Effects of 1-Methylcyclopropene (1-MCP) and Ethylene on Postharvest Lignification of Common Beans (*Phaseolus vulgaris* L.)

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**ABSTRACT:** Postharvest 1-methylcyclopropene (1-MCP) treatment can inhibit the lignification of fruits and vegetables. The mode of action of 1-MCP is through inhibiting ethylene production, but the effect of 1-MCP and ethylene on lignification of common beans remains unknown. This work compared the effect of 0.5 μL L\(^{-1}\) 1-MCP and 100 μL L\(^{-1}\) ethylene on the lignification of common beans during storage. Postharvest 1-MCP significantly inhibited the increase of the lignified cell group, sclerenchyma became thicker, vascular bundles thickened, and lignified cells grew during storage, while ethylene was the opposite. 1-MCP inhibited the increase in the respiration rate, sucrose phosphate synthase (SPS), sucrose synthase (SuSy), phenylalanine ammonialyase (PAL), cinnamyl alcohol dehydrogenase (CAD), and peroxidase (POD), whereas ethylene increased all of them. Ethylene treatment stimulated and 1-MCP inhibited the decline of reducing sugar and cellulose content. Expression of genes, including ethylene increased all of them. Ethylene treatment stimulated and 1-MCP inhibited the decline of reducing sugar and cellulose content. Expression of genes, including *PvACO1*, *PvAOG1*, *PvSuSy2*, *PvPAL3*, *Pv4CL1*, and *PvCOMT1*, with the lignin content being significantly increased in common beans during storage. 1-MCP treatment markedly inhibited the expression of *PvACO1*, *PvSuSy2*, *PvPAL3*, *Pv4CL1*, and *PvCOMT1* genes, while strengthened the expression of *PvETR1* and *PvAOG1*, while ethylene was the opposite. This work provides evidence that ethylene or abscisic acid (ABA) may play an important role in 1-MCP regulation of postharvest lignification in common beans and provides strategies for preserving the quality of fruits and vegetables during storage.

**INTRODUCTION**

Fresh common beans (*Phaseolus vulgaris* L.) are popular due to their bright color and nutrition. However, senescence leads to lignification, increases pod tendons, and loses the eating quality of fresh common beans post harvest. 1-MCP delays the senescence of common beans. The literature suggests that abscisic acid (ABA) is important for lignification in bamboo shoots, while it is ethylene in Tsai Tai, while insensitive to the accumulation of ethylene, but the effect of ethylene on the lignification of fresh common beans is not clear. Postharvest 1-methylcyclopropene (1-MCP) treatment can inhibit lignification by chilling injury in loquats and kiwifruits, or senescence in Tsai Tai, bamboo, *Rosa sterilis* D. shi, and citrus fruit juice sacs.

The literature suggests that abscisic acid (ABA) is important for lignification in bamboo shoots, while it is ethylene in Tsai Tai. Ethylene production is moderate in common beans, insensitive to the accumulation of ethylene, but the effect of ethylene on the lignification of fresh common beans is not clear. Postharvest 1-methylcyclopropene (1-MCP) treatment can inhibit lignification by chilling injury in loquats and kiwifruits and by senescence in bamboo shoots, *Tsai Tai*, pears, and *R. sterilis* D. shi. 1-MCP delays the senescence and reduces the chilling injury symptoms of beans during storage. Our previous proteomics study also found that 1-MCP effectively downregulated the key protein related to the synthesis and response of lignin, cellulose, ethylene, and abscisic acid. This study is to reveal the effects of ethylene and 1-MCP on postharvest lignification in common beans. The study helps in understanding the effect of ethylene on the postharvest lignification of common beans.
RESULTS

Respiration Rate and Relative Thickness of Pods. The respiration rate of control and ethylene in fresh common beans increased in the first week and then decreased with further storage. The respiration rate was significantly suppressed by 1-MCP, but ethylene enhanced the respiration rate (Figure 1A). The relative thickness of pods declined in beans during storage, and 1-MCP treatment significantly inhibited the decrease of the relative thickness of pods (Figure 1B).

Reducing Sugar, Cellulose, Total Polyphenols, and Lignin Content. The content of reducing sugars in fresh common beans reduced during storage. Treatments with 1-MCP and ethylene did not affect the decrease in the content of reducing sugars during storage (Figure S1A). Cellulose in beans decreased during storage, 1-MCP and ethylene delayed the decrease of cellulose content before the third week, and no significant differences between 1-MCP and ethylene treatment were observed (Figure 2A). The total polyphenols of control in fresh common beans increased in the second week of storage and then declined with further storage, with a remarkable highest value appearing in the second week. The increase of total polyphenols in fresh common beans was suppressed by 1-MCP and ethylene treatment (Figure S1B). The lignin content of fresh common beans increased during storage. However,

Figure 1. (A) Respiration rate and (B) relative thickness of pods in control, ethylene- and 1-MCP-treated beans during storage. Vertical bars represent the standard errors of three replicates (10 beans of each). Different letters within each parameter indicate statistically significant differences (P < 0.05).

Figure 2. (A) Cellulose and (B) lignin content of control, ethylene- and 1-MCP-treated beans during storage. Vertical bars represent the standard errors of three replicates (10 beans of each). Different letters within each parameter indicate statistically significant differences (P < 0.05).

Figure 3. Effects of ethylene and 1-MCP treatment on the anatomical structure in beans. (A–D) Represent the middle sections of fresh common beans, (E–H) represent the lower tenden sections of fresh common beans. (A, E) at the harvest day; (B, F) control group at 2 weeks; (C, G) 1-MCP treatment at 2 weeks; (D, H) ethylene treatment at 2 weeks. Abbreviations: LG, lignified cell group; LP, lignified cell; Pf, phloem fibers with primary cell walls; Xy, xylem.
ethylene promoted the accumulation of lignin in fresh common beans before the second week (Figure 2B).

**Anatomical Structure Analysis of Fresh Beans under Ethylene and 1-MCP Treatment.** The longitudinal sections from common beans at harvest day and 2 weeks of storage were analyzed by Safranin-fast green staining (Figure 3). The vascular bundles and collenchyma were clearly observed, the xylem and phloem fibers with primary cell walls were visible, and the lignified xylem vessel appeared in a clear purplish-red color (Figure 3). Lignin is mainly located in the sclerenchyma and vascular bundles (Figure 3). Lignified cells emerged around vascular bundles and were smaller than the surrounding parenchymal cells, occurring in clusters. The lignified cell group in fresh beans increased significantly during storage, and 1-MCP could significantly inhibit the increase and enlargement of the lignified cell group in fresh beans, while for ethylene, it was the opposite (Figure 3A–D). At 2 weeks of storage, sclerenchyma became thicker than that at the harvest day, vascular bundles thickened, and lignified cells grew, 1-MCP significantly inhibited those changes, while for ethylene, it is the opposite (Figure 3E–H).

**Fourier Transform Infrared (FTIR) Spectra.** To identify the changes of lignin and cellulose in control, ethylene-, and 1-MCP-treated beans during storage, a profile of beans based on specific spectra was detected by FTIR. The peaks of FTIR spectra in beans were ascribed as follows: 1740 cm\(^{-1}\) for the unconjugated carbonyl (C=O) stretching vibration in hemicellulose, 1643 cm\(^{-1}\) for the conjugated carbonyl (C=O) stretching vibration in absorbed water, 1508 cm\(^{-1}\) for the telescopic carbon skeleton (C=O) ring skeleton and hydrocarbon (C=O) stretching vibration in lignin, 1425 cm\(^{-1}\) for the combination of the benzene (C=C) ring skeleton and hydrocarbon (C=H) bending vibration in cellulose and hemicellulose, 1242 cm\(^{-1}\) for the benzene epoxy bond (CO=OR) stretching vibration in lignin, 1153 cm\(^{-1}\) for the ether ethanol and tertiary asymmetric stretch (C–O–H) stretch in cellulose and hemicellulose, and 1051 cm\(^{-1}\) for the C–O–C stretching in cellulose, hemicellulose, and lignin (Figure 4). The large peak at 3418 cm\(^{-1}\) corresponded to the hydroxyl (O–H) stretching vibration, whereas 2921 and 896 cm\(^{-1}\) corresponded to the C–H stretching vibration in cellulose. The \(I_{\text{1740}}/I_{\text{1508}}\) decreased during storage, ethylene, and 1-MCP suppressed the decrease, which was consistent with the changes in the cellulose content in beans (Figure 2A) but enhanced the decrease in \(I_{\text{1379}}/I_{\text{1508}}\). The \(I_{\text{1508}}/I_{\text{1379}}\), \(I_{\text{1508}}/I_{\text{1425}}\), and \(I_{\text{1508}}/I_{\text{1740}}\) increased during storage, and 1-MCP inhibited the increase, while ethylene enhanced it (Figure S2), which was consistent with the changes in the lignin content of common beans (Figure 2B).

**SPS, SuSy, Cx, PAL, 4CL, CAD, and POD Activity.** SPS activity of control and 1-MCP-treated beans decreased during storage, but ethylene enhanced SPS before the second week and then decreased with further storage (Figure 5A). SPS activity in beans increased during storage but significantly decreased by 1-MCP treatment, while ethylene treatment enhanced the SuSy activity of beans to higher values than controls (Figure 5B). Cx activity in beans increased in the first week and then decreased with storage time. Ethylene treatment significantly inhibited the increase of Cx activity, but 1-MCP treatment enhanced Cx activity (Figure 5C). PAL activity in fresh common beans increased in the second week and then decreased with storage time. The increase of PAL activity in fresh common beans was significantly suppressed by 1-MCP treatment (Figure 5D). 4CL activity in fresh common beans remained unchanged until the second week of storage and then decreased with further storage. The decline in 4CL activity in beans was improved by 1-MCP and ethylene treatment (Figure 5E). The CAD activity of control and 1-MCP-treated beans decreased in the second week and then increased with further storage. However, the CAD activity of ethylene in fresh common beans increased in the first week and then decreased with further storage (Figure 5F). POD activity of fresh...
common beans decreased in the first week and then increased with further storage. The POD activity in fresh common beans was significantly suppressed by 1-MCP ($P < 0.05$). However, the ethylene-treatment-enhanced POD activity in fresh common beans during storage (Figure 5G).

Expression of $PvACO1$, $PvETR1$, $PvPYR1$, and $PvAOG1$ Genes during Postharvest Storage. The $PvACO1$ genes showed differential expression between control and treated fresh common beans during storage (Figure 6A). $PvACO1$ in fresh common beans showed an increasing trend during storage. The $PvACO1$ gene was significantly enhanced by ethylene but significantly suppressed by 1-MCP during storage. The expression of $PvETR1$ was stimulated by ethylene and 1-MCP (Figure S3A). Expression of $PvETR1$ significantly increased by 1-MCP before the second week of storage. However, expression of $PvETR1$ was significantly inhibited by 1-MCP and ethylene treatment at the third week of storage, while there was no significant difference between 1-MCP and...
ethylene treatment. \( \text{PvPYR1} \) in control and treated fresh common beans showed a downward trend during storage. The effect of 1-MCP and ethylene was a maintained expression pattern of \( \text{PvPYR1} \) in the second week of storage, but there was no significant difference between 1-MCP- and ethylene-treated fresh common beans (Figure S3B). The expression of \( \text{PvAOG1} \) showed an upward tendency during storage. Expression of \( \text{PvAOG1} \) in common beans treated with 1-MCP increased in the second week of storage, while the expression of \( \text{PvAOG1} \) was inhibited by ethylene in the third week of storage (Figure 6B).

**Expression of Lignin Synthesis Genes during Postharvest Storage.** Expression of \( \text{PvSuSy2}, \text{PvPAL3}, \text{Pv4CL1}, \) and \( \text{PvCOMT1} \) in control and 1-MCP-treated beans increased; ethylene significantly stimulated their expression, while 1-MCP significantly suppressed their expression (Figure 7). Expression of \( \text{PvCAD6} \) in common beans decreased during storage, and the decrease of expression was accelerated by 1-MCP and ethylene treatment at the first week of storage and then was inhibited by 1-MCP treatment (Figure S4A). Ethylene and 1-MCP showed significantly increased expression of \( \text{PvPOD1} \) before the second week of storage. However, expression of \( \text{PvPOD1} \) was significantly inhibited by treatment compared to the control, but not significantly between ethylene and 1-MCP at 3 weeks of storage (Figure S4B).

**DISCUSSION**

In the lignification process of fruits and vegetables, cellulose was synthesized, which formed fiber bundles. Lignin was synthesized and deposited in the fiber bundle grid. As the cell lengthens and the secondary wall thickens, the tissue became rough and fibrous, which leads to lignification.\(^{1}\) Tissue lignification gathered the increase of firmness in loquat fruits and accompanied by lignin biosynthesis and cellulose hydrolysis.\(^{16,41}\) In this work, postharvest 1-MCP treatment suppressed the respiration rate and retarded the decrease in the relative thickness of pods (Figure 1A). Others have reported that 1-MCP treatment remarkably suppressed the respiration rate of fresh common beans during storage.\(^{33,34}\) Our results showed that the relative thickness of the pods decreased because of the consumption of carbohydrates by self-respiration during storage (Figures 1A and 2B). It has been reported previously that phenolics are precursors of lignin biosynthesis, and coumaric acid, caffeic acid, and ferulic acid are the main phenolics in asparagus stalks.\(^{17,21}\) Our results showed that total polyphenols increased first and then decreased with storage time. The increase in total polyphenols was significantly suppressed by ethylene and 1-MCP treatment (Figure S1A). Lignification in loquat fruits is the result of the coordinated regulation of lignin biosynthesis and cellulose hydrolysis.\(^{16,41}\) 1-MCP effectively inhibited the decrease of cellulose and the increase of lignin in common beans during storage, while ethylene enhanced them (Figure 2). 1-MCP inhibited the decrease of cellulose and the increase of lignin by influencing the proteins related to the synthesis and degradation of cellulose and lignin.\(^{3}\) Our results showed that the lignified cell group increased, sclerenchyma became thicker, vascular bundles thickened, and lignified cells grew in common beans during storage (Figure 3), which were consistent with ‘Xuxiang’ kiwifruits,\(^{3}\) and 1-MCP inhibited significantly those changes in common beans (Figure 3). \( \text{I}_{1740}/\text{I}_{1508} \) decreased during storage, ethylene and 1-MCP suppressed the decrease, which were consistent with the changes in the cellulose content (Figure 2A), while 1-MCP enhanced the decrease in \( \text{I}_{1379}/\text{I}_{1508}, \text{I}_{1508}/\text{I}_{1379}, \text{I}_{1508}/\text{I}_{1425}, \) and \( \text{I}_{1508}/\text{I}_{1740} \) increased during storage, 1-MCP inhibited this increase, while ethylene enhanced it (Figure S2), which were consistent with the changes in the lignin content (Figure 2B).

Our results showed that postharvest treatment with 1-MCP inhibited lignin accumulation by restraint of the SPS, SuSy, PAL, CAD and POD activities, while that with ethylene enhanced (Figure 5A,B,D,F,G), consistent with loquat fruits,\(^{29}\) water bamboo shoots,\(^{7,30,42}\) R. sterilis D. shi,\(^{14}\) and common beans.\(^{3}\)

The literature suggests that lignification was involved in ethylene in Tsai Tai,\(^{10}\) while ABA/GA\(_3\) in bamboo shoots.\(^{25}\) Exogenous ABA downregulated the expression of genes involved in lignin biosynthesis,\(^{73}\) but the phytohormones that

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**Figure 7.** Expressions of (A) \( \text{PvSuSy2} \), (B) \( \text{PvPAL3} \), (C) \( \text{Pv4CL1} \), and (D) \( \text{PvCOMT1} \) genes of control, ethylene-, and 1-MCP-treated beans during storage. Vertical bars represent the standard errors of three replicates (10 beans of each). Different letters within each parameter indicate statistically significant differences (\( P < 0.05 \)).

**Figure 8.** Expressions of (A) \( \text{PvSuSy2} \), (B) \( \text{PvPAL3} \), (C) \( \text{Pv4CL1} \), and (D) \( \text{PvCOMT1} \) genes of control, ethylene-, and 1-MCP-treated beans during storage. Vertical bars represent the standard errors of three replicates (10 beans of each). Different letters within each parameter indicate statistically significant differences (\( P < 0.05 \)).
affect the lignification in fresh common beans are not clear. The presented results show significantly increased expression of \( \text{PvACO1} \) by ethylene treatment during storage. 1-MCP treatment produced effects opposite to those of ethylene (Figure 6A). However, treatment with ethylene and 1-MCP heightened the \( \text{PvETR} \) in beans in the second week and then inhibited it during further storage (Figure S3A). Treatment with 1-MCP enhanced the expression of \( \text{PvAOG1} \) in beans and inhibited the decline of \( \text{PvPYR1} \) during storage (Figures 6B and S3B), Expression of \( \text{PvAOG1} \) significantly increased during storage as a result of pronounced 1-MCP treatment. Treatment with 1-MCP produced effects opposite to those of ethylene, which provides added evidence for the role of these genes concerning lignin content.10

Expression of genes related to lignin biosynthesis, including \( \text{PAL} \), \( \text{4CL} \), \( \text{CAD} \), and \( \text{COMT} \), upregulated in the process of lignification.11,13,15,21 Our results showed that 1-MCP dramatically suppressed the expression of genes, including \( \text{PvSuSy2} \), \( \text{PvPAL3} \), \( \text{Pv4CL1} \), and \( \text{PvCOMT1} \) in common beans, while ethylene treatment increased (Figure 7). Expression of \( \text{PvCAD6} \) was suppressed by 1-MCP and ethylene treatment in the first week of storage and then inhibited the decline of expression (Figure S4A), in contrast to the results in Tsai Tai treated,10 but are consistent with the results of kiwifruits treated with 1-MCP.9 Expression of \( \text{PvPOD1} \) was enhanced in beans by ethylene and 1-MCP compared to control before the second week of storage (Figure S4B). These results agree with previous findings that 1-MCP markedly increases the expression of \( \text{AcPOD1} \) in kiwifruit core tissue.9

**CONCLUSIONS**

The effects of ethylene and 1-MCP on postharvest lignification of fresh common beans were evaluated. Where lignification was reinforced by ethylene treatment, or retarded by 1-MCP, the inhibition of lignin biosynthesis and the enzyme was consistently enhanced or retarded. Expression correlated well with the lignification and in response to the treatments by ethylene and 1-MCP. This work provides further information on the role of gene expression in lignin biosynthesis in common beans during storage and may be helpful in understanding ethylene involvement in lignification in common beans. Overall, the results indicate that ethylene or ABA may play an important role in 1-MCP regulation of postharvest lignification in common beans, while the interaction of ethylene and ABA on the lignification of fresh beans still needs further study.

**MATERIALS AND METHODS**

**Plant Materials.** Fresh common beans (\( \text{Phaseolus vulgaris} \), cv. Qingbangdou) of commercial maturity were hand-harvested from a garden in Guanling County, Guizhou, China. The beans without physical defects and with uniformity in color and length were selected.

Three treatments were performed, namely 100 \( \mu \text{L} \) \( \text{L}^{-1} \) ethylene and 0.5 \( \mu \text{L} \) \( \text{L}^{-1} \) 1-MCP for 20 h at 25 °C and the control with air. All treatments use a mini fan to maintain air circulation. Then, all common beans were placed into commercial polyethylene bags for storage at 12 ± 1 °C for 3 weeks with a relative humidity of 85%. The common beans were frozen immediately in liquid nitrogen and stored at −80 °C until further analysis. The treatments were carried out on three biological replicates.

**Evaluation of the Respiration Rate and Relative Thickness of Pods.** The respiration rate and relative thickness of pods were determined according to Xie et al.3 The respiration rate was reported in mg kg\(^{-1}\) h\(^{-1}\) CO\(_2\), and the relative thickness of pods was reported in percentage.

**Determination of Reducing Sugar, Cellulose, Total Polyphenols, and Lignin Content.** The reducing sugar content was measured by the 3,5-dichlorosalicylic acid (DNS) method, and the results were reported as % (Fw).35 The cellulose content was determined by the acid detergent method, and results were reported as % (Fw).1 Total polyphenols were quantified by Folin-C reagent, and the results were reported in g kg\(^{-1}\) (Fw).36 The lignin content was determined according to Liu et al., and the results were recorded as A\(_{280}\) g\(^{-1}\).35

**Histochemistry for Identifying Cellulose and Lignin Morphology and Distribution.** For this, 10 μm thick paraffin sections were prepared according to the method described by Chu et al. and Li et al.9,37 The microstructures of beans under an optical microscope were captured with a microscopy imaging system (OLYMPUS, Japan).

**FTIR Measurements.** The FTIR spectra of beans were recorded with an IRAfinity-1 FTIR spectrometer, using the KBr disk standard technique (1 mg of beans powder with 100 mg of KBr). Each spectrum was an average of 32 scans over the range of 4000–400 cm\(^{-1}\) at a resolution of 4 cm\(^{-1}\). To eliminate the influence of bean powder difference and operation error on the experimental results, \( I_{1579}/I_{1508} \) and \( I_{1740}/I_{1508} \) were used to characterize the cellulose content and \( I_{1508}/I_{1579} \), \( I_{1508}/I_{1425} \) and \( I_{1508}/I_{1740} \) were used to characterize the lignin content.38

**Evaluation of \( \text{SPS} \), \( \text{SuSy} \), \( \text{Cx} \), \( \text{PAL} \), \( \text{4CL} \), \( \text{CAD} \), and \( \text{POD} \) Activity.** \( \text{SPS} \) and \( \text{SuSy} \) activities were determined according to Grof et al. and Cunha et al., and the results were expressed as mol h\(^{-1}\) kg\(^{-1}\). Cellulase (Cx) activity was determined according to Cai et al.,16 and the results were expressed as U g\(^{-1}\). \( \text{PAL} \) and \( \text{CAD} \) activities were determined according to Li et al.,9 and the results were expressed as U g\(^{-1}\). \( \text{4CL} \) activity was determined according to Luo et al.,40 and the results were expressed as U g\(^{-1}\). \( \text{POD} \) activity was determined according to Xie et al.,14 and results were expressed as U g\(^{-1}\).

**Total RNA Isolation, cDNA Synthesis, and Real-Time q-PCR Assays.** Based on preliminary proteomic results, the genes involved in lignification, ethylene, and abscisic acid were identified and confirmed. The expression of genes related to ethylene synthesis and response (\( \text{PvACO1} \) and \( \text{PvETR1} \)), \( \text{ABA} \) synthesis and response (\( \text{PvAOG1} \) and \( \text{PvPYR1} \)), cellulose synthesis gene (\( \text{PvSuSy2} \)), and lignin synthesis genes (\( \text{PvPAL3} \), \( \text{Pv4CL1} \), \( \text{PvCOMT1} \), \( \text{PvCAD6} \), and \( \text{PvPOD1} \)) (Figure S5) was examined in fresh common beans. The primers were designed by Primer Premier 5.0 software and are listed in Table S1. Real-time q-PCR was carried out according to Xie et al.3 Samples from day 0 (assigned an arbitrary quantity of 1) were used as a calibrator to calculate the relative quantity of the results. Three replicates were performed for each sample.

**Statistical Analysis.** Statistical tests were performed using the SPSS Statistical Software 22.0 (IBM). The means and significant differences were carried out by Duncan’s multiple range tests at 0.05 probability (\( P < 0.05 \)). The results were reported as the mean ± standard error.
Dear Editor:

I have read the comments and recommendations provided by the reviewers. I would like to thank them for their time and effort in evaluating my manuscript. I have carefully considered their suggestions and addressed them in the following:

1. **In Vivo and In Vitro Analysis**: The in vivo analysis was expanded to include more detailed observations, while the in vitro analysis was refined to better align with the in vivo results. This integration has provided a more comprehensive understanding of the effects of the treatment.

2. **Addition of Additional References**: I have included several new references that address recent developments in the field. These references will help to contextualize my findings.

3. **Figure Enhancements**: The figures have been updated to include more data and visual aids. The descriptions have also been revised to clearly explain the significance of each figure.

I believe that these changes will strengthen the manuscript and make it more valuable to the scientific community. Thank you again for your feedback.

Sincerely,

[Your Name]
(20) Liu, J.; Huang, Q. H.; Kang, P. Z.; Liang, L.; Chen, J. J. Lignin Accumulation in Three Pomelo Cultivars in Association with Sucrose and Energy Depletion. *Biomolecules* 2019, 9, No. 701.

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