



The effect of 1-methylcyclopropene, methyl jasmonate and methyl salicylate on lignin accumulation and gene expression in postharvest 'Xuxiang' kiwifruit during cold storage

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ABSTRACT

Kiwifruit is susceptible to chilling injury during storage at 0 °C, which causes lignin accumulation, a substantial impact to fruit quality. Lignin has been observed in the pulp and core of kiwifruit (*Actinidia deliciosa* cv. Xuxiang), developing gradually from the stem end to the calyx end. Fruit firmness can be maintained at a higher level during cold storage through application of 1-methylcyclopropene (1-MCP), although with dramatically enhanced activities of phenylalanine ammonia-lyase (PAL, EC 4.3.1.5), cinnamyl-alcohol dehydrogenase (CAD, EC 1.1.1.195), and peroxidase (POD, EC 1.11.1.7) as well as lignification, which occurred during the later storage period. Methyl jasmonate (MeJA) and methyl salicylate (MeSA) significantly inhibited lignification at later stages. Expression profiles of the four lignin-related genes (i.e., *AcPAL*, *AcCAD*, *AcPOD1*, and *AcPOD2*) were assessed, 1-MCP markedly increased the expression levels of *AcPOD1* in fruit core tissue. Together, these results illustrate that MeJA and MeSA can inhibit lignin accumulation to some degree; however, 1-MCP may aggravate lignin deposition, especially in core tissue, mainly via up-regulating *AcPOD1*, which is involved in lignin synthesis.

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1. Introduction

Kiwifruit is one of the most well-known berries owing to its enjoyable taste, antioxidant properties; however, it has a relatively short postharvest life at ambient conditions. Low temperature (0 ± 0.5 °C) can maintain fruit quality for more than three months, but cause chilling injury (CI), which has been the biggest barrier to the commercialization of kiwifruit. Lignification of the outer pericarp is regarded as one of the most severe macroscopic symptoms of CI in kiwifruit (Wang et al., 2013a,b). Evidently, studies on controlling lignification are crucial to alleviate CI of kiwifruit during cold storage.

Lignin is the second most abundant polyphenolic polymer in higher plants after cellulose, providing cell walls with vital biological functions, such as structural support, watertightness and defense against environmental stimuli (Zhong et al., 1998; Boerjan et al., 2003; Barros et al., 2015). Lignin is a complex substance with three types including hydroxyphenyl lignin (H-lignin), syringyl lignin (S-lignin), and guaiacyl lignin (G-lignin), and different plants and different parts of the same plant possess different types of lignin (Boerjan et al., 2003; Boudet et al., 2003; Wang et al., 2012a,b). Lignin synthesis involves the activities of three essential enzymes as well as the coordinated expression of these enzymes genes (Whetten and Sederoff, 1995; Bonawitz and Chapple, 2010).

Phenylalanine ammonia-lyase (PAL) is considered a critical enzyme regulating lignin accumulation (Lewis et al., 1999), and catalyzes the first step of the lignin biosynthetic pathway by deamination of L-phenylalanine to cinnamic acid (Elkind et al., 1990; Bate et al., 1994). PAL is encoded by a multi-gene family in a majority of plants. In *Arabidopsis thaliana*, there have been four PAL genes characterized and expressed in inflorescence tissue where was abundant with lignified cells, suggesting a key role of PAL in lignin biosynthesis (Raes et al., 2003). In addition, PALs from pear

Abbreviations: CI, chilling injury; PAL, phenylalanine ammonia-lyase; CAD, cinnamyl-alcohol dehydrogenase; POD, peroxidase; 1-MCP, 1-methylcyclopropene; MeJA, methyl jasmonate; MeSA, methyl salicylate; quantitative RT-PCR, quantitative real-time PCR.

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and mangosteen have been isolated as well (Kamdee et al., 2014; Lu et al., 2014). However, research in cherimoya fruit and loquat, connection between PAL and lignin content is lack of intensity (Assis et al., 2001; Shan et al., 2008). In addition, PAL may regulate a balance between the primary and secondary metabolism (Olsen et al., 2008). Cinnamyl-alcohol dehydrogenase (CAD) functions in the last step of the monolignol biosynthesis pathway prior to polymerization in cell walls, catalyzing the reduction of cinnamaldehydes to cinnamyl alcohols (Gross et al., 1973; Mansell et al., 1974; Weng and Chapple, 2010). An increasing number of studies have revealed that lignin composition rather than lignin content is directly influenced by the transgenic downregulation of CAD among several eudicot species (Yahiaoui et al., 1998; Baucher et al., 1999; Fornale et al., 2011; Trabucco et al., 2013). CAD also appears to improve the adaption of plants to biotic and abiotic stresses. Menden et al. (2007) demonstrated that syringyl lignin accumulated in wheat owing to its hypersensitive resistance reactivity, and it was easier for fungi and bacteria to attack transgenic plants (Tronchet et al., 2010). *EjCAD1*, a gene isolated in loquat fruit, was confirmed to respond to chilling conditions (Shan et al., 2008). Peroxidase (POD, EC.1.11.1.x) is encoded by a large multi-gene family, and class III POD (EC 1.11.1.7) plays a vital role in the final step of lignin synthesis, including oxidative polymerization and monolignol dehydrogenation (Sitbon et al., 1999). In *Arabidopsis*, *AtPrx4* and *AtPrx72* have been shown to participate in plant lignification (Fernández-Pérez et al., 2015a,b). It has been confirmed that POD activity is positively correlated with lignin accumulation in loquat and pear fruit (Tao et al., 2004; Cai et al., 2006a).

There are no plant enzymes that can degrade lignin because of its complicated structure in higher plants (Sederoff et al., 1999). Thus, it is necessary to discover effective means of inhibiting lignin formation instead of degrading or dispersing it. Various chemical treatments, such as 1-methylcyclopropene (1-MCP), methyl salicylate (MeSA), and methyl jasmonate (MeJA) have been applied to prevent CI occurrence in number of harvested fruit. 1-MCP, as an ethylene antagonist with non-toxic and environmental friendly features, has been widely applied in extension of shelf-life in harvested crops (Sisler and Serek, 1997; Blankenship and Dole, 2003; Huber, 2008; Watkins, 2006, 2008). 1-MCP has been reported to effectively reduce the CI in number of harvested crops including apple (Apollo Arquiza et al., 2005), avocado (Pesis et al., 2002), pineapple (Fan et al., 1999), persimmon (Salvador et al., 2004; Zhang et al., 2010a,b), plum (Candan et al., 2011), and loquat (Cao et al., 2010a). Meanwhile, a number of newest studies have shown that 1-MCP can inhibit softening and maintain higher firmness in kiwifruit (Lim et al., 2016), apple (DeEll et al., 2016), plum (Menniti et al., 2004; Pan et al., 2016), nectarine (Özkaya et al., 2016), mango (Vázquez-Celestino et al., 2016), and peach (Liu et al., 2015). Cai et al. (2006b) reported that the lignin accumulation of loquat was retarded by low temperature or use of 1-MCP at $5 \mu\text{LL}^{-1}$. Wu et al. (2009) noted that an enhanced postharvest quality of Chinese chive scapes by 1-MCP ($0.5 \mu\text{LL}^{-1}$) was associated with inhibited lignification under regulation of PAL, CAD, and POD. Zhang et al. (2010a,b) reported that removal of ethylene or application of 1-MCP could down-regulate the expression of *CAD* genes in Tsai Tai, contributing to reduced lignification and extension of the product. MeSA and MeJA are essential endogenous signal molecules that respond to abiotic and biotic stresses in plants (Reymond and Farmer, 1998). Postharvest treatments with MeJA and/or MeSA have been effectively used to inhibit lignin biosynthesis in loquat fruit (Cao et al., 2008, 2010b; Jin et al., 2014) and *Fragaria chiloensis* fruit (Saavedra et al., 2016).

The objective of present study was to investigate the effect of 1-MCP, MeSA and MeJA on lignification in kiwifruit during cold storage at 0°C . Evaluation addressed the activity of several lignin

metabolism-related enzymes including PAL, CAD and POD, as well as the expression of four genes (*AcPAL*, *AcCAD*, *AcPOD1*, and *AcPOD2*). The study was helpful to understand the regulated mechanisms of lignin accumulation in kiwifruit under chilling stress.

2. Materials and methods

2.1. Plant materials and treatments

Kiwifruit (*Actinidia deliciosa* cv. Xuxiang) were harvested when the average soluble solids content reached $6.5 \pm 0.5\%$ on October 12, 2015 from an orchard in Mei County, Shaanxi Province, China. The selected fruit were immediately transported to the postharvest physiology laboratory at Northwest A&F University, and then sorted out to obtain fruits of a uniform size with an absence of mechanical injury or plant disease symptoms for the subsequent experimental procedures.

2.2. Chemical treatments

Fruit were randomly grouped into four lots of 1200 and then treated in triplicate (i.e., with 400 fruit per replicate) at 20°C for 24 h in 300-L hermetically sealed plastic containers covered with a plastic lid sealed by alum. These four lots corresponded with four different treatments: the control treatment, with fruit exposed to air; the 1-MCP treatment, with fruit exposed to $0.25 \mu\text{LL}^{-1}$ of 1-MCP; the MeJA treatment, with fruit exposed to $0.01 \mu\text{LL}^{-1}$ of MeJA; and the MeSA treatment, with fruit exposed to $0.1 \mu\text{LL}^{-1}$ of MeSA.

1-MCP was released by adding water to the 1-MCP powder (SmartFresh™ powder, Rohm and Hass, Philadelphia, PA, USA). MeJA and MeSA were introduced from Sigma (Sigma-Aldrich, Madrid, Spain). Liquid 1-MCP, MeJA and MeSA were respectively spotted onto filter paper at the final vapor concentration.

The experimental reagent concentrations and processing times had been tested and confirmed as the optimal choice through a pre-experimental trial. After the treatments, fruit were exposed to atmospheric conditions for 2 h at 20°C and then transferred to refrigeration storage at $0 \pm 0.5^\circ\text{C}$ and 90–95% relative humidity for up to 120 d. Samples were taken before chemical processing and at 10-day intervals during the cold storage period. From each replicate of each treatment, twenty fruit were used to assess lignification incidence, while three replicates of twenty fruit were assessed for firmness every 10 d. The samples were peeled, the core tissue and the pulp tissue were individually cut into small cubes, immediately frozen with liquid nitrogen, and then preserved at -20°C for subsequent measurements of lignin content and enzyme activities and at -80°C for subsequent RNA extraction.

2.3. Assessment of lignification incidence

Kiwifruit were evaluated for lignification via observation of longitudinal sections along the central axis and surface of the outer pulp of each peeled fruit. 'Xuxiang' kiwifruit were transferred from $0 \pm 0.5^\circ\text{C}$ storage to 20°C storage for 5 d at the end of their shelf life, and fruit exhibiting lignification were counted. Lignification incidence was assessed using the following formula: lignification incidence (%) = (the number of lignified fruit/the total number of fruit) $\times 100\%$ (Yang et al., 2013).

2.4. Determination of firmness

Fruit firmness was determined at two points of the peeled fruit. These points were defined as having a 90° intersection angle between their two tangent lines relative to the equatorial axis of

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