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Light quality affects flavonoid biosynthesis in young berries of Cabernet Sauvignon grape

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ABSTRACT

Biosynthesis of phenolic compounds is known to be sensitive to light environments, which reflects the possible role of these compounds for photoprotection in plants. Herein, the effects of UV and visible light on biosynthesis of flavonoids was investigated, i.e., proanthocyanidins (PAs) and flavonols, in young berry skins of a red-wine grape, *Vitis vinifera* cv. Cabernet Sauvignon. Shading with light-proof boxes from the flowering stage until 49 days after treatment (DAT) partially decreased PA concentrations, and completely decreased flavonol concentrations in the berry skins. Shading decreased the transcript abundance of a flavonol-related gene more remarkably than those of PA-related genes. In addition, light exclusion influenced the composition of PAs, such as the decrease in the proportion of trihydroxylated subunits and the mean degree of polymerization (mDP) within PAs. However, solar UV exclusion did not affect the concentration and composition of PAs, whereas this exclusion remarkably decreased the flavonol concentration. Consistently, UV exclusion did not influence the transcript levels of PA-related genes, whereas it dramatically decreased that of flavonol-related genes. These findings indicated a different light regulation of the biosynthesis of these flavonoids in young berry skins of wine grape. Visible light primarily induces biosynthesis of PAs and affects their composition, whereas UV light specifically induces biosynthesis of flavonols. Distinct roles of members of a MYB transcription factor family for light regulation of flavonoid biosynthesis were proposed.

1. Introduction

Higher plants require visible solar radiation to provide energy for photosynthetic activity. When harvesting light, the photosynthetic organs of the plants are inevitably exposed to relatively high doses of harmful UV radiation. In response to elevated doses of solar radiation, including UV radiation, higher plants have evolved a number of protective mechanisms (Jansen et al., 1998; Merzlyak et al., 2002). One effective strategy is accumulation of phenolic compounds that selectively absorb UV radiation in the plant cuticle and epidermis (Bieza and Rodrigo, 2001; Casati and Walbot, 2003; Schmitz-Hoerner and Weissenböck, 2003; Solovchenko and Schmitz-Eliberger, 2003). These compounds also act as scavengers of reactive oxygen species (ROS) in living cells to counteract the consequences of irradiation (Landry et al., 1995; Olsson et al., 1998; Gould et al., 2002; Ryan et al., 2002; Nagata et al., 2003).

Phenolic compounds in fruits have received much attention for their potential contribution to human health through their antioxidant, antimicrobial, antiviral, and anticarcinogenic characteristics (Jackson, 2000b). In addition, they are important contributors to organoleptic qualities of fresh fruit, fruit juices, and wine (Cheynier et al., 1999; Cheynier, 2005). Phenolic compounds are biosynthesized through the phenylpropanoid and flavonoid pathways originated from phenylalanine (**1**), which are among the most characterized secondary metabolic pathways in plants (Fig. 1) (Winkel-Shirley, 2001; Davies and Schwinn, 2003). Phenolic compounds include non-flavonoid compounds, such as hydroxycinnamic acid esters (**3**) and stilbenes, as well as flavonoid compounds, such as anthocyanins, flavonols, and proanthocyanidins (PAs) (**11**).

Flavonoid compounds are abundant in grape berry skins. Anthocyanins are responsible for the red and purple colors that accumulate during ripening in berry skins of red varieties. Flavonols are yellow pigments that are synthesized in berry skins during two distinct periods: from flowering to the early stages of berry development and during ripening (Downey et al., 2003; Fujita et al., 2006). PAs (**11**), which are polymers of flavan-3-ol units (e.g., catechin (**7**), epicatechin (**8**), epicatechin-3-*O*-gallte (**9**), and epigallocatechin (**10**)), represent the most abundant class of phenols in grape berries, and these are responsible for the bitter and astringent properties of red wine (Vidal et al., 2003). PA (**11**) biosynthesis occurs early in berry development and is completed around veraison, which is the developmental stage when anthocyanin synthesis begins in red varieties (Downey et al., 2004; Fujita et al., 2007). PA

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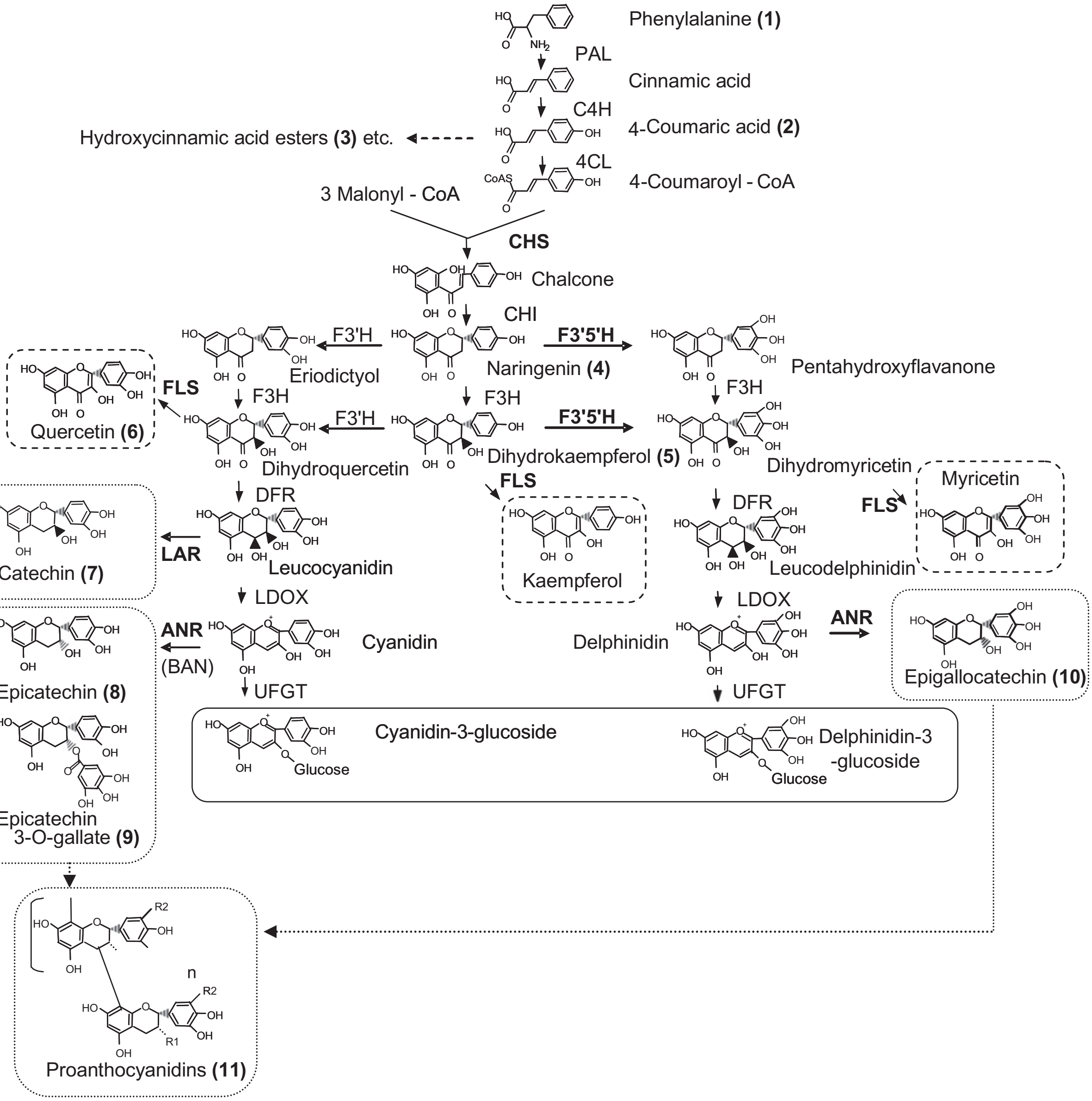

Fig. 1. Schematic representation of general phenylpropanoid and flavonoid pathways in grape skins. Enzyme names are abbreviated as follows: PAL, phenylalanine ammonia-lyase; C4H, cinnamate 4-hydroxylase; 4CL, 4-coumarate:CoA-ligase; CHS, chalcone synthase; CHI, chalcone isomerase; F3H, flavanone-3-hydroxylase; F3’H, flavonoid 3′-hydroxylase; F3′5′H, flavonoid 3′,5′-hydroxylase; FLS, flavonol synthase; DFR, dihydroflavonol 4-reductase; LAR, leucoanthocyanidin reductase; LDOX, leucoanthocyanidin dioxygenase; ANR, anthocyanidin reductase; and UFGT, UDP-glucose:flavonoid 3-*O*-glucosyltransferase. The products in the solid-line box are the members of anthocyanins. The products in the dotted-line boxes are members of flavan-3-ols and their polymer, proanthocyanidins (PAs). The products in the broken-line boxes are members of flavonols. The mechanism of the condensation reactions of PAs shown by the dotted arrows has not been fully understood yet. Transcripts of genes shown with the bold character were analyzed in this study.

(11) concentrations decrease during ripening, possibly because of a decrease in the ratio of extractable PAs **(11).**

Transcriptional regulation of the structural genes on the flavonoid pathway by the complex of DNA-binding R2R3 MYB transcription factors, basic helix-loop-helix, and other classes of transcription factors has been found in several plant species (Weisshaar and Jenkins, 1998; Davies and Schwinn, 2003; Baudry et al., 2004; Hartmann et al., 2005). In grapes, different regulators belonging to the MYB transcription factor superfamily were recently reported to regulate structural genes on specific branches of the pathway, which contribute to the biosynthesis of flavonoids: VvMYBA1 (Kobayashi et al., 2004) and VvMYBA2 (Walker et al., 2007) regulated the anthocyanin branch; VvMYB5a (Deluc et al., 2006), VvMYB5b (Deluc et al., 2008), VvMYBPA1 (Bogs et al., 2007), and VvMYBPA2 (Terrier et al., 2009) appeared to regulate the general branch of the pathway as well as the PA branch; and VvMYBF1 (Czemmel et al., 2009; Matus et al., 2009) regulated the general branch and the flavonol branch. The mRNA levels of these MYB genes were influenced by environmental factors, such as light, heat, and water relations, as well as plant hormones, which correlates to mRNA levels of the structural genes of flavonoid pathways (Jeong et al., 2004; Yamane et al., 2006; Castellarin et al., 2007; Czemmel et al., 2009; Matus et al., 2009).

Flavonoids in fruits were found to be particularly sensitive to light environments around clusters, which reflects a possible role of these compounds for photoprotection (Jackson and Lombard, 1993; Downey et al., 2006). The synthesis of anthocyanins and its regulation in response to light conditions have been studied in several types of fruit (Jaakola et al., 2002; Jeong et al., 2004; Steyn et al., 2004; Tsuda et al., 2004; Takos et al., 2006b), however,