenas na casca, enquanto a atividade da SOD não foi induzida por MeJA na casca e na polpa. Embora o aumento da CAT a partir do terceiro dia de armazenamento possa ter contribuído para a redução da peroxidação lipídica na casca, a redução do MDA na polpa não pode ser explicada apenas pela atividade da CAT. Em resumo, a aplicação de MeJA em mamão 'Golden' reduziu a incidência e severidade da antracnose, diminuiu a respiração, a produção de etileno e a peroxidação lipídica. Conclui-se que a aplicação de MeJA em baixa concentração (10 µmol L-1) pode contribuir para o controle da antracnose em mamão ´Golden` e retardar o amadurecimento dos frutos.*
**Palavras-chave**: *Carica papaya, Colletotrichum gloeosporioides, peroxidação lipídica, respiração, amadurecimento.*

## INTRODUCTION

Jasmonic acid (JA) and its methyl ester, methyl jasmonate (MeJA), are potential substances that reduce postharvest biotic and abiotic injuries on a number of horticultural crops, and have been tested to improve the postharvest life of many fruit species (WANG et al., 2021). MeJA treatments decreased fruit decay infected by *Colletotrichum gleosporioides* and *Alternaria alternata* (GONZÁLEZ-AGUILAR

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et al. 2003), among other pathogens, and beneficial effects on fruit quality have also been reported such as reduced losses in fruit weight, firmness, and organic acids and enhanced anthocyanin, total phenolic and ascorbic acid contents (GARCÍA-PASTOR et al., 2019, WANG et al., 2021).

The exogenous application of MeJA can induce a series of physiological and biochemical changes that make fruits acquire resistance to a series of stresses such as oxidative stress that occurs at ripening. Thus, it is not surprising that during postharvest storage with MeJA application an intricate biochemical network of the oxidative network is triggered, such as induction of oxidant and antioxidant enzymes (SERNA-ESCOLANO et al., 2021) as well as physicochemical changes, such as respiration and ethylene production (GLOWACZ & REES, 2015). The effects of exogenous application of MeJA on ethylene production during the ripening process are still not clear enough and seem to be dependent on the species, cultivars, and the physiological state of the fruits at the time of application of the regulator (WANG et al., 2021). Most studies with MeJa on postharvest are focused on its relationship with resistance to pathogens and cold stress (WANG et al., 2019; REHMAN et al., 2018) and few species have been investigated, especially when tropical species are concerned.

This research has the objective to test the hypothesis that the application of MeJA in 'Golden' papaya can delay ripening by decreasing ethylene production and oxidative damage in addition to reducing anthracnose incidence.

## MATERIALS AND METHODS

*Fruit material and MeJA treatment*

Papaya fruit (*Carica papaya* L.) cv. Golden were harvested from a commercial orchard in Linhares, (Espírito Santo State, Brazil) at maturity stage 1 (yellow color covering less than 15% of skin surface) and then transported at 10 ºC to Campinas (São Paulo State, Brazil).

Half of the fruits were placed into hermetic chambers (200 L) containing filter papers moistened with MeJA (10 µmol $L^{-1}$) for 24 h at 24 ºC. The other half was placed in other hermetic chamber at the same temperature conditions but only with distillated water.

*Pathogen inoculation and disease lesion measurement*

After the hormonal treatment, the fruits were placed at 24 ºC and 80-90% RH. Immediately after being removed from the chamber (24 h after initiation of treatment) and after one day of removal (48 h after initiation of treatment), fruits were inoculated with *Colletotrichum gloeosporioides.*, which was isolated from naturally infected papaya fruits showing typical symptoms of anthracnose. The fungus was grown on potato dextrose agar (PDA) for 8 days in growth chambers at 25 °C. A *C. gloeosporioides* spore suspension was prepared by adding 15 mL of distilled water, followed by filtering through sterile cheesecloth. The resulting spore suspension was adjusted to $10^5$ conidia $mL^{-1}$ by using a hemacytometer. 'Golden' papaya was superficially wounded with a chromatographic syringe (Hamilton®) at the equatorial region, and into the wound 10 µL of *C. gloeosporioides* suspension was dispensed (CIA et al., 2007). The fruits were stored at 25 ± 2 °C / 80 ± 5 % RH for 9 days and daily assessed by measuring lesion diameter, with a digital caliper, and rot incidence. The experimental design was completely randomized with three replications and eight fruits per set.

*Physico-chemical analyses*

The physico-chemical analyses were performed in non-inoculated fruit, with or without MeJA treatment. Measurements of pulp firmness and skin color were taken at two opposite positions at the largest diameter of the fruit and then averaged. Fruit skin color was measured using the hue angle (Hº) with a colorimeter (Minolta Chromameter 300, Minolta Camera Co., Japan) and firmness data were recorded in Newtons (N) using a digital penetrometer (53200, Tr Turoni, Italy) fitted with an 8 mm diameter probe tip. Seven replications were used for skin color and pulp firmness analyses, each of which consisted of a single fruit.

Soluble solids (SS) were determined in the juice from pulp using a digital refractometer (Atago PR-101, Atago, Japan), with results expressed in ºBrix. The titratable acidity (TA) was determined by titration with sodium hydroxide (NaOH) 0.1 mol $L^{-1}$ and the results were expressed as % of citric acid. The quantity of ascorbic acid (AA) was determined by adding 5 g of papaya pulp to 25 mL of 1% oxalic acid and then titration this solution with DCIP (2.6-dichlorophenol-indophenol sodium) until the pink color was persistent for 15 seconds. The results were expressed as mg of ascorbic acid per 100 g of pulp (CARVALHO et al., 1990). For SS, AT, and AA four biological replicates were used, each of which consisted of a single fruit.

The samples for respiratory activity and ethylene production were analyzed by gas chromatograph Thermo Finnigan Trace 2000GC

(EUA). The respiration and ethylene production were determined by the difference between the initial (when the vials were closed) and final (after 1 h) gas concentration, expressed as mL $CO_2$ $kg^{-1}$ $h^{-1}$ and µL $C_2H_4$ $kg^{-1}$ $h^{-1}$, respectively (BRON & JACOMINO, 2009). Ten biological replicates were used for respiration and ethylene production, each of which consisted of a single fruit.

*Analysis of lipid peroxidation and antioxidant enzymes*

The analyses were performed in non-inoculated fruit, with or without MeJA treatment. All tissue samples were maintained at -80 °C until they were analyzed. Lipid peroxidation was determined by estimating the content of thiobarbituric acid reactive substances (TBARS) (HEATH & PACKER, 1968). The concentration of malondialdehyde (MDA) equivalents were calculated using an extinction coefficient of $1.55 \times 10^{-5}$ $mol^{-1}$ $cm^{-1}$.

For the extraction and analysis of antioxidant enzymes, the following steps were carried out at 4 ºC unless stated otherwise. Skin and pulp were homogenized (2:1, buffer v/w) in a mortar with a pestle in 100 mM potassium phosphate buffer (pH 7.5) containing 1 mM ethylenediaminetetraacetic acid (EDTA), 3 mM DL-dithiothreitol and 5% (w/v) insoluble polyvinylpolypyrrolidone (GRATÃO et al., 2015). The homogenate was centrifuged at 10,000 *g* for 30 min, and the supernatant was stored in separate aliquots at -80 ºC prior to enzymatic analysis.

CAT (EC 1.11.1.6) activity was assayed spectrophotometrically at 25 ºC in a reaction mixture containing 10 mL 100 mM potassium phosphate buffer (pH 7.5) and 2.5 µL $H_2O_2$ (30% solution), prepared immediately before use. The reaction was initiated by the addition of 35 µL of fruit extract, and the activity was determined by monitoring the removal of $H_2O_2$ at 240 nm over one minute against a plant extract-free blank. CAT activity was expressed as µmol $min^{-1}$ $mg^{-1}$ protein (GRATÃO et al., 2015).

SOD (EC 1.15.1.1) activity staining was carried out as described by BORGES et al. (2018). After non-denaturing-PAGE separation, the gel was rinsed in distilled-deionized water and incubated in the dark, at room temperature, in 50 mM potassium phosphate buffer (pH 7.8) containing 1 mM EDTA, 0.05 mM riboflavin, 0.1 mM nitroblue tetrazolium (NBT) and 0.3% N,N,N′,N′-tetramethylethyllenediamine (TEMED). After 30 min, the gels were rinsed with distilled-deionized water and then illuminated in water until the development of achromatic bands of SOD activity on a purple-stained gel. One unit of bovine liver SOD (Sigma, St. Louis, USA) was used as a positive control of activity.

The protein content was determined by the Bradford method using bovine serum albumin as a standard (BRADFORD, 1976).

For lipid peroxidation and antioxidant enzymes four biological replicates were used, each of which consisted of a single fruit.

*Statistical analysis*

The experimental design was completely randomized, and the dataset was subjected to analysis of variance (ANOVA) and means separated by the Tukey test at 10% of probability by the statistical program SISVAR.

## RESULTS AND DISCUSSION

The application of MeJa 24 h before fruit inoculation did not reduce the incidence and/or severity of anthracnose (data not shown). However, when the inoculation was performed after 48 hours, the regulator reduced the anthracnose incidence from the 7th day of storage (Table 1). Seven days after inoculation the percentage of infection was significantly reduced in the wound sites treated with MeJA (8%) compared to non-treated fruits (38%). Moreover, the lesion area after infection was also reduced (Table 1). Studies have shown that MeJA induces resistance in the host against pathogens (PAN et al., 2020). It is believed that the period used was sufficient for the induction of a resistance response against the pathogen since the induction of systemic resistance and protection happens gradually. The acquired resistance is dependent on signaling mediated by jasmonate to induce secondary metabolites and host resistance to pathogens, as well as stimulating plant stress resistant proteins and defense gene expression (SAAVEDRA et al., 2017). Jasmonate activates genes that transcribe proteins with an anti-fungal action such as thionin (ANDRESEN et al., 1992), osmotina (XU et al., 1994), and several genes involved in the biosynthesis of phytoalexins (GUNDLACH et al., 1992). MeJA has also been effective in reducing injuries caused by *C. gloeosporioides* in ´Sunrise' papaya fruit treated with MeJA at 10 and 100 µmol $L^{-1}$, and stored at 20 ºC (GONZÁLEZ-AGUILAR et al., 2003), indicating that MeJA could be an effective factor for inducing resistance mechanisms in this plant species.

MeJA increased CAT activity in the skin on the third, fourth, and fifth days of storage (Figure 1A) ($P \leq 0.10$). In the pulp, MeJA did not induce CAT activity

Table 1 - Incidence and severity of anthracnose in 'Golden' papaya inoculated after 48 hours of methyl jasmonate (MeJA) treatment*.

| | MeJA | | | |
|---|---|---|---|---|
| | Incidence (%) | | Severity (mm) | |
| Days of storage | 0 µmol $L^{-1}$ | 10 µmol $L^{-1}$ | 0 µmol $L^{-1}$ | 10 µmol $L^{-1}$ |
| 6 | 8 aA | 0 aA | 0.1aA | 0 aA |
| 7 | 38 bB | 8 aAB | 1.7 aA | 0.5 aA |
| 8 | 58 bBC | 29 aBC | 6.5 bB | 3.5 aB |
| 9 | 71 bC | 42 aC | 10.3 bC | 6.3 aC |

*Means followed by the same case letter in the line and capital letter in the column do not differ, by the Tukey test at 10% probability. CV = 32.9 %.

(Figure 1C) ($P \geq 0.10$). During papaya ripening, biochemical changes follow an oxidative burst in the pulp, leading to a higher activity of enzymatic (CAT, SOD) and non-enzymatic (glutathione and ascorbate) antioxidant scavenger systems. Herein, both pulp and peel were analyzed separately. ZHANG et al. (2019), verified differences in tissue structure, antioxidant compounds, and water content between peel and pulp when analyzing table grapes scavenger system and quality attributes. Results showed a clear difference

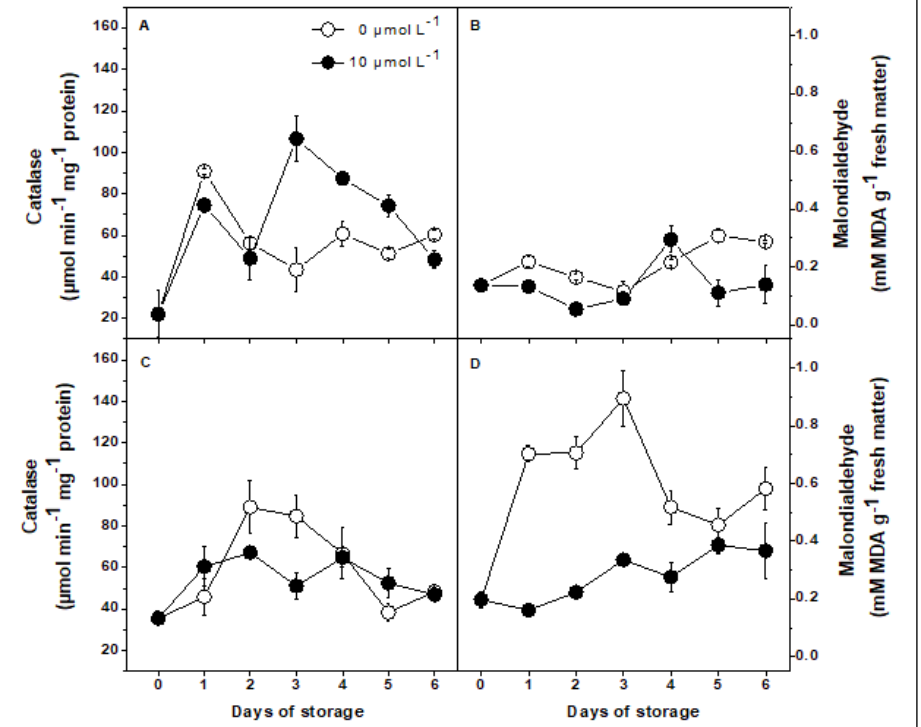


Figure 1 - Activity of catalase (CAT) and lipid peroxidation (MDA) in the skin (A and B) and in the pulp (C and D) of 'Golden' papaya treated with methyl jasmonate and stored at 24 ± 1 °C and 80-90% RH during 6 days. Vertical bars indicate the standard error (n = 4).

between both tissues in 'Golden' papayas, and it is believed that the factors mentioned above might be causing a higher defense ability of papaya skin than pulp under oxidative damage, as also pointed out by ZHANG et al. (2019).

Moreover, the SOD isoenzyme activity pattern, which was observed using non-denaturing PAGE, was not induced by MeJA in both skin and pulp (Figure 2 and 3) ($P \geq 0.10$). Such a result suggested that other components of the antioxidative network are involved in the response to abiotic and biotic stresses (SOARES et al., 2019, CARVALHO et al., 2020) may also be taken part in the response and future research should consider other enzymes and non-enzimatic compounds. MeJA treatment has been extensively associated with the induction of antioxidant compounds in different plant organs of a wide range of species. According to WEI et al., (2017), MeJA increased several antioxidant enzymes activities, such as SOD and CAT. Furthermore, the authors explain that a decrease in CAT activity is expected after the activation of systemic acquired resistance, allowing $H_2O_2$ levels to increase, acting as a second messenger in response to biotic and abiotic stresses (SOARES et al., 2019). WANG et al. (2019), reported an increase in $H_2O_2$ levels after MeJA treatment (10, 50 and 100 µmol $L^{-1}$) concomitantly with an increased CAT activity, and suggested that the $H_2O_2$ role may be complicated by MeJA application with the purpose to regulate postharvest fruit quality.

Much of the research that evaluates CAT and other antioxidants in fruits treated with MeJA is related to cold damage; however, considering the ripening as an oxidative event it is interesting to increase the antioxidant capacity as a way to retard ripening, mainly in tropical fruits. Besides, we showed that CAT is altered and we are now exploring in papaya other compounds, such as a wide range of antioxidant and reactive oxygen species (ROS), under MeJA treatments during biotic and abiotic injuries.

Although, the increase of CAT from the third day of storage may have contributed to reduction of lipid peroxidation in the skin (Figure 1B), the MDA reduction in the pulp cannot be explained only by CAT activity ( Figure 1D). According to ZHANG et al. (2019), MDA is the most important product of membrane lipid peroxidation in fruit. According to WANG et al., (2019), a lower level of MDA and a higher value of DPPH were observed in blueberry MeJA treated with 50 and 100 µmol $L^{-1}$, which could be triggered by the increase of non-enzymatic and enzymatic antioxidants. Certainly, other mechanisms, including other enzymes and ROS are involved in the reduction of lipid peroxidation. In fact, hydrogen peroxide ($H_2O_2$) seems to be a fundamental ROS acting as a signal molecule (SOARES et al., 2019), which is involved, for example, in the increase of host resistance to infection.

Most of the studies demonstrated that the application of exogenous jasmonate promotes the ripening of climacteric fruits by stimulating the production of ethylene. The stimulation of ethylene production is apparently due to the increase in the ethylene forming enzymes, ACC synthase, and ACC oxidase (CZAPSKI & SANIEWSKI, 1992). Differently, we observed that $CO_2$ and ethylene production were reduced during the storage (Figure 4A and C) ($P \leq 0.10$). The effects of exogenous application of MeJA on the production of ethylene during the ripening process are still not sufficiently clear, and appear to be dependent on species, cultivars, concentration, and the physiological state

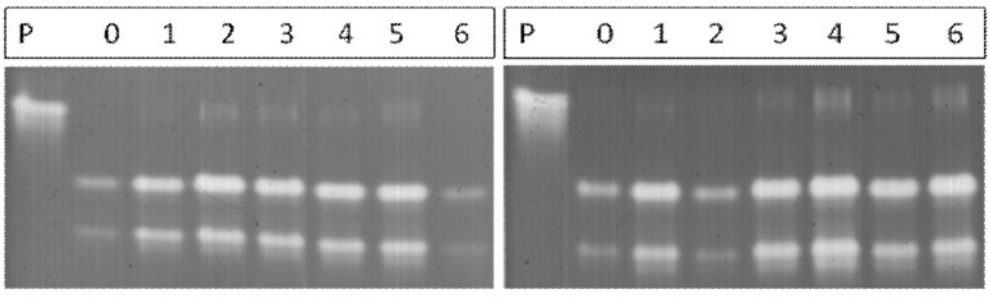


Figure 2 - Activity of superoxide dismutase (SOD) in PAGE gel in the skin of 'Golden' papaya treated (left) and untreated (right) with methyl jasmonate and stored at 24 ± 1 ° C and 80-90% RH for 6 days. Pattern (P) bovine SOD, 0, 1, 2, 3, 4, 5 and 6 represent the days of storage of fruits.

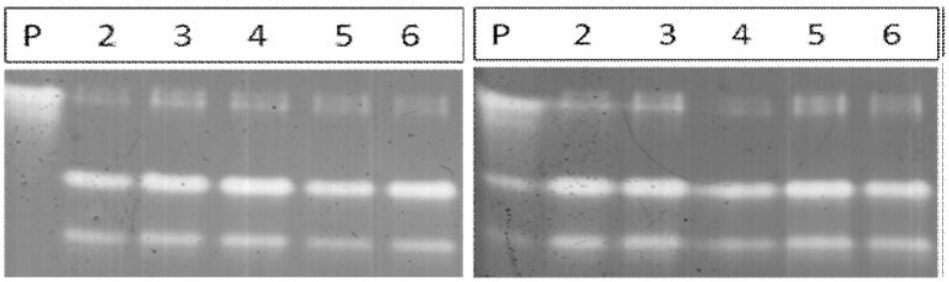


Figure 3 - Activity of superoxide dismutase (SOD) PAGE gel in the pulp of 'Golden' papaya treated (left) and untreated (right) with methyl jasmonate and stored at 24 ± 1 ° C and 80-90% RH for 6 days. Pattern (P) bovine SOD, 0, 1, 2, 3, 4, 5 and 6 represent the days of storage of fruits.

of fruits at the time of application of the regulator. Treatment with MeJA at 0.5 % and 1.0 % promoted ethylene production in apples in the pre-climacteric stage, but reduced the ethylene production when applied in the post-climacteric stage (SANIEWSKI et al., 1987). According to ZAPATA et al. (2014), 'Royal Rosa' plums treated with 2.0 mM MeJA showed increased ethylene production; conversely, when 0.5 mM was applied ethylene was inhibited and the concentration of 1.0 mM MeJA did not show any significant effects. The response to MeJA is also dependent on the cultivar. 'Delicious' apples showed

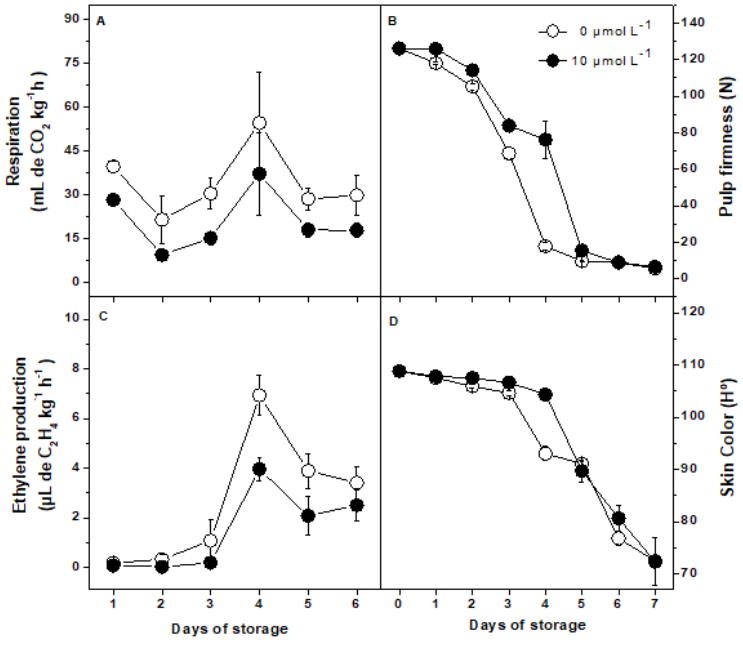


Figure 4 - Respiration (A), ethylene production (C), pulp firmness (B) and skin color (D) of 'Golden' papaya treated with methyl jasmonate and stored at 24 ± 1 ° C and 80-90% RH for 6 days. Vertical bars indicate the standard error of mean (n = 10).

a decrease in ethylene production, while 'Golden Delicious' showed an increase in the production of this hormone (KONDO et al., 2005).

The mechanism by which MeJA affects ethylene production seems to be regulated at a molecular level, with stimulation or inhibition of the responsible genes for its biosynthesis being species specific. Thus, the inhibition of ethylene production by MeJA is supported by the reduced expression of ACC synthase, ACC oxidase, and ethylene receptors transcripts (RUIZ et al., 2013).

The reduction in ethylene production (Figure 4C) ($P \leq 0.10$) was accompanied by a reduction in respiration in treated fruits. The relationship between respiratory rate and MeJA treatment seems to be dependent on species, since, e.g. in mango MeJA did not increase respiration rate (GONZÁLEZ-AGUILAR et al., 2000), whereas in strawberries the contrary was observed (PEREZ et al., 1997). Other studies reported no difference in the respiration rate between treated and untreated fruits, e.g. in mangos treated with MeJA at 100 µmol $L^{-1}$ for 24 h, and subsequently stored at 7 °C (GONZALEZ-AGUILAR et al., 2000), and in papaya treated with MeJA at 10 and 100 µmol $L^{-1}$, stored at 10 °C (GONZALEZ-AGUILAR et al., 2003).

We observed a slight retention in firmness and skin color ($P \leq 0.10$) in MeJA treated fruit (Figure 4B and D). The firmness loss is closely related to the activity of these pectinolytic enzymes, whose activity is related to ethylene with different dependence degrees (JEONG, HUBER & SARGENT, 2002). Loss of firmness was also reduced in papaya MeJA treated at 10 and 100 µmol $L^{-1}$ and stored at 10 °C (GONZALEZ-AGUILAR et al., 2003). The firmness, as well as other characteristics evaluated, seems to be really dependent upon concentration, plant species, and even cultivars. The positive effects of jasmonates on fruit firmness were associated with delayed ripening and senescence (SAYYARI et al., 2011), and reduced oxidative stress (JIN et al., 2012).

Although, MeJA did reduce fruit acidity, ascorbic acid and soluble solids content was not altered during storage with hormonal treatment ($P \geq 0.10$) (Figure 5).

Our results showed that MeJA at low concentration (10 µmol $L^{-1}$) reduced the anthracnose incidence and decreased the respiration, ethylene and

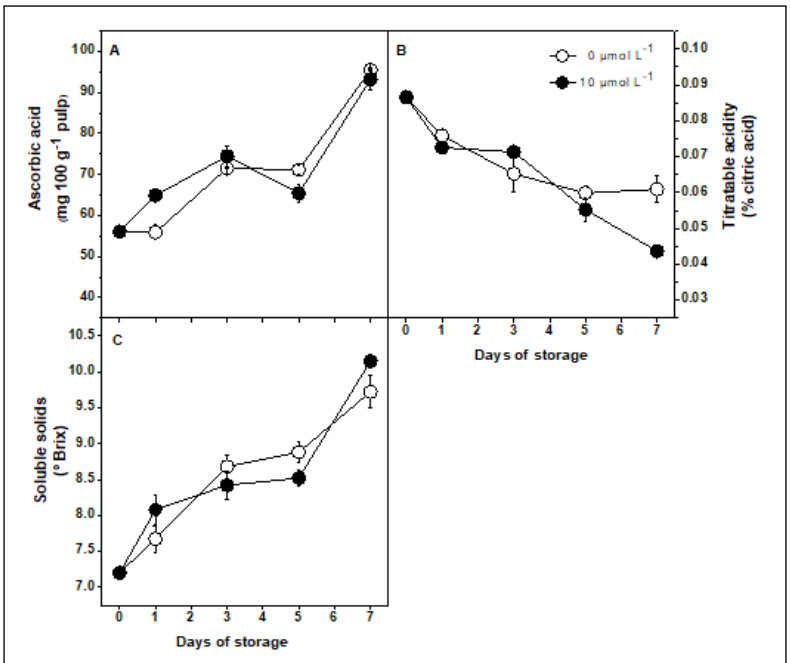


Figure 5 - Ascorbic acid (A), titratable acidity (B) and soluble solids (C) in 'Golden' papaya treated with methyl jasmonate and stored at 24 ± 1 °C and 80-90% RH for 7 days. Vertical bars indicate the standard error of mean (n = 4).

lipid peroxidation. Since MeJA treatment is influenced by several parameters, further investigations are still necessary, mainly in tropical fruits, species with less published studies.

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## DECLARATION OF CONFLICT OF INTEREST

The authors declare no conflict of interest. The founding sponsors had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, and in the decision to publish the results.

## AUTHORS ' CONTRIBUTIONS

IUB, PC, RAA designed the experiments. RPM, ECOR performed the experiments. IUB supervised and coordinated the experiments. BMPS performed the statistical analysis and assisted in the data interpretation. APJ coordinated the ethylene and respiration analyses. RFC assisted in data interpretation and translation. All authors assisted in the writing and critically reviewed the manuscript and approved the final version.

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