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Effects of ethylene and 1-methylcyclopropene (1-MCP) on lignification of postharvest bamboo shoot

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Abstract

The effects of 1-methylcyclopropene (1-MCP) and ethylene on quality and lignification of postharvest bamboo shoot (*Phyllostachys praecox* f. *prevernalis*.) were examined during storage at 20 °C. Disease incidence and respiration rate of control bamboo shoot increased, while total sugar (TS) content decreased quickly. Reducing sugar (RS) content and ethylene production increased at first and then decreased quickly. Increased shoot firmness after harvest was positively correlated with higher lignin and cellulose contents. Accumulation of lignin in flesh tissue was also positively correlated with activities of phenylalanine ammonia lyase (PAL), cinnamyl alcohol dehydrogenase (CAD) and peroxidase (POD). Ethylene treatment enhanced firmness, respiration rate and ethylene production increase, promoted TS decrease, but retarded disease incidence. 1-MCP treatment resulted in lower firmness, higher disease incidence and TS content, inhibited respiration rate and ethylene production, delayed the activities of PAL, CAD and POD, and retarded lignin and cellulose accumulation. The present findings show that ethylene is involved in bamboo shoot lignification, and suggest that 1-MCP could be used commercially to control this important postharvest physiological disorder in bamboo shoot.

Keywords: Bamboo shoot; Lignification; 1-methylcyclopropene; Ethylene

1. Introduction

Bamboo shoot is the young, tender stalk emerging from nodes of the (pseudo-) rhizome of bamboo plants. The edible parts consist of meristematic cell tissue with regions of rapid cell division and differentiation, enveloped in protective, non-edible leaf sheaths (Kleinhenz et al., 2000). They are frequently used in Asian cuisine. Commercially canned bamboo shoot is common, but fresh, locally grown bamboo has far better flavour and texture and the market share of fresh shoots may increase in the future.

Studies on causes of postharvest deterioration of quality in bamboo shoots are limited. In local markets of China, bamboo shoot is usually stored and sold at ambient temperatures. However, during transport from production sites into urban centres, the deterioration of bamboo shoot is characterized by an unusual increase in firmness and toughness of the flesh from the cut end toward the tip during storage. The increase in firmness may be the result of tissue lignification due to a wound (Xi, Luo, Cheng, Feng, & Zhang, 2001). The plant hormone ethylene is produced in response to various kinds of environmental stress, including wounding (Henstrand & Handa, 1989), and wound-induced ethylene is involved in plant lignification (Liu & Jiang, 2006). Therefore, inhibiting ethylene biosynthesis or its action may play an important role in slowing the lignification process and extending storage-life of bamboo shoot. Lignin comprises polyphenolic polymers derived from the oxidative polymerization of different monolignols, including *p*-coumaryl alcohol, coniferyl alcohol and sinapyl alcohol (Whetten & Sederoff, 1995). The biochemistry of lignin biosynthesis is a complex process, involving the action of several enzymes of primary phenylpropanoid metabolism, as well as of lignin biosynthetic branching enzymes (Boudet, 2000). Following the

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deamination of phenylalanine to cinnamic acid by phenylalanine ammonia-lyase (PAL), the lignin biosynthetic branching pathway is operative and the key enzymes involved are hydroxylases, *O*-methyl transferases, COA ligases and alcohol dehydrogenases (Kuboi & Yamada, 1978). In addition, peroxidases are also involved in the last step for the polymerisation of cinnamyl alcohols to form lignin (Imberty, Goldberg, & Catesson, 1985).

1-Methylcyclopropene (1-MCP) has been shown to compete with ethylene for the binding site on the ethylene receptor in plant tissue, which prevents ethylene from exerting its physiological action (Sisler & Serek, 1997). 1-MCP has a non-toxic mode of action, a negligible residue and is active at very low concentrations (E.P.A., 2002); it has been considered non-toxic for humans and the environment (Blankenship & Dole, 2003). It has been used experimentally on fruits and vegetables including, broccoli (Fan & Mattheis, 2000; Ku & Wills, 1999), parsley leaf (Ella, Zion, Nehemia, & Amnon, 2003), green asparagus (Liu, Lv, & Jiang, 2003), lettuce (Saltveit, 2004), and cucumber (Nilsson, 2005). These reports indicate that 1-MCP has commercial potential to control ripening and senescence in harvested fruits and vegetables.

To our knowledge, there is no study on the role of 1-MCP in postharvest quality loss and lignification of bamboo shoots. To understand whether 1-MCP can be commercially practical for bamboo shoot, it is important to determine how it affects the lignification process, so that it can be used in a predictable and reliable manner by the industry. The present study was performed to characterise the physiological and biochemical responses of bamboo shoot to ethylene and 1-MCP treatment and to evaluate its ability as a postharvest tool for regulating the lignification of bamboo shoot. The effects of 1-MCP and ethylene treatment on firmness, disease incidence, total sugar (TS) and reducing sugar (RS) content, respiration and ethylene production, lignin and cellulose content, and the activities of PAL, CAD and POD were examined during storage at 20 °C.

2. Materials and methods

2.1. Plant materials

Bamboo shoot (*P. praecox* f. *prevernalis.*) was harvested from a plantation in Lin'an, Zhejiang Province of China. The shoot was then packed in fiberboard cartons, and transferred to the laboratory in 3 h, where shoot of uniform size and freedom from blemishes were selected.

The shoots were divided into nine sets of 120. Three replicates were used for each of the following treatments: (1) control shoot (0 $\mu l\, l^{-1}$ of 1-MCP or ethylene), (2) 1 $\mu l\, l^{-1}$ of 1-MCP, (3) 500 $\mu l\, l^{-1}$ of ethylene, applied for 8 h at 20 °C in an airtight 200 l container. The treated shoots were then stored at 90% relative humidity at 20 °C for 12 days. Shoot firmness, disease incidence, respiration and ethylene production were assessed every three days. Shoot flesh samples (about 100 g each) were frozen in liquid nitrogen and stored at −70 °C until used for the measurement of total sugar (TS), reducing sugar (RS), lignin and cellulose contents, and PAL, CAD and POD activities.

2.2. Texture measurement

Texture measurements were conducted using a texture analyzer (TA-XT2i, Stable Micro Systems Ltd, UK), incorporating a 5 mm diameter probe. Firmness was measured on the middle of the shoot. At least eight shoots were measured for each treatment and the firmness was expressed as Newton (N).

2.3. Disease incidence

Disease incidence was measured by observing visible fungal growth or bacterial lesions on the shoot surface, and the percentage of infected shoot was recorded every 3 days.

2.4. RS and TS contents determination

Frozen shoot samples (5 g) were ground and extracted for 30 min with 50 ml of ethanol at 25 °C. The mixture was centrifuged at 14,000*g* for 15 min and 5 ml of the supernatant were brought to 50 ml with H_2O. The content of RS was determined spectrophotometrically at 520 nm, using dinitrosalicylic acid as a colouring agent, according to Miller (1959). For TS determination, the samples were first hydrolyzed with 0.1 M HCl for 10 min and then processed as described above. Results were expressed as g of glucose per 100 g fresh fruit.

2.5. Respiration and ethylene evaluation

Respiration was measured as CO_2 production. Three pairs of bamboo shoots (two bamboo shoots per chamber) from each treatment were enclosed in a chamber and air was passed through the chamber. The effluent air was connected to a GXH-3051 (Institute of Junfang Scientific Instrument of Beijing, China) infrared gas analyzer (IRGA) and respiratory rate was measured. The results were expressed as ml of $CO_2\, h^{-1}\, kg^{-1}$ fresh weight.

For ethylene determination, three pairs of bamboo shoots (two shoots per jar) from each treatment were enclosed in about 1000 ml air-tight jars for 1 h at 20 °C. A 1 ml gas sample, collected by syringe, was taken for ethylene determination. The samples were injected into a SP 6800-A gas chromatograph (Lunan Chemical Engineering Instrument Ltd, Shandong Province, China) equipped with a flame ionization detector and an alumina column.

2.6. Lignin and cellulose determination

About 5 g of frozen samples were extracted four times with 50 ml 1% (v/v) 11 M HCl in methanol for 1 h, each

time under continuous stirring and centrifuged at 14,000*g* for 10 min. The final residue was used for analysis of lignin. Lignin (Klason-lignin) content was determined gravimetrically after acid hydrolysis of the insoluble-alcohol residue under previously established conditions (Saura-Calixto, Goñi, Mañas, & Abia, 1991). This residue was mixed with 12 M H_2SO_4 (1:9, w/v) and hydrolysed for 3 h at 20 °C with stirring. The solution was then diluted with distilled water up to 1 M H_2SO_4, and heated for 2.5 h at 100 °C with continuous shaking, cooled, vacuum-filtered through an acid-treated 0.45 μm Millipore HVLP filter, and rinsed with 100 °C distilled water. The filter, containing Klason-lignin, was air-dried at 60 °C overnight and weighed. Results were expressed as g lignin per 100 g fresh weight.

Cellulose was extracted and measured by the method described by Oomena et al. (2004) with modifications. For the isolation of cell wall material (CWM), 10 g of frozen tissue powder was extracted into a 50 mM Tris:HCl, pH 7.2 solution containing 1% SDS for 3 h at room temperature with continuous shaking. The CWM was pelleted by centrifugation at 14,000*g* for 15 min. Subsequently, the residue was washed with water, ethanol, and acetone and air-dried. Fifty milligrammes of CWM was incubated for 90 min at 120 °C in 5 ml of 2 M trifluoroacetic acid. The remaining cellulose was pelleted and washed with water and ethanol. The pellet was solubilized in 67% (v/v) H_2SO_4 at 37 °C, 60 min and diluted appropriately to determine the cellulose content colorimetrically, using anthrone as a colouring agent. Quantification was achieved by using glucose as a standard.

2.7. PAL activity assay

About 5 g of frozen samples were homogenised for 2 min in 15 ml 0.1 M borate buffer (pH 8.8) containing 6 g polyvinylpyrrolidone (PVPP), 5 mM β-mercaptoethanol, and 2 mM EDTA, according to the method of Cheng and Breen (1991). The homogenate was centrifuged for 15 min at 14,000*g* and the supernatant collected for enzyme activity determination. PAL activity was measured by incubating 0.5 ml of supernatant with 2 ml of 0.1 M borate buffer (pH 8.0) containing 3 mM *L*-phenylalanine for 1 h at 30 °C. Increase in absorbance at 290 nm, due to the formation of trans-cinnamate, was measured spectrophotometrically. PAL activity was expressed as change in OD_{290} per minute per kg fresh weight.

2.8. CAD activity assay

About 5 g of frozen samples was extracted by using 10 ml Tris:HCl buffer (200 mM, pH 7.5), as described by Mansell, Gross, Stockight, Frand, and Zenk (1974). The homogenized mixture was centrifuged at 14,000*g* for 15 min and the supernatant liquid was used as an extract of the enzyme.. For assaying the CAD activity, the formation of coniferyl aldehyde from coniferyl alcohol was monitored spectrophotometrically by measuring the increase in absorbance at 400 nm at 37 °C for 2 min. The reaction mixture contained 100 mM Tris:HCl (pH 8.8), 20 mM coniferyl alcohol, 5 mM $NADP^+$, and 50 μl of extract. One unit of CAD activity was defined as change in OD_{400} per minute per kg fresh weight.

2.9. POD activity assay

About 5 g of frozen samples was homogenized with 0.5 g of PVPP and 20 ml of a phosphate buffer (50 mM, pH 7). The homogenized mixture was centrifuged at 14,000*g* for 15 min and the supernatant liquid was used as an extract of the enzyme. The POD activity was determined spectrophotometrically according to a modification of the method described by Aydin and Kadioglu (2001). The assay mixture contained 1 ml of 0.05 M phosphate–citrate buffer (pH 4.6), 1 ml of 40 mM guaiacol and 0.5 ml of 26 mM H_2O_2. The mixture was incubated for 15 min at 25 °C and, finally, 0.5 ml of the enzyme extract was added to the cuvette. Changes in the absorbance at 420 nm were measured for 3 min by spectrophotometer. POD activity was expressed as change in OD_{420} per minute per kg fresh weight.

2.10. Statistical analysis

The experiments were conducted in a completely randomized design. Analysis of variance (ANOVA) was performed; means were compared by the least significant difference, tested at a significance level of 0.05.

3. Results and discussions

3.1. Effect of ethylene and 1-methylcyclopropene treatment on firmness and disease incidence of bamboo shoot

Tissue softening of fruits and vegetables is often the most apparent change that occurs after harvest. In bamboo shoot, however, firmness tended to increase quickly (Fig. 1a), after 12 days of storage at 20 °C; firmness increased by 26.3%. This increase in firmness has been suggested to be the result of tissue lignification (Xi et al., 2001). An increase of lignification has also been found in mangosteen after impact (Ketsa & Atantee, 1998).

1-MCP retarded the firmness increase which, at 12 days after treatment, corresponded to a 17.8% increase over that at 0 day, while ethylene treatment promoted higher firmness.

Disease incidence of control shoot increased sharply during storage at 20 °C (Fig. 1b). 1-MCP treatment accelerated disease incidence increase. Ethylene treatment delayed changes in disease incidence of bamboo shoot. This indication that ethylene retards disease incidence, has also been reported in 'Shamouti' orange (Porat et al., 1999).

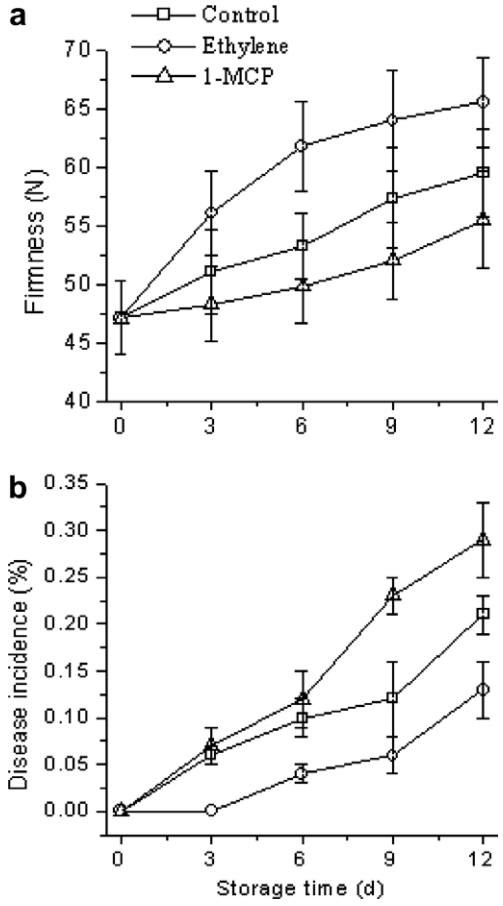

Fig. 1. Firmness (a) and disease incidence (b) following ethylene and 1-MCP treatment in bamboo shoot during storage at 20 °C. Each data point is the average of eight independent shoots. Vertical bars represent standard deviation of the mean.

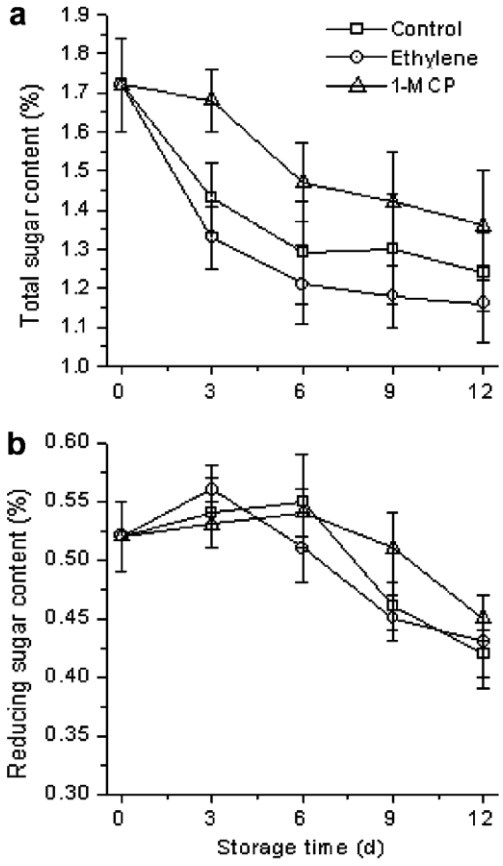

Fig. 2. TS (a) and RS (b) contents following ethylene and 1-MCP treatments in bamboo shoot during storage at 20 °C. Each data point is the average of three independent samples. Vertical bars represent standard deviation of the mean.

3.2. Effect of ethylene and 1-methylcyclopropene treatment on TS and RS contents in bamboo shoot

TS content in bamboo shoots decreased quickly from 1.72% to 1.24% from harvest to day 12 (Fig. 2a). A more rapid decrease in ethylene-treated shoots was observed during storage at 20 °C, while 1-MCP treatment delayed the TS decrease.

RS content in control bamboo shoots increased slowly during the first 6 days of storage at 20 °C (Fig. 2b), but this was followed by a 22.3% decrease. The RS content of ethylene - and 1-MCP-treated bamboo shoots showed patterns similar to the control shoot. The increase in content of reducing sugar may be the result of sugar (e.g., sucrose) hydrolysis, releasing glucose and fructose, while the decrease in RS might be due to a consumption of RS for respiration in fresh-cut bamboo shoot (Lu & Xu, 2004).

3.3. Effect of ethylene and 1-methylcyclopropene treatments on respiration and ethylene production of bamboo shoot

Respiration is a major factor contributing to postharvest loss, which converts stored sugar to energy in the presence of an oxygen substrate, thus advancing senescence (Nourian, Ramaswamy, & Kushalappa, 2003). Control of respiration rate becomes very important. Lowering the respiration rate extends the shelf-life and preserves the quality of products (McLaughlin & O'Berne, 1999). The rate of CO_2 production showed similar patterns in ethylene-treated, 1-MCP-treated and control shoots. It increased slowly during storage at 20 °C (Fig. 3a). 1-MCP treatment inhibited the respiration, while ethylene treatment promoted respiration. This indicated that 1-MCP treatment can effectively suppress CO_2 production. Similar results were reported in 'Bartlett' pears (Ekman, Clayton, Biasi, & Mitcham, 2004).

Ethylene production of control fruit increased slowly and reached maximum values on day 6; thereafter, the ethylene production decreased quickly (Fig. 3b). A more rapid increase, in ethylene treated shoots was observed within 6 days, while 1-MCP treatment inhibited ethylene production increase. Inhibition of ethylene production by 1-MCP treatment has also been reported for coriander leaf (Jiang, Sheng, Zhou, Zhang, & Liu, 2002).

3.4. Effect of ethylene and 1-methylcyclopropene treatment on lignin and cellulose contents in bamboo shoot

Lignin is a complex polymer of phenylpropanoid residues mainly deposited in cell walls (Whetten & Sederoff,

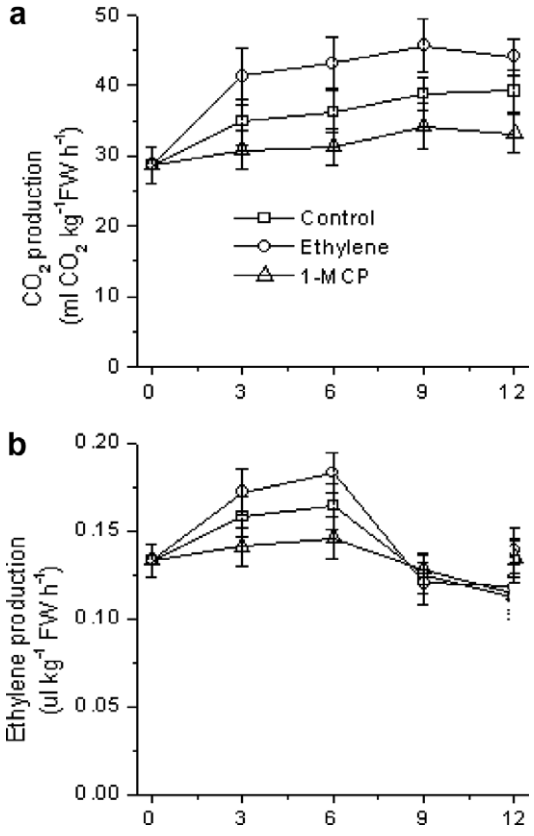

Fig. 3. Respiration (a) and ethylene production (b) following ethylene and 1-MCP treatments in bamboo shoot during storage at 20 °C. Each data point is the average of three pairs of shoots (two shoots per pair). Vertical bars represent standard deviation of the mean.

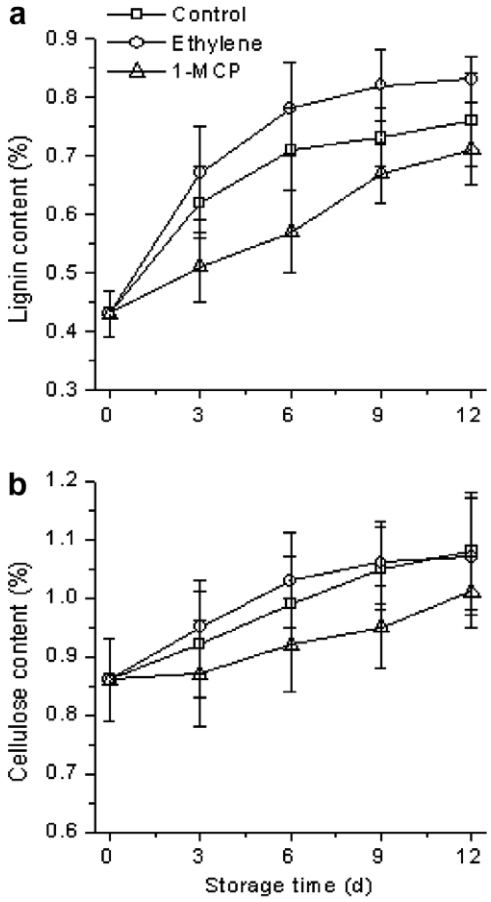

Fig. 4. Lignin (a) and cellulose (b) contents following ethylene and 1-MCP treatment in bamboo shoot during storage at 20 °C. Each data point is the average of three independent samples. Vertical bars represent standard deviation of the mean.

1995), which imparts rigidity to cell walls (Hu et al., 1999). The lignin content of bamboo shoots increased quickly during storage at 20 °C (Fig. 4a), giving approximately 76.7% increase within 12 days. There was a positive correlation between firmness and lignin increases ($r = 0.92^{**}$). Accumulation of lignin was accelerated by ethylene treatment; the content of lignin increased by 93% after 12 days, while 1-MCP treatment retarded the lignin increase.

A moderate increase in cellulose content of bamboo shoot was observed during storage at 20 °C (Fig. 4b). There was a positive correlation between firmness and cellulose content ($r = 0.99^{**}$). 1-MCP treatment retarded cellulose increase, while ethylene treatment promoted cellulose accumulation.

3.5. Effects of ethylene and 1-methylcyclopropene treatments on activities of PAL, CAD and POD of bamboo shoot

Lignin synthesis involves PAL, CAD and POD (Whetten & Sederoff, 1995). PAL, in catalysing deamination of phenylalanine to *trans*cinnamate, is believed to be the critical enzyme controlling accumulation of lignin in plants (Boudet, 2000). CAD catalyzes the last step of the monolignol pathway, while POD catalyzes the polymerization of monolignol to complete the process of lignification (Imberty et al., 1985). These enzymes, that are all part of the lignification pathway, may have profound effects on the lignification of plant tissues.

PAL activity of bamboo shoots increased during storage. A rapid increase in PAL activity was observed over 6 days at 20 °C, by 87.1%, but this was followed by a slow increase (Fig. 5a). There was a significant positive correlation between lignin content and PAL activity ($r = 0.99^{**}$). Ethylene treatment promoted the PAL activity increase, while 1-MCP treatment retarded the PAL activity increase.

CAD activity of bamboo shoot increased quickly during storage at 20 °C, giving approximately 44.8% increase within 12 days (Fig. 5b). There was a significant positive correlation between lignin content and CAD activity ($r = 0.91^{**}$). CAD activity of bamboo shoot was promoted by ethylene treatment, but suppressed by 1-MCP treatment.

POD activity of bamboo shoot increased quickly and reached maximum values on day 6 of storage at 20 °C, (34.1%), but this was followed by a slow decrease (Fig. 5c). There was a significant positive correlation between lignin content and POD activity ($r = 0.91^{**}$). POD activity of 1-MCP treated bamboo shoot was inhibited,

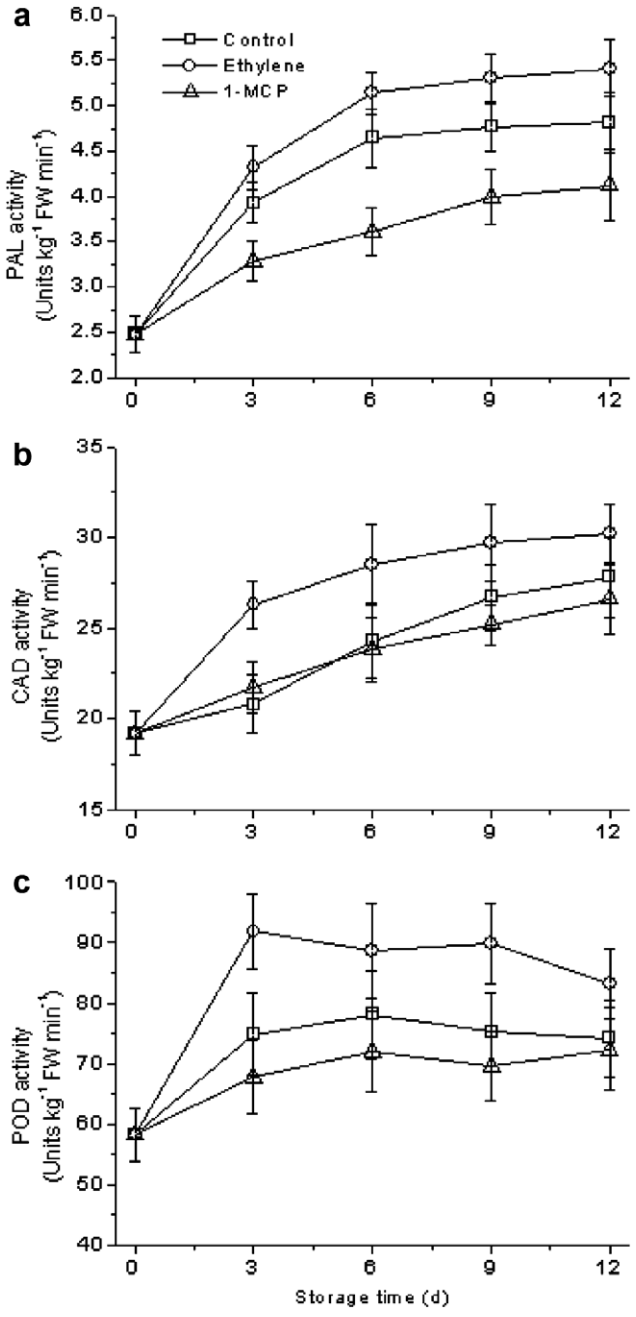

Fig. 5. PAL (a), CAD (b) and POD (c) activities following ethylene and 1-MCP treatments in bamboo shoot during storage at 20 °C. Each data point is the average of three independent samples. Vertical bars represent standard deviation of the mean.

while ethylene treatment promoted a POD activity increase.

4. Conclusions

An increase in shoot firmness after harvest was positively correlated with increases of lignin and cellulose contents. Accumulation of lignin in flesh tissue was also positively correlated with the increased activities of PAL, CAD and POD. Ethylene treatment enhanced firmness, respiration rate and ethylene production, promoted TS decrease, but retarded disease incidence. 1-MCP treatment was associated with lower firmness, higher disease incidence and TS content, inhibited respiration rate and ethylene production, delayed activities of PAL, CAD and POD, and retarded lignin and cellulose accumulation. These results indicated that 1-MCP could be considered for use commercially to maintain postharvest quality and control lignification disorder in bamboo shoot.

Acknowledgements

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