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Low temperature storage reduces aroma-related volatiles production during shelf-life of banana fruit mainly by regulating key genes involved in volatile biosynthetic pathways

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ABSTRACT

Banana fruit is sensitive to chilling injury, which not only causes physical damage but also dramatically reduces fruit flavor. In this work, we evaluated the influence of non-chilling low temperature (NCT, 13 °C) and chilling temperature (CT, 5 °C) storage on volatiles production in banana in comparison to control conditions (20 °C) and evaluated the possible mechanisms. We found that CT storage caused chilling injury, which negatively affected the physical appearance of the fruit and dramatically reduced volatiles production, especially fruity note volatiles, such as esters. In contrast, NCT storage only reduced the production of a few specific volatiles. Both NCT and CT affected volatile-related amino acid and biosynthetic precursors of fatty acid compositions. The expression levels of the volatiles biosynthesis-related genes, *MaHPL, MaLOX,* and *MaAAT,* were repressed by low temperature (NCT and CT), particularly chilling temperature, while *MaADH* and *MaPDC* were up-regulated. These results suggest that CT significantly reduces volatiles production by regulating different key enzymes and genes involved in volatiles biosynthetic pathways and is mainly mediated via the repression of the lipoxygenase and amino acid metabolic pathways.

1. Introduction

Banana is a globally popular and economically important fruit. However, it ripens and decays rapidly at ambient temperatures. As a widely used postharvest management strategy, cold storage is an effective way to prolong the storage of fresh produce (Brosnan and Sun, 2001; Skog and Chu, 2001; Zhang et al., 2016). However, banana fruit is highly sensitive to low temperature, which can induce chilling injury (CI) when the fruit is stored at temperatures lower than 13 °C (Huang et al., 2016). Physiological disorders develop faster and more intensely when banana is stored at temperatures below a critical level of 11 °C, and cellular membrane damage is a typical early CI response (Jiang et al., 2004). Unsuitable low temperatures not only cause CI to the fruit (Shah et al., 2016) but also result in flavor loss (Zhang et al., 2016) by impairing the production of volatiles, as has been documented in various fruits, including tomato (Zhang et al., 2016), peach (Zhang et al., 2011), and mango (Zhang et al., 2017).

As a typical climacteric fruit, banana undergoes significant changes during ripening, including changes in respiration, ethylene production, color, volatiles production, and texture (Yang et al., 2011). The production of aromatic volatile compounds is important for maintaining the flavor of banana fruit, and more than 250 volatile compounds have been identified in banana (Shiota, 1993). The characteristic banana aroma is not derived from just one or a few volatile compounds but results from a complex mixture of volatile compounds (Wyllie and Fellman, 2000), including C_6 aldehydes and alcohols, such as hexanal and (E)-2-hexenal, and esters, such as isoamyl acetate and 2-methylbutyl acetate (Zhu et al., 2010). Generally, esters, such as butyl acetate, isoamyl acetate, ethyl acetate, butyl butanoate, and isoamyl isobutanoate, are responsible for the characteristic aroma of fresh banana fruit and constitute the major class of volatile compounds present in banana fruit (Shivashankara, 2016).

With regards to the biosynthesis pathways, the C_6 aldehydes and alcohols are generated using linoleic and linolenic acids as precursors

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via the lipoxygenase (LOX) pathway (Schwab et al., 2008). LOX and hydroperoxide lyase (HPL) convert linoleic and linolenic acids to hexanal and hexenal, respectively, via 9- and 13-hydroperoxide isomers. The aldehydes can then be reduced to the corresponding C_6 alcohols by alcohol dehydrogenase (ADH) (Baldwin et al., 2000). The aromatic esters are produced through alcohol acyltransferase (AAT), which catalyzes the final linkage of acyl-CoA and alcohol. Some branched-chain carbon skeleton esters are derived from branched chain amino acids, such as leucine, isoleucine, and valine, by branched chain aminotransferase (BCAT), ADH, and AAT (Schwab et al., 2008). When banana fruit is over-ripe, considerable amounts of alcohol and ethyl acetate are generated, which are derived from aldehyde and catalyzed by pyruvate decarboxylase (PDC) (Dixon and Hewett, 2000). As mentioned above, the characteristic banana volatiles are mainly derived from the LOX pathway and amino acid metabolism. The activities of enzymes involved in both the LOX pathway and amino acid metabolism pathways and the gene expression of AAT during fruit ripening have been reviewed (Echeverría et al., 2004; El Hadi et al., 2013; Zhang and Chen, 2014), but little information on the roles of other key enzymes in banana is available.

Several studies have investigated the volatile profiles of banana fruit during fruit ripening and low temperature storage (Luo et al., 2017; Wyllie and Fellman, 2000), but the effects of cold or chilling temperature (CT) on volatiles production and the associated mechanisms have not been clearly addressed. In the present work, the effects of low temperature [non-chilling low temperature (NCT) and CT] storage on volatiles production, the volatile precursor contents, and the expression profiles of genes related to volatile biosynthesis during banana fruit ripening were studied, with the aim of revealing the possible mechanism of fruit volatiles synthesis under low temperature storage. This study will provide a theoretical basis for reducing quality loss in banana fruit following cold storage.

2. Materials and methods

2.1. Plant material and experimental design

Mature-green (75–80% plump stage) ‘Brazil’ banana (*Musa* spp. AAA group) was harvested from Panyu, Guangdong province, China. The fruit was cleaned and soaked in a 0.2% hypochloride solution for 10 min and then soaked in 0.2% (w v^{-1}) Sporgon solution (Bayer, Leverkusen, Germany) for 1 min to eliminate potential microbes, and then allowed to air-dry at room temperature for 3 h. Bananas free from visual signals of any disease or blemishes and of uniform weight, shape, and maturity were selected and then treated as described below.

All the selected bananas were divided randomly into three groups. The fruit in the control group was treated with an ethephon solution at 1000 μl L^{-1} for 1 min after being pre-handled, and then directly placed at 20 °C. The fruit in the other two groups was stored at 13 °C and 5 °C, respectively. The bananas were then placed into unsealed plastic bags (0.02 mm thick). After one week of storage, the bananas in these two groups were removed and placed at room temperature for 4 h, and then treated with ethephon solution at 1000 μl L^{-1} for 1 min and stored at 20 °C under high humidity (RH 80–90%). The samples were obtained at 0, 1, 3, 5, 7, and 9 d after ethephon treatment and three replicates were tested for each treatment on each sampling date. For all fruit samples, the fruit pulp was chopped up, frozen in liquid nitrogen, and then stored at −80 °C until further use.

2.2. Fruit ripening evaluation

Ten individual bananas were used for peel color determination for each treatment. Four points around the equatorial region on each fruit were selected for color measurement using a Chromameter-2 reflectance colorimeter (Minolta, Osaka, Japan) equipped with a CR-300 measuring head, and recorded as lightness (L), hue angle, or chroma.

Fruit firmness was determined using an Instron 5542 penetrometer (Instron, Norwood, MA, USA) equipped with a cylindrical flat-surfaced plunger (8 mm in diameter). A small slice of banana skin was removed and fruit firmness was measured at a penetration depth of 10 mm on three different fruit at three different points per fruit. Fruit firmness (N) was expressed as the mean value of these measurements.

2.3. Volatiles analysis

Volatiles production was determined by using the solid-phase microextraction (SPME) technique as described previously (Zhu et al., 2010), with minor modifications. Briefly, 5.0 g of pulp sample from three bananas per replicate was homogenized and placed in a 20 mL sealed vial. Polydimethylsiloxane (PDMS) fiber (DVB/CAR/PDMS 50/30 μm, SUPELCO, USA) was inserted into the vial and kept at room temperature (20 °C) for 30 min. The fiber was then inserted into the gas chromatograph (GC; G-3900, HITACHI, Japan) injection port at 220 °C and desorbed for 5 min (splitless). Separation was achieved on a capillary column (DB-1, 30 m × 0.53 mm, 0.1 μm, Agilent Technologies, USA). The program was optimized for volatiles determination. The major volatile components of the banana fruit were identified using gas chromatograph-mass spectrometry (GC/MS) and then confirmed by matching the mass spectra with those available in the National Institute of Standards and Technology Library (http://www.nist.gov) of authentic standards. Total volatile production was determined by calculating the relative concentrations of selected volatile compounds in relation to an internal standard. Ten volatile compounds (Supplementary Table 1), which were representative of banana volatiles, were quantified using authentic external standards (Sigma-Aldrich, St. Louis, MO, USA).

2.4. Determination of free amino acid content

The contents of amino acids, including leucine, isoleucine, and valine, were determined as described previously (Zeng et al., 2015). One gram of banana pulp was homogenized and centrifuged. The supernatant was filtered through a 0.45-μm filter membrane, diluted 10-fold with water, and then derivatized using the AccQ-Fluor™ reagent kit. An amino acid standard mixture (valine, isoleucine, and leucine) was prepared for the calibration. All the samples were prepared in triplicate. The separation and measurements were performed on an Agilent 1200 series high-performance liquid chromatography (HPLC) system (Agilent Technologies, Inc., CA, USA) consisting of a G1315D diode array detector. The separation was carried out using Agilent ZORBAX Eclipse Plus C18 column (4.6 × 250 mm, 5 μm). A binary gradient system was used. The contents of free amino acids were determined by calculating the relative concentrations of selected amino acid in relation to an internal standard.

2.5. Fatty acids assay

Lipids were extracted using a previously described method (Ohkawa et al., 1979). Briefly, 1.5 g of banana pulp in 3 mL of petroleum ether/toluene (v/v = 1:1) and 3 mL of 0.4 mol L^{-1} sodium hydroxide/methanol was combined after stirring at 4 °C for 24 h. Methyl esterification was allowed for 2 h after vortexing at room temperature, after which the solution was centrifuged at 10,000 g for 10 min. Liquid (1.0 μL) was withdrawn from the supernatant and the methylated fatty acid content was assayed using a Hitachi G3900 GC (Japan) equipped with FIDs, and separation was achieved on a Supelco wax™-10 (30 m × 0.53 mm, 1 μm). The flow rate of the carrier gas (helium) was 1.0 mL min^{-1}. The detector temperature was maintained at 250 °C. The injector temperature was 220 °C and the column temperature was maintained at 100 °C for 5 min, after which it was increased to 200 °C at a rate of 10 °C min^{-1} and maintained for 5 min. Fatty acids were identified using methylated standards by comparing their retention times (RT). The concentrations

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