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Postharvest light irradiation and appropriate temperature treatment increase anthocyanin accumulation in grape berry skin

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ABSTRACT

Grape skin color is important because consumers generally prefer well pigmented grapes, and the high marketability of these fruit is important for farmers. Poor coloration, caused mainly by high temperatures during maturation, is a common problem. We investigated the effect of 7- to 9-day light irradiation and temperature treatment at 10, 15, 20, and 25 °C on anthocyanin accumulation in harvested berries of grape accessions. Anthocyanin accumulation of berries, mainly in red- to purple-skinned accessions, could be increased by combining postharvest light irradiation (white light + *UV* light, or blue LED light) with 15–25 °C treatments. Our data suggest that the optimal temperature (15–20 °C) improves anthocyanin accumulation without a decline in titratable acidity and berry weight. The coordinated induction of anthocyanin biosynthesis–related genes under these conditions might explain the accumulation of anthocyanins. These findings will help us to develop techniques for stable production of well colored grapes.

1. Introduction

Anthocyanins are polyphenolic compounds that accumulate in flowers, leaves, and fruit. The color of grape berry skin is determined mainly by the quantity and composition of anthocyanins, and red- to black-skinned accessions accumulate anthocyanins. Anthocyanins protect plants against *UV* light and pathogens, and attract animal pollinators (Harbone and Williams, 2000; Koes et al., 2005). Anthocyanins in grapes and wines have antioxidant and anticancer activity, and counter coronary heart disease, type II diabetes, and retinal degeneration (Harbone and Williams, 2000; Martin et al., 2011). Consumers prefer well colored grapes, and high marketability of these fruit is important for farmers. However, poor coloration, caused mainly by high temperatures during maturation in regions with a warm climate, has become a common problem (Teixeira et al., 2013). Therefore, it is important to understand how anthocyanin biosynthesis is affected by temperature and light, as this knowledge will help us to develop techniques for stable production of well colored grapes in the face of global warming.

In general, the accumulation of anthocyanins in grape skin begins after the onset of ripening (veraison). Exposure of grape bunches to light increases anthocyanin accumulation, whereas shading severely reduces it (Cortell and Kennedy, 2006; Downey et al., 2004; Fujita et al., 2006; Jeong et al., 2004; Kataoka et al., 2003; Matus et al., 2009). Low ambient temperature during maturation increases anthocyanin accumulation in grape berries, whereas high temperature decreases it (Kataoka et al., 1984; Mori et al., 2005a; Tomana et al., 1979a, b). Kliewer and Torres (1972) reported that 'Tokay' grapes developed the strongest fruit coloration at day temperatures between 15 and 25 °C and night temperatures between 10 and 20 °C, and that 35 °C during the day or 30 °C at night inhibited color development.

The genes encoding the enzymes of the anthocyanin biosynthesis pathway in grape have been isolated (Sparvoli et al., 1994), and some MYB-related transcription factors such as VvMYBA1, VvMYBA2, VlMYBA1-2, VlMYBA1-3, and VlMYBA2 regulate anthocyanin biosynthesis (Azuma et al., 2008; Kobayashi et al., 2002, 2004; Walker et al., 2007). Exposure of grape bunches to light significantly increases the expression of anthocyanin biosynthesis–related genes, whereas shading reduces it (Cortell and Kennedy, 2006; Downey et al., 2004; Fujita et al., 2006; Jeong et al., 2004; Matus et al., 2009). Low ambient temperature during maturation increases the expression of genes related to anthocyanin biosynthesis, whereas high temperature decreases it and increases anthocyanin degradation (Mori et al., 2005a, 2007; Yamane et al., 2006). Previously, we found that anthocyanin accumulation depends on both light and low temperature, which synergistically affect the expression of anthocyanin biosynthesis genes (Azuma et al., 2012a).

The difficulty of obtaining an ideal color of grape berries is well

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known; to overcome this difficulty, various approaches have been reported, such as appropriate fruit load control (Kitamura et al., 2005; Sato et al., 1997), trunk girdling at the onset of coloration (Yamane and Shibayama, 2007; Yuki et al., 2016), and exogenous abscisic acid (ABA) application to grape clusters (Ferrara et al., 2013; Jeong et al., 2004; Katayama-Ikegami et al., 2016; Peppi et al., 2007). Irradiation with light-emitting diodes (LEDs) at night, when the ambient temperature decreases, enhances the expression of genes related to anthocyanin biosynthesis and accelerates anthocyanin accumulation during maturation of grape berries (Azuma et al., 2012b; González et al., 2015; Kondo et al., 2014; Rodyoung et al., 2016). These studies showed that blue LED light is the most effective visible wavelength for enhancing anthocyanin accumulation. Most recently, Sheng et al. (2018) reported that *UV*-B or *UV*-C treatment during storage (45 d in the dark) at 4 °C increases the synthesis of phenolic compounds and antioxidant activity. Low-temperature treatment of grape bunches during maturation enhances the accumulation of anthocyanins in grape skin (Koshita et al., 2007, 2015; Tomana et al., 1979a, b). However, no information is available on the effect of short-term visible-light irradiation and temperature treatments on anthocyanin accumulation in harvested berries of different grape genotypes.

In the present study, we used the harvested berries of various grape accessions to investigate the effect of 7–9 d light irradiation and temperature treatment on anthocyanin accumulation and the expression levels of anthocyanin biosynthesis–related genes. Our results will be helpful to understand the mechanism underlying the responses of harvested berries of grape accessions to light and temperature and contribute to develop postharvest techniques for stable production of well colored grapes.

2. Materials and methods

2.1. Postharvest light and temperature treatments of poorly colored grape berries

At harvest time, grape bunches were collected from mature vines of the black-skinned accessions 'Kyoho' and 'Pione' and the red- to purple-skinned accessions 'Aki Queen', 'Akitsu 28', 'Oriental Star', 'Queen Nina', 'Ruby Roman' (*Vitis vinifera* × *V. labrusca*), 'Kaiji', 'Sekirei' (bud sports of 'Kaiji'), and 'Ruby Okuyama' (*V. vinifera*) growing in a vineyard at the Division of Grape and Persimmon Research, Institute of Fruit Tree and Tea Science, National Agriculture and Food Research Organization (NARO), Higashihiroshima, Hiroshima, Japan. Detached poorly colored berries with pedicels were used. The total anthocyanin contents of the berry skin and fruit qualities before treatment are shown in Table S1. The surface of the berries was washed in sterile distilled water, and the berries were immediately packaged in 150 mm × 200 mm pouches of P-Plus (25 µm thickness; Sumitomo Bakelite Co. Ltd, Tokyo, Japan), an oriented polypropylene packaging material. After heat sealing, the packages were immediately incubated under the following conditions.

The red-skinned 'Queen Nina' was used to investigate the effect of postharvest light and temperature treatments on anthocyanin accumulation in berry skin. Ten berries per treatment were incubated in a multi-incubator (LH-30-8CT, Nippon Medical & Chemical Instruments Co., Ltd., Osaka, Japan) for 9 d under one of eight conditions: 10, 15, 20, or 25 °C, either in the dark or under continuous irradiation with a mixture of white light provided by a cold cathode fluorescent lamp and *UV* light provided by an FL10BLB lamp (peak wavelength, 352 nm; Toshiba, Tokyo, Japan) at a total of 80 µmol m^{-2} s^{-1}. In each treatment, the relative humidity (RH) inside P-Plus pouches was measured with a TR-72wf-H Thermo Recorder (T&D Corporation, Nagano, Japan), and vapor pressure deficit (VPD) was calculated from RH and temperature (Campbell and Norman, 1998; Table 1).

All accessions were used to investigate the effect of postharvest temperature treatments under blue LED irradiation on anthocyanin accumulation in the skin. Berries (10–20 per treatment) were incubated in a multi-incubator for 7–9 d at 10, 15, 20, or 25 °C with continuous irradiation with blue LED light (peak wavelength, 445 nm; 100 µmoL m^{-2} s^{-1}). This experiment was performed in 2014 and again in 2015. After incubation, the berry skins were peeled off, immediately frozen in liquid nitrogen, and kept at −80 °C until analysis.

2.2. Analysis of anthocyanin contents and fruit qualities

Anthocyanins were extracted from berry skins by the method of Shiraishi et al. (2007). Skin (1 g per treatment) collected from 10 random berries was placed in 10 mL of 50% acetic acid (*v/v*) for 24 h at 4 °C in the dark. Total anthocyanin content (n = 3) was expressed as milligrams of cyanidin-3-monoglucoside (Extrasynthèse, Genay, France) equivalent per gram of fresh berry skin. Berry firmness (n = 8) was determined at two points on the surface using a durometer (KR-27E, compression force range of 0 to 8.05 N; Kori Seiki MFG. Co., Ltd., Tokyo, Japan) with a 5.42 mm diameter spherical head. The soluble solids content (SSC) of juice (n = 3) was measured with a digital refractometer (PR-100α; Atago, Tokyo, Japan). The titratable acidity (n = 3) was measured by neutralizing the juice with 0.1 N NaOH and expressed as the mass (g) of tartaric acid equivalent per 100 mL of juice. Anthocyanin contents and fruit qualities were measured before and after treatment.

2.3. Quantitative real-time PCR analysis

Total RNA was extracted as described by Reid et al. (2006) (n = 3 per treatment), and cDNA was synthesized with a PrimeScript II cDNA synthesis kit (Takara, Shiga, Japan) as described in the manufacturer's manual. The following groups of genes were analyzed: (1) anthocyanin biosynthesis-related genes *VvMYBA1*, *VlMYBA1-2*, *VlMYBA1-3*, *VlMYBA2*, *chalcone synthase 3* (*CHS3*), *flavonoid 3′-hydroxylase* (*F3′H*), *flavonoid 3′5′-hydroxylase* (*F3′5′H*), *dihydroflavonol 4-reductase* (*DFR*), *leucoanthocyanin dioxygenase* (*LDOX*), *UDP-glucose:flavonoid 3-O-glucosyltransferase* (*UFGT*), *anthocyanin O-methyltransferase* (*AOMT*), *glutathione-S-transferase* (*GST*), *anthocyanin multidrug and toxic extrusion* (*antho-MATE*); (2) ABA-related genes *open stomata 1* (*OST1*), *enhanced response to ABA 1* (*ERA1*), and *9-cis-epoxycarotenoid dioxygenase 1* (*NCED1*); (3) light signaling–related genes *elongated hypocotyl 5* (*HY5*), *HY5 homolog* (*HYH*), *UV-B receptor* (*UVR1*), and *DNA-repairing enzymes* (*FOT6-4*); (4) flavonol biosynthesis-related genes *MYBF1*, *flavonol synthase* (*FLS4*), and *flavonol-O-glycosyltransferase 5* (*GT5*); and (5) *MYB4a*, which encodes a repressor of flavonoid biosynthesis. Quantitative real-time (qRT) PCR (n = 3 per treatment) was performed on a 7300 Real-Time PCR system (Applied Biosystems, Foster City, CA, USA) with a QuantiTect SYBR Green PCR kit (Qiagen, Hilden, Germany) as described in the manufacturers' manuals with primers listed in Table S2. Relative gene expression was calculated by the $2^{-\Delta\Delta Ct}$ method. The amounts of transcripts were normalized against *VvUbiquitin1* (Bogs et al., 2006). The average expression level of each gene was calculated as the molar ratio relative to the copy number of *VvUbiquitin1*.

2.4. Statistical analysis

Light and temperature conditions were compared by two-way ANOVA. Temperature conditions were compared by one-way ANOVA and Tukey–Kramer test. Correlations among anthocyanin contents and the levels of gene expression were analyzed by Pearson's product–moment correlation coefficient. All statistical tests were performed in JMP v. 13 software (SAS Institute Inc., Cary, NC, USA).

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