



Article

Comparative Analyses of Ripening, Texture Properties and Cell Wall Composition in Three Tropical Fruits Treated with 1-Methylcyclopropene during Cold Storage

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Abstract: Regulation of fruit ripening is one of the most important topics in postharvest storage. Effects of 1-methylcyclopropene (1-MCP) greatly depend on the responsiveness of fruit cultivar to this molecule. Although 1-MCP has been used in postharvest preservation of many fruit species, its effects on ripening process, including ethylene production, and softening of banana, mango, and papaya are still not very clear. In the present study, we comparatively investigated the effects of 1-MCP fumigation treatment (1 $\mu\text{L L}^{-1}$ for 20 h) on ripening behavior and texture qualities of the three fruits during storage at 15 °C. Results showed that 1-MCP treatment not only suppressed the production but also delayed the peak points of ethylene in banana and mango. However, it only significantly delayed the emergence of peak, but didn't suppress the production of ethylene in papaya. Meanwhile, 1-MCP treated papayas showed the lowest malondialdehyde (MDA) content, cell membrane permeability (CMP) and activities of polygalacturonase (PG) and cellulose (CX), accompanied by the highest firmness and protopectin content. Furthermore, 1-MCP treatment slowed down the changes of pulp cell structure in three kinds of fruit. Thus, the findings suggest that postharvest application of 1-MCP has potential in banana and mango fruits due to both prolonging storage-life and ensuring the texture quality, whereas it is not suitable for papaya fruit because of the abnormal softening and the poor texture.

Keywords: ethylene-responsive inhibitor; tropical fruits; ripening and softening; pulp; cell structure



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1. Introduction

Banana (*Musa spp.* AAA Group), mango (*Mangifera indica* L.) and papaya (*Carica papaya* L.), are three of the most extensively explored tropical fruits. For typical climacteric fruits, the large release of ethylene can stimulate the ripening process, leading to rapid softening and deterioration, which results in massive economic loss [1,2]. 1-methylcyclopropene (1-MCP), as a well-established competitive inhibitor of ACC oxidase (ACO) and ethylene synthase (ACS) [3], has become useful tools to delay fruit softening process and maintain postharvest fruit quality [4].

Fruit softening is typical and important characteristic for ripening and senescence process, it is mainly caused by the changes of fruit cell wall structure and composition [5,6]. fruit softening is due to the progressive disassembly of the primary cell wall structure and components including pectin substances, hemicellulose, and cellulose [7,8]. During ripening period of persimmon fruit, flesh cell structure changes obviously, with the extension of storage time, cell vacuolization, separation of cell wall is observed, and cell compositions breakdown in the end of storage time [9].

Numerous studies documented that degradation of cell wall is ascribed to activities of cell wall degrading enzymes, including polygalacturonase (PG), endoglucanase (GLU),

cellulase (CX), pectin methylesterase/pectate lyase (PME/PL), and so on [10]. Moreover, it has been reported that 1-MCP treatment can delay fruit softening through suppressing activities of enzymes involved in cell wall metabolism. Among various cell wall degrading enzymes, PG and CX are thought to be responsible for softening of banana fruit [11].

As a kind of ethylene receptor inhibitors, 1-MCP has several characteristics that make it conveniently useful by the fresh produce industry [12]. Previous research demonstrated that the effects of 1-MCP depended greatly on the responsiveness of the variety to the molecule. The unreasonable use of 1-MCP could lead to certain detrimental effects on fruit, such as peel scalds, rubbery texture, higher electrolyte leakage, abnormal ripening, and so on [13].

Banana, mango, and papaya are all popular and tropical fruits, they play important roles in the economic development in tropical area [14–16]. Despite the abundance of reports regarding the effects of 1-MCP on storage life and fruit quality of the three fruits, the information about their special responses to 1-MCP treatment is still insufficient. Therefore, the objective of this study is to explore the different effects of 1-MCP on ripening, cell wall composition and texture properties of ‘Brazil’ banana, ‘Guifei’ mango and ‘Risheng’ papaya fruits. Results in this work provide a base for elucidating molecular mechanism of regulating ripening and softening of climacteric fruit, and provide a reference for appropriate application of 1-MCP in agricultural practice.

2. Materials and Methods

2.1. Fruit Materials

The whole experiment in this study was conducted from 2020 to 2021. Banana fruit (*Musa* spp. AAA Group, cv. ‘Brazil’, with 80% mature degree, fruit weight 120–140 g of each fruit) were harvested from a banana plantation located in Hongqi Town of Haikou City. Mango fruit (*Mangifera indica* L., cv. ‘Guifei’, with 80% mature degree, 130 d after flowering, fruit weight 130–150 g of each fruit) were harvested from a mango plantation in Changjiang City of Hainan. Papaya fruit (*Carica papaya* L., cv. ‘Risheng’, with 80% mature degree with pink flesh, fruit weight 350–400 g of each fruit) were harvested from a papaya plantation located in Yunlong Town of Haikou City. The fruits were transported to the laboratory immediately after harvest. Each banana hand was split into individual fingers, fruit stalks of mango and papaya were cut off and 0.5 cm stem was left. The uniform fruit without disease and mechanical damage was dipped in 1.0 g L⁻¹ sodium hypochlorite solution for 5 min, washed with 0.05% (*w/v*) SporGon (Bayer, Berlin, Germany), and then dried naturally at 25 °C.

2.2. Postharvest Treatments

Three kinds of fruit were randomly divided into two groups, respectively; each group contained 100 fruit. The first groups of three kinds of fruit were placed in a 100 L chamber and exposed to 1-MCP at 1.0 µL L⁻¹ for 20 h at 25 °C [17]. 1-MCP gas was generated from a commercial powdered formulation (SmartFresh EthylBloc 0.14%). The second groups of three kinds of fruit were control, using distilled water instead of 1-MCP.

All the treated fruits were placed into 0.02 mm thick PE bags (Gang Tai[®], Jieyang, China), about 9 fruit for one bag, and stored at 15 ± 0.5 °C with 90–95% relative humidity for up to 40 days (for mango) or 50 days (for banana and papaya). Three kinds of fruit were sampled with 5-days intervals. All assays were performed with three biological triplicates, and one replicate containing 3 fruit.

2.3. Color Variations

Measurement of fruit surface color was performed with a colorimeter (Konica Minolta CM-700D, Aichi, Japan). Three test points are randomly selected in the equatorial site of each fruit. Color changes were expressed as CIE a* (green to red).

2.4. Ethylene Production

Production of ethylene was determined with a gas chromatograph (TRACE 1300, Thermo Fisher Scientific, Waltham, MA, USA) according to the method of Huan (2018) [18] with some modifications. Three fruits were sealed in an 11.2 L airtight jar for 2 h at 25 °C. The gas samples were collected from each jar headspace by syringe (1 mL) and injected into the chromatograph. The condition of gas chromatography column was HP-55% capillary column, the column temperature was 60 °C, temperature of inlet was 100 °C, the detector was flame ionization (FID), and temperature was 250 °C, carrier gas was N₂ with 9 mL min⁻¹ flow rate, burning gas was H₂ with 40 mL min⁻¹ flow rate, the combustion gas was air with 400 mL min⁻¹ flow rate, ethylene release rate was calculated as $\mu\text{L h}^{-1} \text{kg}^{-1} \text{FW}$. Each treatment had three replicates, 3 fruit for one replicate.

2.5. Detection of Fruit Firmness

Fruit firmness was measured with a Penetrometer (Model FHM-1, Takehara, Japan) fitted with an 8.0-mm probe. For banana, each banana finger was cut into three sections and two faces of every midsection were detected at two different points on each face (fruit pulp). Average of the four readings was taken as the firmness for this finger. For mango and papaya, after removing fruit peel (1 mm thick), flesh firmness was measured at two opposite points at equatorial region of each fruit. Each measurement containing three replicates, 3 fruit for one replicate, and the results were expressed as newton (N).

2.6. Cell Membrane Permeability (CMP) and Malondialdehyde (MDA) Content

The CMP was measured by a conductivity instrument (ECOSCAN, Singapore). Fruit peel discs (5 mm diameter) were separated from the equatorial section. Fifteen discs from three fruit (five discs per fruit) were dipped into a 50 mL tube containing 25 mL distilled water. Each tube was placed at 25 °C for 3 h and the conductivity (C1) was recorded. After that, the covered tube was heated, boiled for 15 min. After cooling to room temperature (25 °C), the conductivity (C2) was recorded. The CMP was calculated by relative conductivity [(C1/C2) × 100].

MDA content was determined according to Luo et al. (2015) to reflect the lipid peroxidation during postharvest storage of fruit [19]. Results were presented as mmol g⁻¹ FW.

2.7. Activities of Cell Wall-Degrading Enzymes

Enzyme extraction was conducted according to the methods of Zaharah and Singh (2011) [20] with some modifications. Fruit pulp (1.0 g) was ground with 5 mL of cold NaAc solution (50 mM, pH 5.2) containing 100 mM NaCl, 2% (v/v) mercaptoethanol, and 5% (w/v) polyvinyl pyrrolidone (PVP). Then, the homogenate was centrifuged at 10,000 rpm for 30 min, and the supernatant was dialyzed at 4 °C for 24 h, and the dialyzed solution was used to analyze enzyme activities.

The PG activity was analyzed referring to the protocol of Gwanpua et al. (2016) [21]. The assay system contained 0.5 mL enzyme extract, 1.5 mL sodium acetate buffer (0.1 mol L⁻¹, pH 4.6), 0.5 mL PGA (0.1%) and 0.5 mL distilled water. The mix solution was incubated at 37 °C for 1 h and the reaction was terminated with 1 mL DNS (3,5-Dinitrosalicylic acid reagent). After that, the mix solution was put into boiling water for 10 min and cooled to room temperature (25 °C). The absorbance was determined at 540 nm. The enzyme extract boiled for 10 min served as control group. D-galacturonic acid was used to make the standard curve. PG activities were expressed as $\mu\text{mol h}^{-1} \text{g}^{-1} \text{FW}$.

The CX activity was measured as the method described in Figueroa et al. (2010) [22] with some modification. The reaction mixture contained 1.0 mL CMC (0.625%), 1.0 mL of 0.2 mol L⁻¹ sodium acetate buffer (pH 4.6) and 1.0 mL enzyme extract. The mixture was incubated at 37 °C for 1 h. The reaction was terminated with 1 mL DNS, incubated in boiling water for 5 min, and cooled to room temperature (25 °C). The OD values were measured at 540 nm. Glucose was used to make the standard curve, and CX activities were expressed as $\mu\text{mol h}^{-1} \text{g}^{-1} \text{FW}$.

2.8. Contents of Protopectin and Water-Soluble Pectin (WSP)

The protopectin and WSP contents were determined using carbazole colorimetric method as described by Selcuk and Erkan (2015) [23].

2.9. Mornitering Pulp Cell Structure Using Electron Microscopy

The pulp tissue under 5 mm peel in the middle of fruit was taken, and cut it into the size of 4 mm × 4 mm × 3 mm, there were 8–10 pieces for each sample. Plant section was made using conventional paraffin wax method [24]. Plant material was fixed in 50% FAA solution, and was dehydrated, trans parented, paraffined, paraffin embedded by graded ethanol, then was sliced with thickness of 8 to 10 µm, and stained by safranin and fast green, then mounted by neutral gum. It was taken graph using optical microscope (OLYMPUSBH-2 model, Toyoko, Japan).

2.10. Chemicals

Polygalacturonic acid, galacturonic acid, and solid green were all purchased from Sigma company (St. Louis, MO, USA), carbazole was obtained from Fluka company (Everett, MA, USA). Other chemicals are domestic products (all analytical grade).

2.11. Statistical Analysis

The entire experiment was done three times each with three replicates (three fingers or three fruits for one replicate). Data are expressed as mean ± standard error. Statistical comparisons of the data obtained were performed by Sigma Plot 12.0 software (Jandel Scientific, San Rafael, CA, USA). Differences between the means of two treatments were analyzed using Student's *t*-test, with $p < 0.05$ being considered significant.

3. Results

3.1. Effects of 1-MCP Treatment on Production of Ethylene

As shown in Figure 1, 1-MCP treatment not only inhibited ethylene productions, but also delayed the peaks of ethylene by 10 d and 5 d in banana and mango, respectively. However, for papaya fruit, although 1-MCP treatment delayed ethylene climacteric time for 10 d than the control, the ethylene peak value was 61.54% higher than that of control ($p < 0.05$).

3.2. Effects of 1-MCP on Sensory Quality and Fruit Firmness

The fruit peel colour changed from green to yellow or red during cold storage (15 °C) of fruits, a^* values increased gradually during the storage, 1-MCP had obvious effect on delaying color change (Figure 2A,B). The inhibition effects of 1-MCP were very different among three kinds of fruit, the a^* values of banana, mango, and papaya peel at the end of storage time were lower 1.49, 0.55, and 10.33 than those in beginning time, respectively ($p < 0.05$).

Fruit firmness in all groups tended to decrease during storage (Figure 2C). Compared with 1-MCP treated fruit, firmness of control fruit declined at a higher rate. Moreover, firmness of 1-MCP treated fruit showed a slow decline, especially papaya fruit, its firmness decreased slightly during the whole storage period. On 30 d, the firmness of treated banana, mango and papaya were higher 0.582 N, 0.218 N and 0.751 N than those of control, respectively ($p < 0.05$).

3.3. Effects of 1-MCP Treatment on CMP and MDA Content of Postharvest Fruits

CMP increased gradually over storage time, regardless of fruit kinds and treatments (Figure 3A). 1-MCP treatment could significantly suppress the increase of CMP. Moreover, the inhibition effect of 1-MCP in papaya fruit was most obvious, it's followed by banana fruit ($p < 0.05$). MDA concentrations in fruits increased at early storage time and then decreased for all treatments (Figure 3B), however, the MDA contents were significantly reduced by 1-MCP treatment, and there was significant difference between 1-MCP -treatments, the lowest concentration of MDA in papaya fruit were observed ($p < 0.05$) during the whole storage period.

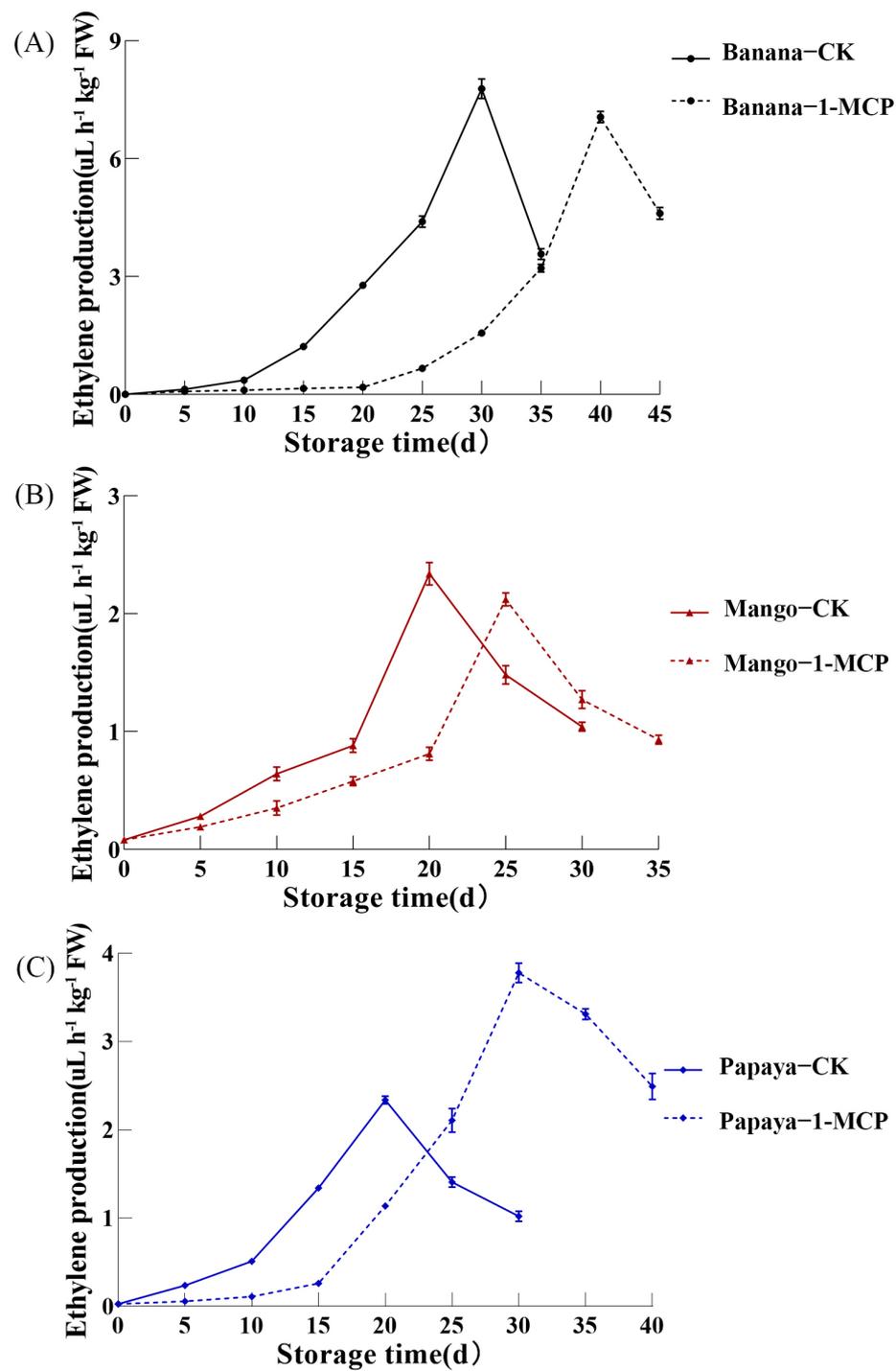


Figure 1. Effects of 1-MCP treatment on ethylene productions of banana (A), mango (B) and papaya (C) fruits during storage at 15 °C. The values are expressed as mean \pm SE ($n = 3$). Vertical bars indicate standard error of means for three replicates.

3.4. Effects of 1-MCP Treatment on Activities of PG and CX in Postharvest Fruits

At early stage of the storage (10 d), the increases in PG activities of banana and mango fruit were significantly faster than that of papaya fruit ($p < 0.05$) (Figure 4A). 1-MCP could inhibit the rise of PG activities of three kinds of fruit. On 30 d, PG activity of banana, mango and papaya fruit were lower 24.71%, 0.12% and 65.41% than those of control, respectively ($p < 0.05$)

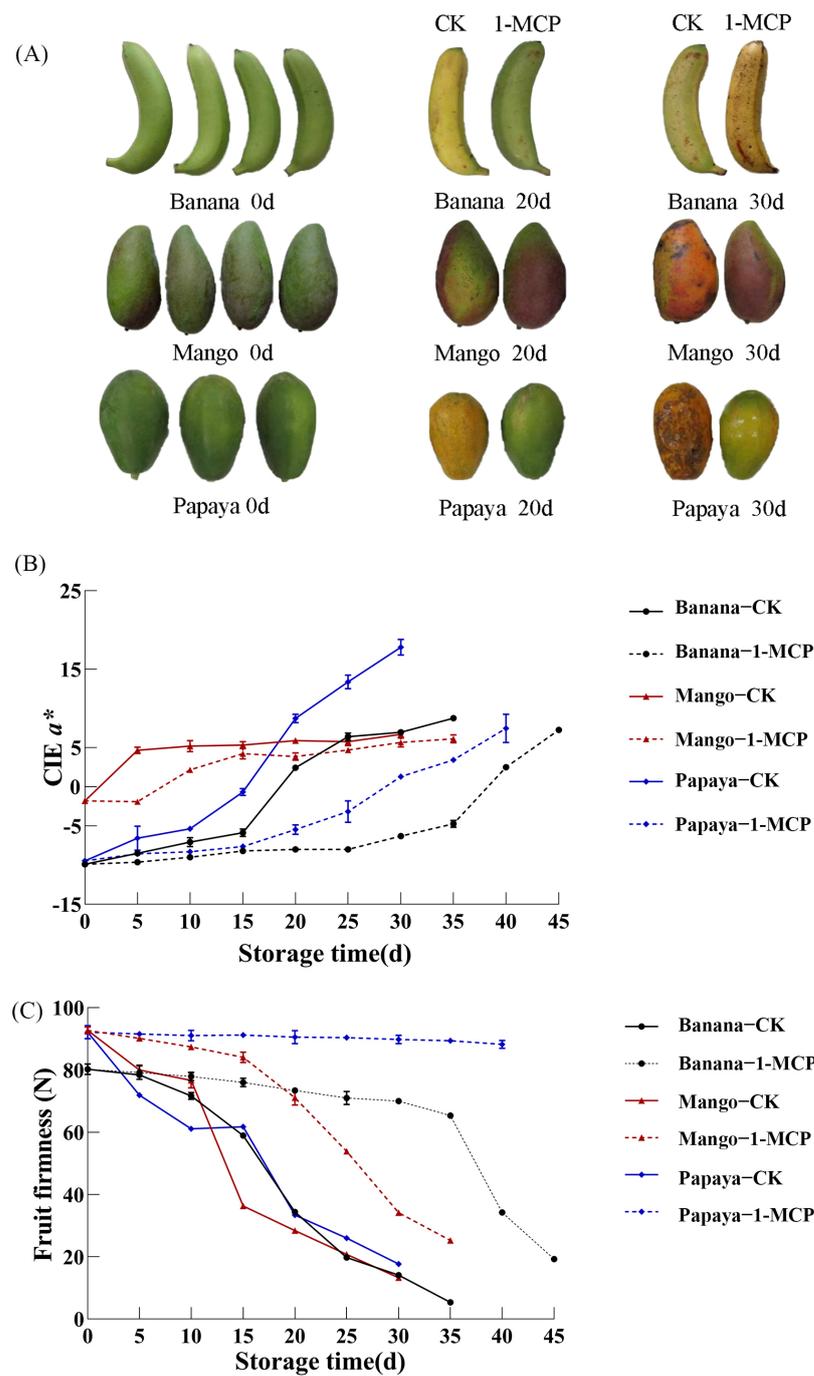


Figure 2. Effects of 1-MCP treatment on fruit appearance (A), CIE a^* (B) and firmness (C) of banana, mango, and papaya fruits during storage at 15 °C. The values are expressed as mean \pm SE ($n = 3$), and vertical bars indicate standard error of means for three replicates.

For three kinds of un-treated fruit, CX activity of mango fruit was the lowest, CX activity of papaya fruit was the highest ($p < 0.05$) (Figure 4B). 1-MCP treatment significantly inhibited the CX activities in three kinds of fruit, in the medium of storage (20 d), CX activities of banana, mango and papaya fruit were 11.93, 12.56 and 8.51 $\mu\text{mol h}^{-1} \text{g}^{-1}$, respectively, and they were reduced by 37.6%, 1.95% and 69.72% than CK fruit ($p < 0.05$) (Figure 4B). Results suggested that the inhibitory effects of 1-MCP on activities of PG and CX in papaya fruit was the most obvious, and it was followed by banana fruit.

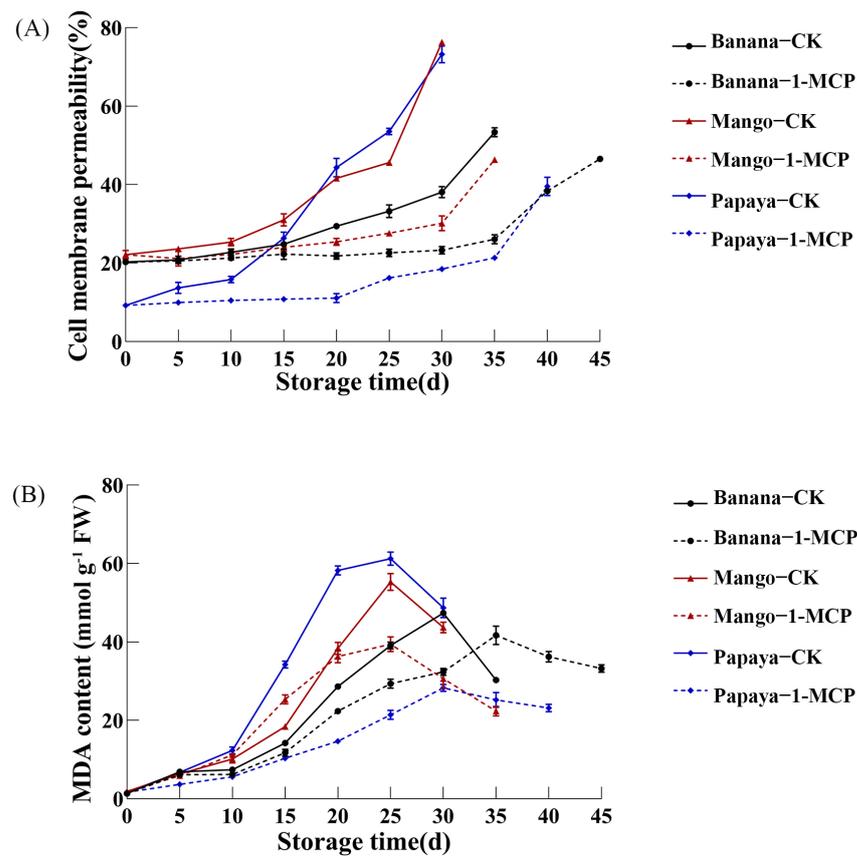


Figure 3. Effects of 1MCP treatment on CMP (A) and MDA content (B) of banana, mango, and papaya fruits during storage at 15 °C. The values are expressed as mean \pm SE ($n = 3$), and vertical bars indicate standard error of means for three replicates.

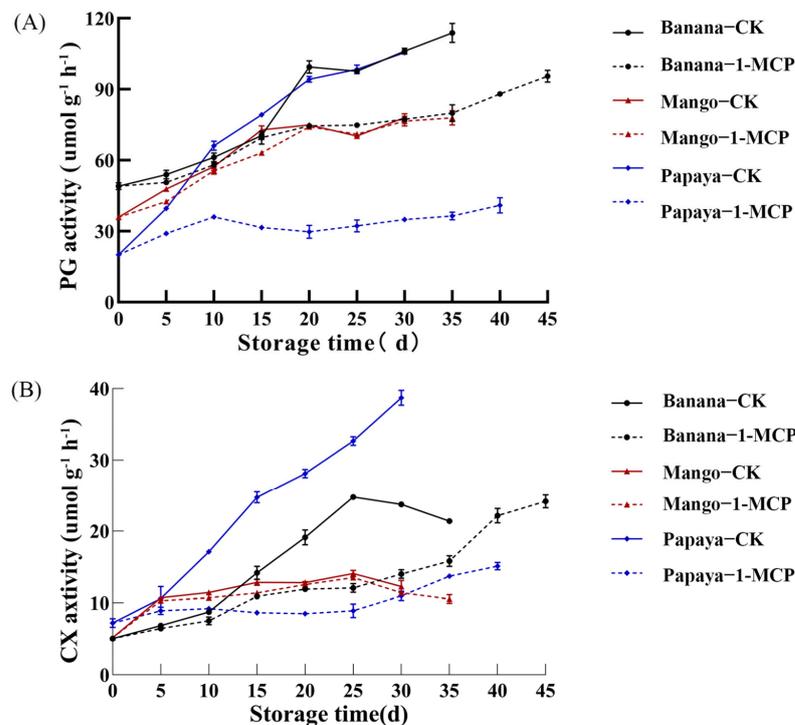


Figure 4. Effects of 1-MCP treatment on activities of PG (A) and CX (B) of banana, mango, and papaya fruits during storage at 15 °C. The values are expressed as mean \pm SE ($n = 3$). Vertical bars indicate standard error of means for three replicates.

3.5. Effects of 1-MCP Treatment on Contents of Protopectin and WSP in Postharvest Fruits

As shown in Figure 5, the decrease in protopectin and the increase in WSP were observed in different fruits and treatments. 1-MCP treatment greatly inhibited the decreases of protopectin contents in three kinds of fruit, it was most obvious in papaya fruit (Figure 5C). For 1-MCP treated fruit, WSP content in papaya fruit remained stable, which increased by 0.113% throughout the whole storage period (Figure 5F). However, the contents of WSP of banana and mango fruit increased by 262.4% and 364.5%, respectively ((Figure 5D and E, $p < 0.05$).

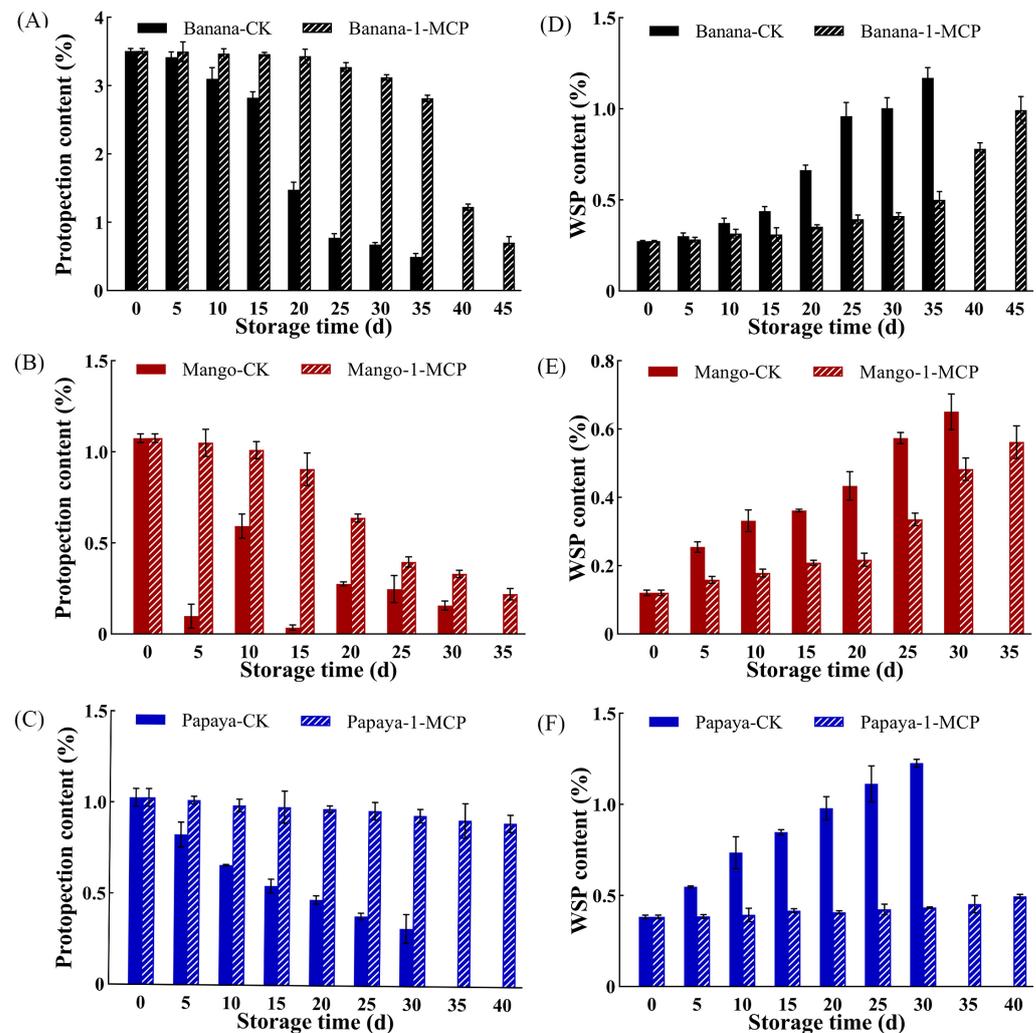


Figure 5. Effects of 1-MCP treatment on protopectin contents of banana (A), mango (B) and papaya (C) and WSP contents of banana (D), mango (E) and papaya (F). The values are expressed as mean \pm SE ($n = 3$), and the vertical bars indicate standard error of means for three replicates.

3.6. Effects of 1-MCP Treatment on Changes of Cell Microstructure in Postharvest Fruits

The pulp cell structures of the three kinds of fruits were presented in Figure 6 (0 d). The cell of banana pulp was small and arranged closely, which was filled with large amounts of starch grains. Moreover, the banana cell wall on 0 d was smooth. However, the cells of mango fruit were bigger and the cell wall was thinner than that of banana fruit. There was a large amount of plump starch grains in mango cells on 0d. The pulp cells of fresh papaya on 0 d were large, vacuolated, and irregularly shaped, and its cytoplasm was extruded into a thin layer. It was closely to the thick cell wall, and the intercellular space was smaller.

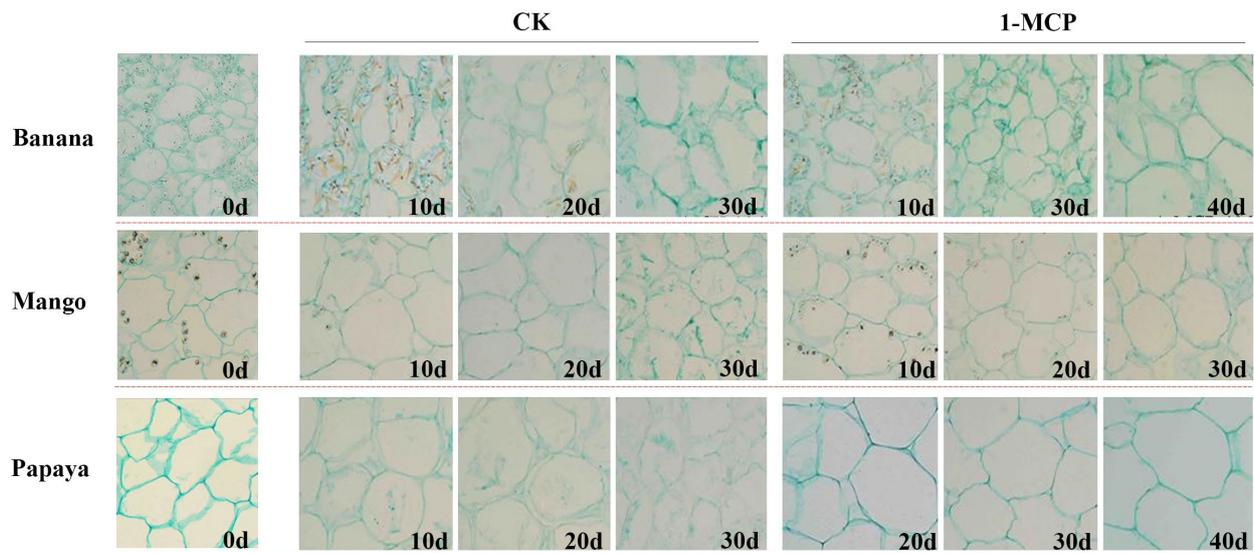


Figure 6. The flesh microstructure ($\times 400$) of CK and 1-MCP treated banana, mango, and papaya fruits on 0, 10, 20, 30 or 40 days after harvest.

Flesh cell structure of the control and 1-MCP treated fruits all changed obviously with the extension of storage time (Figure 6B), but the change rates for three kinds of fruit and treatments were obviously different. Banana pulp cells changed most slowly during early stage of storage. There were still many starch grains in cells on 10 d, but the cell volume obviously increased, the cell combination was loosely. In 1-MCP treated banana fruit, the few starch grains could be seen and cell structure was visible clearly until 30 d, and the cell structure on 40 d was the seem as control fruit on 30 d.

Mango fruit changed most quickly during storage. On 10 d, the most starch grain in the pulp cells had disappeared, volume of part cell enlarged, but cell wall structure remained intact. At the end of storage time, we could see the starch grains was disappeared completely, the protoplast was disintegrated, cytoplasm was flocculated, and then cell wall enlarged and degraded. When fruit treated by 1-MCP, the changes in pulp cell structure was delayed. Although the starch grains also disappeared on 30 d, the degradation of components was not obvious, and only a few cells wall were broken, major cell structure was still intact.

Pulp cell volume gradually expanded in postharvest papaya fruit. The cells became loosely and plasmolysis occurred. Meanwhile, cells began to have programmed death. Most of the cell structure was not complete, cell morphology was fuzzy, pulp tissue gradually disintegrated until to 30 d. Although the flesh structure of papaya treated by 1-MCP also showed a little change, pulp cells still arranged very closely on 40 d. Its cellular components remained intact and firmly bond the adjacent cells, only a little increase in cell volume could be found (Figure 6).

4. Discussion

In this study, we investigated the effects of 1-MCP treatment on ripening and softening properties of banana, mango, and papaya fruits from the views of postharvest physiology, material composition and cell micro-structure. We compared and analyzed the response of three kinds of fruit to 1-MCP treatment during the storage for the first time. Our findings support that the responses of banana, mango, and papaya fruits to the same concentration of 1-MCP were obviously different, the most distinct inhibitory effects of 1-MCP on fruit ripening and softening occurred in papaya, it was followed by banana fruit. This difference in ripening and softening characteristics are closely related to the physiological changes, cell wall composition, cell wall metabolism enzymes, and changes of cell structure in three kinds of fruit during the storage.

Ethylene release is the most typical characteristic of fruit ripening and senescence, especially for respiratory climacteric fruits [25]. As an inhibitor of ethylene activity, the resistance of 1-MCP to the physiological effect of ethylene has been confirmed in many horticultural products [26]. Banana, mango, and papaya all belong to climacteric fruits. However, the behavior of ethylene in three kinds of fruit treated by 1-MCP were obviously different in this study (Figure 1). When banana and mango fruit were treated by 1-MCP, not only the time of ethylene peak was delayed, but also the production of ethylene was reduced. These results were consistent with the report of banana fruit in Duan et al. (2008) [27] and the report of mango fruit in Zerbini et al. (2015) [28]. For papaya fruit, although 1-MCP dramatically delayed the time of ethylene peak, the production of ethylene did not be suppressed by 1-MCP, ethylene production in 1-MCP treated fruit was significantly higher than that in control at the end of storage time. It seemed not to support the conclusion that higher ethylene production usually paralleled to higher softening rate [29]. It may be explained that self-catalysis occurred at the late storage time, which promotes the increase of ethylene release of papaya fruit.

Additionally, the increase of CMP and the accumulation of MDA are also important indicators of fruit ripening and senescence. In this work, the most obvious inhibitory effect of 1-MCP on increase of CMP and MDA content were observed in papaya fruit, it was followed by banana fruit (Figure 3). Moreover, it was found that the profile of ethylene of three kinds of fruit had significant positive correlation with CMP and MDA accumulation, which is consistent with many previous studies [30].

It is well established that fruit softening is closely linked to the activities of cell wall metabolism enzymes, such as PG, CX, xylanase, and so on [31]. In this study, we found that 1-MCP treatment significantly inhibited the rise of PG and CX activities of banana, mango, and papaya fruit. The lower protopectin contents, and higher WSP contents were detected in control fruit, which was in coincident with the higher PG and CX activities. Whereas in 1-MCP-treated fruit, we detected the lower activities of PG and CX and a significant suppression of protopectin degradation (Figures 4–6). The results were supported by many other researches [32]. Nevertheless, there are still great differences in the changes of cell wall structural substances and enzyme activities of the three fruits treated by 1-MCP. The changes in softening characters of papaya fruit were the slowest, whereas those of mango fruit were the fastest, which explained why 1-MCP has the best preservation effect on papaya fruit and the worst preservation effect on mango fruit. Additionally, these results prove once again that the effects of 1-MCP treatment depend on fruit varieties, and the response of different fruits to 1-MCP application is significantly different. It is worth noting that the firmness value of mango fruit treated with 1-MCP was significantly higher than that of the control fruit (Figure 2), indicating that 1-MCP inhibits the softening of mango fruit, but there was no significant difference in the changes of PG and CX activities between the treated fruit and the control fruit. It is speculated that some other cell wall degrading enzymes, such as pectin methylesterase (PME), β -galactosidase (β -Gal) or some key genes, such as expansin gene, *MiExpA1* play a key regulatory role in softening of mango fruit [33,34].

The decline of fruit firmness determines the process of fruit ripening and senescence to some extent [35]. In the present study, after 1-MCP application, the firmness change of three kinds of fruit is obviously different. For banana and mango, 1-MCP could both control fruit softening in the early storage time, and ensures the normal fruit softening at the end of storage time (Figure 2). However, for papaya, the fruit treated by 1-MCP still maintained very high firmness (still maintained 89.42 N) at the end of storage time (40 d), which means that fruit cannot completely soften until the fruit collapsed. Meanwhile, the fruit lose normal flavor, and the taste was the seem as 'carrot', it could be called as 'rubber phenomenon'. This result agrees with the result in Thumdee et al. (2010) [36]. The reason for this phenomenon can be attributed to two aspects, one is that no new synthetic ethylene receptor protein is taking at the end of storage period, hence, the fruit could not restore the

sensitivity to ethylene [37]. The other is that transcription factor *CpbHLH3* and *CpXYN1* genes cooperatively counteracted 1-MCP inhibition of softening in postharvest papaya [38].

There are significant changes in cell structure of fruit pulp during fruit ripening and softening. Nunes et al. (2009) [39] reported that the shape, size, and density of the pulp cells all changed obviously as plum ripening and softening using scanning electron microscopy (SEM) techniques. Present research on cell microstructure showed that, for fresh harvested banana and mango fruit, cells had plenty of starch grains, as the proceeding of ripening and softening, the organelle, such as starch grains gradually disappeared (Figure 6). It proved again that the banana and mango belong to starch-convertible types fruit, the breakdown in starch had positive correlation with fruit softening [40]. These results demonstrated again that the structure and function of plant cell are uniform. In addition, the volume of banana, mango and papaya pulp cells gradually enlarged with the extension of storage time, arranged loosely, cell wall expanded loosely, and protoplasm disintegrated (Figure 6). 1-MCP could retard the change in cell microstructure effectively, especially for papaya fruit. The changes in cell microstructure had the close relationship with cell composition, such as original pectin and WSP, which may be closely associated with ethylene production during ripening of banana and papaya fruits.

Interestingly, many previous results showed that the process of fruit ripening, color change and ethylene release were synchronized for most of fruit [41]. In this study, although 1-MCP treatment can significantly inhibit ripening and maintain firmness of papaya, it can't retard the peel color change, and fruit could turn yellow normally in the late storage period, which indicates that ethylene profile, color change and fruit softening may involve in different regulatory pathways, the similar reports were given by Song et al. (2020) [42]. In addition, extensive researches have confirmed that genes and transcription factors involved in cell wall metabolism play critical roles in post-harvest fruit softening [43]. Therefore, it is very necessary for us to do much and comprehensive researches on the molecular mechanism of above conflict and elucidate the regulatory network of ethylene profile, softening, color development of fruit in the future.

5. Conclusions

In this study, 1-MCP is confirmed to delay senescence and maintain quality by suppressing ethylene production and increasing CMP and MDA content in banana, mango, and papaya fruit. The softening inhibition of 1-MCP is accompanied with the slow increase of WSP content, which is mainly attributed to the repression in activities of PG and CX. There are obvious differences on ripening and softening responses of three kinds of fruit to 1-MCP treatment, and the inhibitory effects of 1-MCP in papaya fruit was most significant, followed by banana fruit. Meanwhile, the application of 1-MCP on banana and mango could maintain storage quality as well as ensure texture quality, suggesting its potential utility value in industrial production.

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Conflicts of Interest: The authors declare no conflict of interest.

Abbreviations

1-MCP	1-methylcyclopropene
2-PG	Polygalacturonase
PME	Pectin methylesterase
EXP	Expansins
PL	Pectatelyase
GLU	endoglucanase
CX	cellulase
BGL	Beta-glucosidase
XYN	Endo-1,4-beta-xylanase
GAL	Beta-galactosidase
XTH	Xyloglucan endotransglycosylase
PGA	Polygalacturonic acid
DPPH	1,1-Diphenyl-2-picrylhydrazyl
DNS	3,5-Dinitrosalicylic acid reagent
CMC	Carboxymethyl cellulose
FAA	Alcohol formalin acetate mixture

References

- Maringgal, B.; Hashim, N.; Tawakkal, I.S.M.; Mohamed, M.T.; Hamzah, M.; Ali, M.M.; Razak, M.F.H. Kinetics of quality changes in papayas (*Carica papaya* L.) coated with Malaysian stingless bee honey. *Sci. Hortic.* **2020**, *267*, 109321. [[CrossRef](#)]
- García-Muñoz, M.C.; Henao-Rojas, J.C.; Moreno-Rodríguez, J.M.; Botina-Azain, B.L.; Romero-Barrera, Y. Effect of rootstock and environmental factors on fruit quality of Persian lime (*Citrus latifolia* Tanaka) grown in tropical regions. *J. Food Compos. Anal.* **2021**, *103*, 104081. [[CrossRef](#)]
- Chen, J.Q.; Chen, T.C.; Qiu, M.M.; Li, L.; Zhong, Q.G.; Wei, Q.; Deng, Y.J.; Xie, B.G.; Jiang, Y.J.; Chen, B.Z. Identification of ACC synthetase genes in *Volvariella volvacea* and analysis of their response to ethephon and 1-methylcyclopropene treatments. *Sci. Hortic.* **2021**, *278*, 109848. [[CrossRef](#)]
- Xie, Y.T.; Zhang, F.; Guo, F.Z.; Song, K.Y.; Luo, H.B.; Wang, J.H.; Wang, Y.X.; Jiang, L. Postharvest application of 1-methylcyclopropene delays chloroplast degradation in *Gynura bicolor* DC under sugar scarcity conditions. *Sci. Hortic.* **2022**, *305*, 111342. [[CrossRef](#)]
- Win, N.M.; Yoo, J.G.; Naing, A.H.; Kwon, J.G.; Kang, I.K. 1-Methylcyclopropene (1-MCP) treatment delays modification of cell wall pectin and fruit softening in “Hwangok” and “Picnic” apples during cold storage. *Postharvest Biol. Technol.* **2021**, *180*, 111599. [[CrossRef](#)]
- Liu, J.; Ma, Q.; Liu, D.H.; Meng, C.X.; Hu, Z.Y.; Ma, L. Identification of the cell wall proteins associated with the softening of *Lycium barbarum* L. fruit by using iTRAQ technology. *Food Chem. Mol. Sci.* **2022**, *4*, 100110. [[CrossRef](#)]
- Zhao, Y.T.; Zhu, X.; Hou, Y.Y.; Wang, X.Y.; Li, X.H. Effects of nitric oxide fumigation treatment on retarding cell wall degradation and delaying softening of winter jujube (*Ziziphus jujuba* Mill. cv. *Dongzao*) fruit during storage. *Postharvest Biol. Technol.* **2019**, *156*, 110954. [[CrossRef](#)]
- Ma, Y.Y.; Zhang, X.L.; Li, L.L.; Yang, W.T.; Zhang, W.D.; Cheng, S.B.; Guo, M.R.; Chen, G.G. Delaying fruit softening of ‘France’ prune (*Prunus domestica* L.) using near-freezing temperature storage. *LWT* **2022**, *172*, 114165. [[CrossRef](#)]
- Liu, M.P.; Wang, R.; Sun, W.W.; Han, W.J.; Li, G.; Zong, W.; Fu, J.M. Effects of postharvest calcium treatment on the firmness of persimmon (*Diospyros kaki*) fruit based on a decline in WSP. *Sci. Hortic.* **2023**, *307*, 111490. [[CrossRef](#)]
- Chen, Y.H.; Zhang, S.; Lin, H.T.; Lu, W.J.; Wang, H.; Chen, Y.H.; Lin, Y.F.; Fan, Z.Q. The role of cell wall polysaccharides disassembly in *Lasiodiplodia theobromae*-induced disease occurrence and softening of fresh longan fruit. *Food Chem.* **2021**, *351*, 129294. [[CrossRef](#)]
- Chen, J.; Li, Y.X.; Li, F.F.; Hong, K.Q.; Yuan, D.B. Effects of procyanidin treatment on the ripening and softening of banana fruit during storage. *Sci. Hortic.* **2022**, *292*, 110644. [[CrossRef](#)]
- Wang, N.; Nian, Y.W.; Li, R.; Shao, Y.Z.; Li, W. Transcription Factor CpbHLH3 and CpXYN1 Gene Cooperatively Regulate Fruit Texture and Counteract 1-Methylcyclopropene Inhibition of Softening in Postharvest Papaya (*Carica papaya* L.). *J. Agric. Food Chem.* **2022**, *70*, 9919–9930. [[CrossRef](#)]
- Saba, M.K.; Watkins, C.B. Flesh browning development of ‘Empire’ apple during a shelf life period after 1-methylcyclopropene (1-MCP) treatment and controlled atmosphere storage. *Sci. Hortic.* **2020**, *261*, 108938. [[CrossRef](#)]
- Lawson, T.; Lycett, G.W.; Ali, A.; Chin, C.F. Characterization of Southeast Asia mangoes (*Mangifera indica* L.) according to their physicochemical attributes. *Sci. Hortic.* **2019**, *243*, 189–196. [[CrossRef](#)]
- Ali, A.; Muhammad, M.T.M.; Sijam, K.; Siddiqui, Y. Effect of chitosan coatings on the physicochemical characteristics of Eksotika II papaya (*Carica papaya* L.) fruit during cold storage. *Food Chem.* **2011**, *124*, 620–626. [[CrossRef](#)]

16. Maqbool, M.; Ali, A.; Alderson, P.G.; Zahid, N.; Siddiqui, Y. Effect of a Novel Edible Composite Coating Based on Gum Arabic and Chitosan on Biochemical and Physiological Responses of Banana Fruits during Cold Storage. *J. Agric. Food Chem.* **2011**, *59*, 5474–5482. [[CrossRef](#)]
17. Lwin, H.P.; Choi, J.H.; Chun, J.P.; Watkins, C.B.; Lee, J.W. 1-Methylcyclopropene treatment alters fruit quality attributes and targeted metabolites in ‘Wonhwang’ pears during shelf life. *Sci. Hortic.* **2021**, *284*, 110125. [[CrossRef](#)]
18. Huan, C.; An, X.J.; Yu, M.L.; Li, J.; Ma, R.J.; Tu, M.G.; Yu, Z.F. Effect of combined heat and 1-MCP treatment on the quality and antioxidant level of peach fruit during storage. *Postharvest Biol. Technol.* **2018**, *145*, 193–202. [[CrossRef](#)]
19. Luo, S.S.; Wan, B.; Feng, S.H.; Shao, Y.Z. Biocontrol of Postharvest Anthracnose of Mango Fruit with *Debaryomyces Nepalensis* and Effects on Storage Quality and Postharvest Physiology. *J. Food Sci.* **2015**, *80*, 2554–2563. [[CrossRef](#)]
20. Zaharah, S.S.; Singh, Z. Mode of action of nitric oxide in inhibiting ethylene biosynthesis and fruit softening during ripening and cool storage of ‘Kensington Pride’ mango. *Postharvest Biol. Technol.* **2011**, *62*, 258–266. [[CrossRef](#)]
21. Gwanpua, S.G.; Mellidou, I.; Boeckx, J.; Kyomugasho, C.; Bessemans, N.; Verlinden, B.E.; Hertog, M.L.; Hendrickx, M.; Nicolai, B.M.; Geeraerd, A.H. Expression analysis of candidate cell wall-related genes associated with changes in pectin biochemistry during postharvest apple softening. *Postharvest Biol. Technol.* **2016**, *112*, 176–185. [[CrossRef](#)]
22. Figueroa, C.R.; Rosli, H.G.; Civello, P.M.; Martinez, G.A.; Herrera, R.; Moya-Leon, M.A. Changes in cell wall polysaccharides and cell wall degrading enzymes during ripening of *Fragaria chiloensis* and *Fragaria ananassa* fruits. *Sci. Hortic.* **2010**, *124*, 454–462. [[CrossRef](#)]
23. Selcuk, N.; Erkan, M. The effects of 1-MCP treatment on fruit quality of medlar fruit (*Mespilus germanica* L. cv. Istanbul) during long term storage in the palliflex storage system. *Postharvest Biol. Technol.* **2015**, *100*, 81–90. [[CrossRef](#)]
24. Yang, J.P. The modified method of routine paraffin section. *J. Biol.* **2006**, *23*, 45–46.
25. Tilahun, S.; Lee, Y.M.; Choi, H.R.; Baek, M.W.; Lee, J.S.; Park, D.S.; Kang, H.M.; Jeong, C.S. Modified atmosphere packaging combined with CO₂ and 1-methylcyclopropene prolong the storability and maintain antioxidant properties of cherry tomato. *Sci. Hortic.* **2021**, *288*, 110401. [[CrossRef](#)]
26. Chai, J.X.; Wang, Y.T.; Liu, Y.F.; Yong, K.; Liu, Z.D. 1-MCP extends the shelf life of ready-to-eat ‘Hayward’ and ‘Qihong’ kiwifruit stored at room temperature. *Sci. Hortic.* **2021**, *289*, 110437. [[CrossRef](#)]
27. Duan, X.W.; Cheng, G.P.; Yang, E.; Yi, C.; Ruenroengklin, N.; Lu, W.J.; Luo, Y.B.; Jiang, Y.M. Modification of pectin polysaccharides during ripening of postharvest banana fruit. *Food Chem.* **2008**, *111*, 144–149. [[CrossRef](#)]
28. Zerbini, P.E.; Vanoli, M.; Rizzolo, A.; Grassi, M.; Pimentel, R.M.D.A.; Spinelli, L.; Torricelli, A. Optical properties, ethylene production and softening in mango fruit. *Postharvest Biol. Technol.* **2015**, *101*, 58–65. [[CrossRef](#)]
29. Chang, L.Y.; Brecht, J.K. Responses of 1-methylcyclopropene (1-MCP)–treated banana fruit to pre– and post–treatment ethylene exposure. *Sci. Hortic.* **2023**, *309*, 111636. [[CrossRef](#)]
30. Jung, S.K.; Watkins, C.B. Internal ethylene concentrations in apple fruit at harvest affect persistence of inhibition of ethylene production after 1-methylcyclopropene treatment. *Postharvest Biol. Technol.* **2014**, *96*, 1–6. [[CrossRef](#)]
31. Langer, S.E.; Marina, M.; Francese, P.; Civello, P.M.; Martínez, G.A.; Villarreal, N.M. New insights into the cell wall preservation by 1-methylcyclopropene treatment in harvest-ripe strawberry fruit. *Sci. Hortic.* **2022**, *299*, 111032. [[CrossRef](#)]
32. Hou, Y.Y.; Wu, F.; Zhao, Y.T.; Shi, L.; Zhu, X. Cloning and expression analysis of polygalacturonase and pectin methylesterase genes during softening in apricot (*Prunus armeniaca* L.) fruit. *Sci. Hortic.* **2019**, *256*, 108607. [[CrossRef](#)]
33. Liu, S.M.; Huang, H.; Huber, G.J.; Pan, Y.G.; Shi, X.Q.; Zhang, Z.K. Delay of ripening and softening in ‘Guifei’ mango fruit by postharvest application of melatonin. *Postharvest Biol. Technol.* **2020**, *163*, 111136. [[CrossRef](#)]
34. Sane, V.A.; Chourasia, A.; Nath, P. Softening in mango (*Mangifera indica* cv. *Dashehari*) is correlated with the expression of an early ethylene responsive, ripening related expansin gene, MiExpA1. *Postharvest Biol. Technol.* **2005**, *38*, 223–230. [[CrossRef](#)]
35. Ong, M.K.; Forney, C.F.; Alderson, P.G.; Ali, A. Postharvest profile of a Solo variety ‘Frangi’ during ripening at ambient temperature. *Sci. Hortic.* **2013**, *160*, 12–19. [[CrossRef](#)]
36. Singh, V.; Jawandha, S.K.; Gill, P.P.S.; Gill, M.S. Suppression of fruit softening and extension of shelf life of pear by putrescine application. *Sci. Hortic.* **2019**, *256*, 108623. [[CrossRef](#)]
37. Thumdee, S.; Manenoi, A.; Chen, N.J.; Paull, R.E. Papaya Fruit Softening: Role of Hydrolases. *Trop. Plant Biol.* **2010**, *3*, 98–109. [[CrossRef](#)]
38. Chiriboga, M.A.; Saladié, M.; Bordonaba, J.G.; Recasens, I.; Garcia-Mas, J.; Larrigaudière, C. Effect of cold storage and 1-MCP treatment on ethylene perception, signalling and synthesis: Influence on the development of the ever green behaviour in ‘Conference’ pears. *Postharvest Biol. Technol.* **2013**, *86*, 212–220. [[CrossRef](#)]
39. Nunes, C.; Santos, C.; Pinto, G.; Silva, S.; Lopes-da-Silva, J.A.; Saraiva, J.A.; Coimbra, M.A. Effects of ripening on microstructure and texture of “Ameixad Elvas” candied plums. *Food Chem.* **2009**, *115*, 1094–1101. [[CrossRef](#)]
40. Li, W.; Shao, Y.Z.; Chen, W.X.; Jia, W.J. The Effects of Harvest Maturity on Storage Quality and Sucrose-Metabolizing Enzymes During Banana Ripening. *Food Bioprocess Technol.* **2011**, *4*, 1273–1280. [[CrossRef](#)]
41. Zhang, Y.; Wang, K.; Xiao, X.; Cao, S.F.; Chen, W.; Yang, Z.F.; Shi, L.Y. Effect of 1-MCP on the regulation processes involved in ascorbate metabolism in kiwifruit. *Postharvest Biol. Technol.* **2021**, *179*, 111563. [[CrossRef](#)]

42. Song, Z.Y.; Qin, J.J.; Yao, Y.L.; Lai, X.H.; Zheng, W.; Chen, Y.X.; Zhu, X.Y.; Li, X.P. A transcriptomic analysis unravels key factors in the regulation of stay-green disorder in peel of banana fruit (Fenjiao) caused by treatment with 1-MCP. *Postharvest Biol. Technol.* **2020**, *168*, 111290. [[CrossRef](#)]
43. Shi, L.Q.; Liu, Q.; Qiao, Q.H.; Zhu, Y.L.; Huang, W.; Wang, X.M.; Ren, Z.X. Exploring the effects of pectate and pectate lyase on the fruit softening and transcription profiling of *Solanum lycopersicum*. *Food Control* **2022**, *133*, 108636. [[CrossRef](#)]

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