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Fruit-localized photoreceptors increase phenolic compounds in berry skins of field-grown *Vitis vinifera* L. cv. Malbec

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A B S T R A C T

Sunlight exposure has multiple effect on fruits, as it affects the light climate perceived by fruit photoreceptors and fruit tissue temperature. In grapes (*Vitis vinifera* L.), light exposure can have a strong effect on fruit quality and commercial value; however, the mechanisms of light action are not well understood. The role of fruit-localized photoreceptors in the control of berry quality traits was evaluated under field conditions in a commercial vineyard in Mendoza (Argentina). Characterization of the diurnal dynamics of the fruit light environment in a vertical trellis system indicated that clusters were shaded by leaves during most of the photoperiod. Supplementation of the fruit light environment from 20 days before veraison until technological harvest showed that red (R, 660 nm) and blue (B, 470 nm) light strongly increased total phenolic compound levels at harvest in the berry skins without affecting sugar content, acidity or berry size. Far-red (FR, 730 nm) and green (G, 560 nm) light supplementation had relatively small effects. The stimulation of berry phytochromes and cryptochromes favored accumulation of flavonoid and non-flavonoid compounds, including anthocyanins, flavonols, flavanols, phenolic acids and stilbenes. These results demonstrate that the chemical composition of grape berries is modulated by the light quality received by the clusters under field conditions, and that fruit photoreceptors are not saturated even in areas of high insolation and under management systems that are considered to result in a relatively high exposure of fruits to solar radiation. Therefore, manipulation of the light environment or the light sensitivity of fruits could have significant effects on critical grape quality traits.

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1. Introduction

Fruits are important for seed dispersal and represent a key component of the diet of many animals, including humans. Fleshy fruits are particularly rich in sugars, acids, pigments, minerals and vitamins. A series of coordinated changes in color, texture, flavor, aroma, and chemical characteristics takes place during ripening, rendering the fruits more attractive and nutritionally valuable (Giovannoni, 2004).

Grape berries are fleshy fruits and represent an important source of phytonutrients. Grape berries are particularly rich in antioxidants like phenolic compounds, including flavonoids such as anthocyanins, flavonols (quercetin, kaempferol, etc.), and flavanols (catechins, epicatechins and tannins), as well as non-flavo-

Abbreviations: d, day/s; DAF, days after flowering; h, hour; DW, dry weight; FW, fresh weight; LEDs, light emitting diodes; LMWPC, low molecular weight phenolic compounds; PAR, photosynthetic active radiation; UV-A, UV-A radiation; UV-B, UV-B radiation.

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noids, such as stilbenes, hydroxycinnamic and hydroxybenzoic acids and their derivatives. These compounds are of particular interest since they define organoleptic, nutritional and nutraceutical characteristics of grape berries. Adequate concentrations of phenols, sugars, acids and volatile compounds are desirable attributes in berries, both for fresh consumption and for winemaking (Downey et al., 2006). Anthocyanins have a high antioxidant capacity and, as components of the human diet, they have strong health-promoting effects offering protection against cancer and various age-related degenerative diseases (Martin et al., 2013). Therefore, a better understanding of the mechanisms controlling the accumulation of phenolic compounds could be useful to optimize phytonutrient content of fruits, with potential benefits to reduce the incidence of chronic diseases, and improve the organoleptic characteristics of wines.

Grape berry ripening and, consequently, fruit growth and composition are affected by many environmental factors. The best studied of these factors are light, water status, temperature and pathogens. In general, moderate water deficits, ultraviolet-B (UV-B, 280–315 nm) radiation, and low temperatures positively affect ripening by increasing the content of soluble solids and anthocyanins; while high temperature, pathogens and shade have negative effects on berry quality (Kuhn et al., 2014).

The light environment of grape berries can be influenced by site characteristics, season and the cultural practices that directly affect light penetration through the leaf canopy (i.e. training and trellis system, row orientation, plant density, pruning, shoot thinning and positioning, leaf removal, etc.) (Matus et al., 2009; Smart, 1985, 1988). There are many reports on the effect of light on berry development and metabolite composition. Most of the experimental approaches involved the application of shade treatments, either to the whole plant (Kliewer, 1977; Kliewer and Antcliff, 1970; Smart et al., 1988) or only to the clusters (Cortell and Kennedy, 2006; Dokoozlian and Kliewer, 1996; Downey et al., 2004; Jeong et al., 2004; Koyama and Goto-Yamamoto, 2008; Morrison and Noble, 1990; Niu et al., 2013; Ristic et al., 2007). In other studies, the effect of light on berry development and composition was evaluated by sampling berries from different canopy positions – i.e. shade or sun-exposed berries – (Bergqvist et al., 2001; Crippen and Morrison, 1986a,b; Haselgrove et al., 2000; Kliewer and Lider, 1968; Price et al., 1995; Spayd et al., 2002; Tarara et al., 2008) and also by using different levels of defoliation in the fruit zone (Hunter et al., 1991, 1995; Kliewer and Antcliff, 1970; Matus et al., 2009). All of these studies concluded that sunlight-exposed fruits have (in general) higher levels of total soluble solids, anthocyanins and phenolics, and lower values of titrable acidity, malate, juice pH and berry weight, as compared to shaded fruits. Excessively shaded fruits may even show a delayed ripening and herbaceous aroma, and they may also be affected by fungal diseases (Smart et al., 1988). Additionally, it has been reported that the expression of genes of the flavonoid pathway and various transcription factors involved in its regulation (i.e. *MYBA1*) were up-regulated by visible light and UV radiation (Azuma et al., 2012; Downey et al., 2004; Jeong et al., 2004; Koyama and Goto-Yamamoto, 2008; Koyama et al., 2012; Matus et al., 2009; Zhang et al., 2012). Summarizing, although many studies have characterized the effect of total solar radiation on berry quality traits, the effect

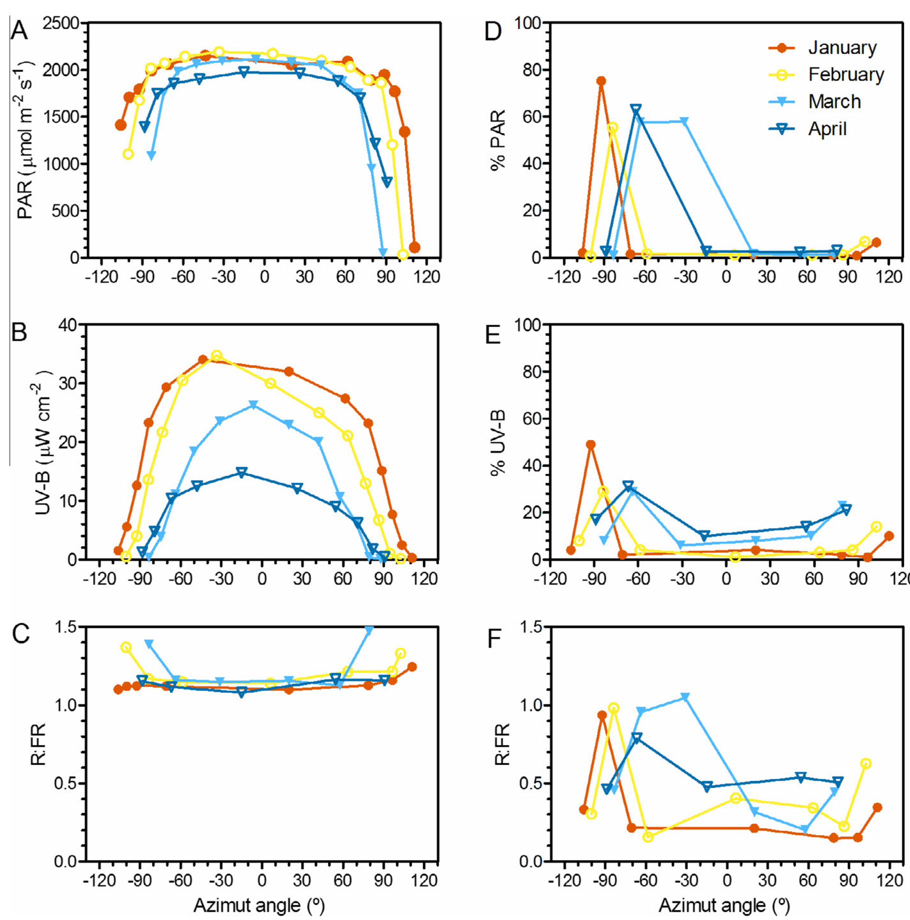

Fig. 1. Cluster zone light environment. Daily course of PAR (A and D), UV-B radiation (B and E) and R:FR ratio (C and F) recorded over the grapevine canopy (left panels) and in the cluster zone (right panels). PAR and UV-B in the cluster zone are expressed as a % of the incident PAR and UV-B, respectively. Solar noon is at 0° azimuth. Date are means ± SE of five measurements.

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