Plant Physiology and Biochemistry 109 (2016) 374–386

Contents lists available at ScienceDirect

Plant Physiology and Biochemistry

journal homepage: www.elsevier.com/locate/plaphy

Research article

Effects of ambient solar UV radiation on grapevine leaf physiology and berry phenolic composition along one entire season under Mediterranean field conditions

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ARTICLE INFO

Article history:
Received 6 September 2016
Received in revised form
8 October 2016
Accepted 18 October 2016
Available online 22 October 2016

Keywords:
UV exclusion
Grapevine
Berry ripening
Flavonols
Phenolic profiles
Phenolic compounds compartmentalization
Field studies

ABSTRACT

In the present study we assessed the effects of ambient solar UV exclusion on leaf physiology, and leaf and berry skin phenolic composition, of a major grapevine cultivar (Tempranillo) grown under typically Mediterranean field conditions over an entire season. In general, the effects of time were stronger than those of UV radiation. Ambient UV caused a little stressing effect (eustress) on leaf physiology, with decreasing net photosynthesis rates and stomatal conductances. However, it was not accompanied by alterations in F_v/F_m or photosynthetic pigments, and was partially counterbalanced by the UV-induced accumulation of protective flavonols. Consequently, Tempranillo leaves are notably adapted to current UV levels. The responses of berry skin phenolic compounds were diverse, moderate, and mostly transitory. At harvest, the clearest response in UV-exposed berries was again flavonol accumulation, together with a decrease in the flavonol hydroxylation level. Contrarily, responses of anthocyanins, flavanols, stilbenes and hydroxycinnamic derivatives were much more subtle or nonexistent. Kaempferols were the only compounds whose leaf and berry skin contents were correlated, which suggests a mostly different regulation of phenolic metabolism for each organ. Interestingly, the dose of biologically effective UV radiation (UV_{BE}) was correlated with the leaf and berry skin contents of quercetins and kaempferols; relationships were linear except for the exponential relationship between UV_{BE} dose and berry skin kaempferols. This opens management possibilities to modify kaempferol and quercetin contents in grapevine through UV manipulation.

1. Introduction

Ultraviolet (UV) radiation is a minor fraction (around 8%) of the solar spectrum reaching the ground level in the Biosphere. At this level, it is composed by two types of wavelengths, being UV-A (315–400 nm) much more abundant than UV-B (280–315 nm). Traditionally, UV radiation (particularly UV-B) has been considered as a generic stressor for plants, inducing diverse damaging processes mainly affecting photosynthesis, DNA, membranes, proteins and hormones. Nowadays, however, there is consistent evidence that natural UV levels act rather as an environmental regulator, controlling gene expression, metabolism, and growth and development (Jansen and Bornman, 2012; Hideg et al., 2013). In crop plants, this new conception opens different management possibilities to improve agricultural products, conferring them an added value and quality differential through UV manipulation. Thus, research on the effects of UV on crop plants has notably increased in recent years (Wargent and Jordan, 2013).

Abbreviations: Ambient, no filter control treatment; ANOVA, analysis of variance; FUV-, UV-blocking filter treatment; FUV+, UV-transmitting filter treatment; HPLC, high-performance liquid chromatography; MIPC, methanol-insoluble phenolic compounds; MSPC, methanol-soluble phenolic compounds; PAR, photosynthetically active radiation; UPLC, ultra-performance liquid chromatography; UV_{BE}, biologically effective UV radiation.

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http://dx.doi.org/10.1016/j.plaphy.2016.10.018
0981-9428/

In grapevine (*Vitis vinifera* L.), one of the main crops worldwide, UV radiation is a key factor regulating the contents of important healthy metabolites that determine berry and wine features, such as aroma, astringency, colour and stability. Additionally, UV radiation may increase tolerance to abiotic and biotic stressors, including pests and diseases (Jug and Rusjan, 2012). Thus, research on the effects of UV radiation on grapevine is strategically important because it offers enormous possibilities of management to improve both the production process and the quality of the final product. These objectives can be investigated through simple cultural practices modifying sun exposure of berries, such as defoliation (Pastore et al., 2013) or shading (Downey et al., 2004). Yet, this kind of methods cannot discriminate between the effects of the different wavelengths of the solar spectrum. To assess the specific effects of UV radiation, two basic manipulation approaches can be applied: UV enhancement using lamps and UV exclusion using filters. Both approaches have been used in grapevine, but many of these studies have focused on leaf physiology (Kolb et al., 2001; Pfündel, 2003; Núñez-Olivera et al., 2006; Pollastrini et al., 2011; Majer and Hideg, 2012; Berli et al., 2013; Alonso et al., 2015; Martínez-Lüscher et al., 2015; Grifoni et al., 2016). Obviously, the results of the studies conducted on leaves have a limited applicability to the production process. Many other studies have analyzed berry traits, particularly phenolic composition and gene expression, and their results may have a greater applicability. However, some of these studies have dealt with plants growing in pots under controlled conditions (Martínez-Lüscher et al., 2014a, 2014b), and thus their results cannot be directly extrapolated to the field. Other studies have been conducted on high-altitude vineyards (Berli et al., 2008, 2011), where plants are exposed to higher UV levels than those received in mid-altitude localities where most of worldwide grapevines are grown. Therefore, studies carried out under typical field Mediterranean environments are scarce (Gregan et al., 2012; Carbonell-Bejerano et al., 2014; Del-Castillo-Alonso et al., 2015; Liu et al., 2015) and badly needed.

Other aspects that remain underexplored in the research on UV and grapevine are, for example: (1) the relationship between phenolic compounds in leaves and berries (Del-Castillo-Alonso et al., 2015); (2) the temporal responses of phenolic compounds to UV radiation over the entire berry ripening process (Gregan et al., 2012), because responses may vary along the development of a specific organ (Wargent and Jordan, 2013); and (3) the cell compartmentalization of phenolic compounds between vacuoles and cell walls. This last point may be relevant for the physiology of the plant, because vacuolar and cell wall-bound compounds can represent different photoprotection modalities (Carbonell-Bejerano et al., 2014; Del-Castillo-Alonso et al., 2015), and also for enological purposes, because the different location of phenolic compounds may influence their extractability in the enological process. Furthermore, it must be pointed out that most studies on the effects of UV radiation on grapevine have been conducted using minor grapevine varieties.

The goal of this study was to assess, under typical mid-altitude Mediterranean field conditions, the effects of solar UV exclusion on grapevine physiology and phenolic composition in leaves and berry skins of *Vitis vinifera* L. cv. Tempranillo at three different phenological stages along berry development (pea-size, veraison and harvest). The accumulation of phenolic compounds was separately analyzed in the methanol-soluble (vacuoles) and -insoluble (cell walls) fractions in both leaves and berry skins. The study was carried out using a major grapevine cultivar, given that Tempranillo is the fourth most used cultivar worldwide, and the first world's fastest-expanding wine grape in the period 2000–2010 (Anderson, 2013). It occupies more than 232,000 ha in the world (5.05% of the total), mostly in Spain.

2. Materials and methods

2.1. Plant material and experimental design

This field experiment was conducted in the 2012 season on a commercial vineyard located in Mendavia (Navarra, northern Spain, 42° 27′ N, 2° 14′ W, 371 m altitude). *Vitis vinifera* L. cv. Tempranillo, grafted onto 110R rootstock and planted in 2007 on clay-loam soil with NE-SW row orientation, was used. The vines were spur-pruned (12 buds per vine) in a bilateral cordon and trained to a vertical shoot positioning trellis system. At pre-bloom (7 June 2012, seven days before flowering), all vines were partially defoliated by removing the first six main basal leaves to increase and homogenize the exposure of fruits to solar radiation. Vines were not irrigated during the growing season.

A completely randomized block design was set-up. Six blocks of nine vines each were divided into three experimental conditions (three vines per replicate): no filter (Ambient); UV-transmitting filter (FUV+); UV-blocking filter (FUV-). The two filtered treatments were established using colourless and transparent polymetacrylate filters (PMMA XT Vitroflex 295 and XT Vitroflex 395 Solarium Incoloro, Polimertecnic, Girona, Spain). PMMA XT Vitroflex 295 filter allowed for the transmission of UV radiation, whereas PMMA XT Vitroflex 395 filter blocked UV transmission. Filters (1.30 × 0.75 m) were placed at 45° from the vertical axis of the plant, on both sides of the canopy, covering the fruiting zone and the first 0.7 m of the canopy of each grapevine. Filters were installed right after defoliation and maintained until harvest (7 September 2012). Spectral irradiances below filters, and also under Ambient conditions, were measured regularly from the beginning of the experiment (Fig. 1) using a spectroradiometer (Macam SR9910, Macam Photometrics Ltd, Livingstone, Scotland), to confirm the stability of their filtering characteristics. Ambient photosynthetic (PAR), UV-A, and UV-B irradiances were continuously recorded close to the experimental plot by broad band radiometers (Skye Quantum SKP 215, SKU 420 and SKU 430, respectively, Skye Instruments Ltd, Powys, UK). The biologically effective UV irradiance (UV_{BE}) was estimated using the action spectrum of Flint and Caldwell (2003). At veraison, fruit and mid-upper canopy temperatures were determined by thermography in each replicate to check the influence of filters. Thermal images were taken at solar noon with a thermal camera (ThermaCAMP640, FLIR

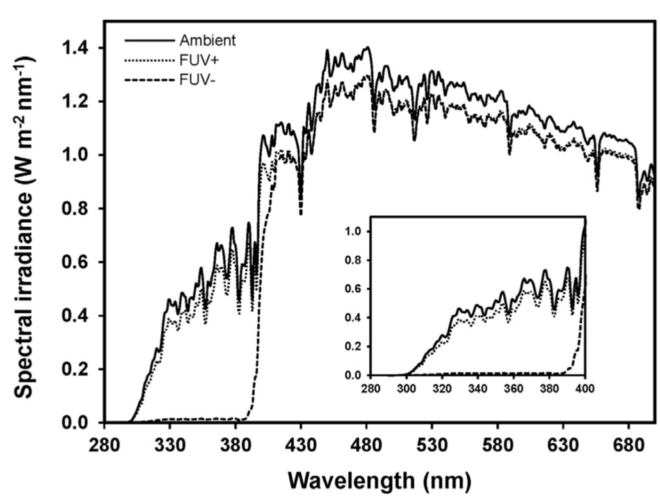

Fig. 1. Spectral irradiances measured around noon on a typical summer sunny day in each of the three experimental conditions used: Ambient, no filter (solid line); FUV+, UV-transmitting filter (dotted line); FUV-, UV-blocking filter (dashed line).