Plant Physiology and Biochemistry 230 (2026) 110863

Contents lists available at ScienceDirect

Plant Physiology and Biochemistry

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

Different responses to steady and fluctuating UV-B radiation treatments between two grapevine cultivars, and the underlying photoreceptor mechanisms involved in *Arabidopsis*

Chenxing Su-Zhou [a,b], Maxime Durand [b], Javier Martinez-Abaigar [c], Alexey Shapiguzov [b,d], Saijaliisa Kangasjarvi [b], Xu Liu [a,f,*], T. Matthew Robson [b,e,**]

[a] College of Enology, Northwest A&F University, Yangling, 712100, Shaanxi, China
[b] Organismal and Evolutionary Biology (OEB), Viikki Plant Science Centre (ViPS), Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, 00014, Finland
[c] Faculty of Science and Technology, University of La Rioja, Madre de Dios 53, La Rioja, 26006, Logroño, Spain
[d] Natural Resources Institute Finland (Luke), Production Systems, Toivonlinnantie 518, FI-21500, Piikkiö, Finland
[e] National School of Forestry, University of Cumbria, Rydal Road, Ambleside, LA22 9BB, UK
[f] Shaanxi Engineering Research Center for Viti-Viniculture, Yangling, 712100, Shaanxi, China

ARTICLE INFO

Keywords:
Ultraviolet radiation
Photoreceptor
Flavonol
Photosystem II
Starch
Acclimation
Grapevine

ABSTRACT

Ultraviolet–B radiation (UV-B) is the most-energetic region of the solar spectrum received by plants and its absorption by leaves requires specialised adaptations. Natural light is essentially dynamic, yet the effects of fluctuating UV-B radiation on plant ecophysiology remain poorly understood. We investigated how two grapevine (*Vitis vinifera*) cultivars, Tempranillo (red) and Viura (white), respond to fluctuating and steady UV-B treatments in a controlled environment, and explored the underlying processes mediating acclimation using photoreceptor mutants of *Arabidopsis thaliana*. Plants were grown in a greenhouse under the same daily dose of fluctuating or steady UV-B radiation, paired with their respective attenuated UV-B controls. Leaf chlorophyll epidermal flavonols and photosynthetic capacity were monitored in both cultivars as well as photoassimilates in *Arabidopsis*. Acclimation was cultivar-specific: whereby flavonol accumulation in response to UV-B was greater in Viura (a 28 % increase), although in Tempranillo within-treatment flavonol accumulation was associated with less inhibition of operating efficiency of photosystem II (ϕ_{PSII}). In *Arabidopsis*, responses to both fluctuating and steady UV-B regimes were primarily mediated by the photoreceptor UV RESISTANCE LOCUS 8, with cryptochromes also contributing to flavonol regulation and playing a greater role in photoassimilate accumulation under steady UV-B. Knowledge of these processes across cultivars and conditions can assist in grapevine selection, to guide photoreceptor-centric approaches on the basis of differences in UV-B-radiation acclimation capacity, and to support vineyard management under naturally variable UV-B conditions. These aspects are increasingly important under current global climate change scenarios for such a widespread crop as grapevine.

1. Introduction

Fluctuating light is ubiquitous over crops and forest canopies in natural environments (Durand and Robson, 2023), hence, plants must be adapted to use and respond to natural fluctuations in irradiance. Despite this, most experiments are done under steady irradiance conditions. Those studies that consider the effects of fluctuating photosynthetically active radiation (PAR, 400–700 nm), typically suggest that it is less efficiently used than steady PAR, because both the frequency and duration of fluctuations impact photosynthetic capacity (Durand et al., 2024; Vialet-Chabrand et al., 2017). Of those spectral regions that fluctuate during the day, solar UV-B radiation (290–315

* Corresponding author. College of Enology, Northwest A&F University, Yangling 712100, Shaanxi, China.
** Corresponding author. Organismal and Evolutionary Biology (OEB), Viikki Plant Science Centre (ViPS), Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, 00014, Finland.
E-mail addresses: szxx@nwafu.edu.cn (C. Su-Zhou), maxime.durand@helsinki.fi (M. Durand), javier.martinez@unirioja.es (J. Martinez-Abaigar), alexey.shapiguzov@luke.fi (A. Shapiguzov), saijaliisa.kangasjarvi@helsinki.fi (S. Kangasjarvi), liuxu@nwafu.edu.cn (X. Liu), matthew.robson@helsinki.fi (T.M. Robson).

https://doi.org/10.1016/j.plaphy.2025.110863
Received 15 September 2025; Received in revised form 25 November 2025; Accepted 2 December 2025
Available online 5 December 2025

nm) holds the highest energy photons reaching the biosphere. However, the effects of fluctuating UV-B radiation on plant ecophysiology are not routinely considered. This gap is critical under climate change, as factors like cloud cover and aerosols overwhelmingly influence surface UV irradiance (Barnes et al., 2023) and projections of increased UV radiation compared with pre-depletion levels in tropical and mid-latitude regions through 2100 (Bernhard et al., 2023; Lamy et al., 2019). Moreover, even a slight change in the amount of incident UV-B radiation at low irradiances can lead to the modulation of gene expression, metabolite accumulation and physiological adjustments (Heijde and Ulm, 2012; Robson et al., 2015). Because of this capacity to perceive and respond to UV-B radiation, examining the effects of fluctuating UV-B on acclimation processes may give us insight into how plants adjust their metabolism and performance to a changing environment.

Grapevine (*Vitis vinifera* L.) is a light-demanding dicot plant, which is an important berry crop around the world. Our previous study on the most common grapevine cultivar, Cabernet Sauvignon, revealed that while grapevines effectively acclimate to both steady and fluctuating UV-B radiation, their photosynthetic acclimation response to fluctuating UV-B radiation is weaker compared to steady UV-B (Su-Zhou et al., 2024). Still, this research did not examine the effects of fluctuating UV-B exposure over a longer period that would better reflect natural conditions. Longer studies are absent from the broader literature (Su-Zhou et al., 2024), although we know that young grapevine leaves are typically more UV-B-sensitive than older leaves. For example, a treatment of 8.04 kJ m^{-2} d^{-1} biologically weighted UV-B radiation reduced the photochemical yield and increased photoprotective pigment accumulation more strongly in 1-to-3-week-old leaves compared to 4-to-6-week-old leaves (Majer and Hideg, 2012). A better understanding of how grapevine leaves acclimate to fluctuating UV-B radiation over their lifespan is needed to reconcile the outcomes of previous studies, and consider the long-term effects of UV-B radiation. Besides, since the effects of UV-B radiation on photosynthesis and metabolites are highly dependent on the cultivar studied (Nunez-Olivera et al., 2006; Matus et al., 2017), we would expect to find cultivar-specific acclimation to fluctuating UV-B radiation, which may guide the strategies for the selection of cultivars better adapted to increasingly variable conditions under climate change.

Specific photoreceptors in plants have been identified to respond to specific regions of sunlight from UV-B to far-red (Galvão and Fankhauser, 2015). The main photoreceptors are UV RESISTANCE LOCUS 8 (UVR8, for UV-B/UV-A regions); cryptochromes (CRYs, blue/UV-A); phototropins (PHOTs, blue/UV-A); and phytochromes (PHYs, red/far-red) (Banerjee and Batschauer, 2005; Briggs and Huala, 1999; Rizzini et al., 2011; Quail, 2002). The absorption spectra of several of these photoreceptors overlap, allowing them to create a coordinated response when plants are exposed to the complex natural light environment (Paik and Huq, 2019). For example, three principal classes of photoreceptor are involved in responses to UV radiation (UVR8, CRYs and PHOTs). UVR8 mediates the photoprotection response, PHOTs regulate light capture, the movement of chloroplasts and stomata, while CRYs regulate plant growth and photomorphogenesis (Guo et al., 1998; Mao et al., 2005; Podolec et al., 2021; Xin et al., 2022). Yet, the extent is still unclear to which these photoreceptors are involved in the differential response of photosynthesis and photoprotection to UV-B photons supplied as fluctuating *vs* steady radiation. Likewise, how much each photoreceptor may contribute to the overall response is still unknown. Given the high functional conservation of photoreceptor pathways between *Arabidopsis* and grapevine (Carbonell-Bejerano et al., 2014; Liu et al., 2024), studying this model system could provide a foundation for future functional studies in grapevine. Additionally, multiple signalling networks contribute to photosynthetic regulation, including reactive oxygen species (ROS) signalling, thiol–redox signalling, 3′-phosphoadenosine 5′-phosphate (PAP), methylerythritol cyclodiphosphate (MEcPP), and tetrapyrroles, phosphorylation cascades such as mitogen-activated protein kinases (MAPK; Baier and Dietz, 2005; Chan et al., 2016; Hernández-Verdeja and Strand, 2018). Among these, sugar signalling plays an important role in feedback loops that respond to environmental factors such as light (Henry et al., 2020; Lastdrager et al., 2014). However, the role of photoreceptors in regulating photoassimilate pools under fluctuating UV-B radiation remains unexplored.

In our previous study only a single cultivar, Cabernet Sauvignon, was chosen and the focus was on acclimation to UV-B radiation after leaf maturation. In contrast, here we investigated how two distinct grapevine cultivars of Mediterranean origin, Tempranillo (a red grape) and Viura (a white grape, also known as Macabeo), acclimate to fluctuating and steady UV-B radiation over their lifespan. These cultivars are cultivated across 219,379 ha and 38,625 ha of vineyards, respectively, which represents 4.9 % (third place) and 0.9 % (20th place) of the total grapevine area globally (Anderson and Nelgen, 2020). To associate analogous responses to fluctuating UV-B radiation in grapevine and *Arabidopsis thaliana* to specific photoreceptors, we also compared photoreceptor-knockout mutants of *Arabidopsis* under the same experimental conditions. Plants were grown under UV-B radiation treatments applied as either fluctuating or steady radiation with equivalent daily UV-B doses and their UV-B attenuated controls, and the consequences for pigment accumulation, photosynthesis and photoassimilates were assessed. The aim of this study is to investigate: (1) whether the differential responses to fluctuating and steady UV-B radiation vary among the selected grapevine cultivars; (2) are photoreceptors involved in the differential response of photoprotection, photosynthesis and photoassimilate to UV-B photons supplied as fluctuating *vs* steady radiation; (3) what are the conserved photoreceptor-mediated mechanisms underlying plant differential response to fluctuating and steady UV-B radiation, as revealed by comparing the responses of grapevine with those of photoreceptor-knockout mutants in *Arabidopsis*?

2. Materials and methods

2.1. Plant material and light treatments

One-year-old grapevine cuttings (*Vitis vinifera* L. cvs Tempranillo and Viura) grafted to 110R rootstocks (Viveros Provedo, Logrono, Spain) were planted in a 7:2:2 mix of peat:sand:vermiculite in 10 L pots. The specific soil mixture used consisted of F6 peat (Kekkilä, Helsinki, Finland), blowing sand 0.5–1.2 mm (Weber, Helsinki, Finland), and Agra-vermiculite 0–2 mm (Pull Rhenen, TX Rhenen, Netherlands). The grapevines were grown in a greenhouse compartment from 06/10/2022 to 13/12/2022.

The following genotypes of *Arabidopsis thaliana* in a background of Landsberg *erecta* (*Ler*) were used in this study*: phot1, uvr8, cry1cry2, uvr8cry1cry2* and the wild type (WT). Their seeds, produced simultaneously under standard conditions, were stratified in water during 24 h at 4 °C in darkness. After that, seeds were sown in a soil mixture: 1:1 mix of B2 peat (Kekkilä, Helsinki, Finland) and Agra-vermiculite 0–2 mm (Pull Rhenen, TX Rhenen, Netherlands). The growth conditions were 12h/12h light/dark photoperiod under photosynthetically active radiation (PAR; 220 μmol m^{-2} s^{-1}), 23 °C/19 °C day/night and constant relative humidity at 60 %. When the first pair of leaves was visible, the seedlings were transplanted to one plant per 6 × 6 cm plots and continued growing under the same conditions.

Twenty days after transplanting, *Arabidopsis* plants were transferred to the same greenhouse and grown from 02/01/2023 to 09/01/2023. The design and implementation of the UV-B treatments and experimental conditions were as described previously in Su-Zhou et al. (2024). Briefly, four UV-B treatments were administered ± 3 h from midday (09:00 to 15:00) local time: (1: FUV) fluctuating UV-B radiation treatment (1.96 ± 0.05 μmol photons m^{-2} s^{-1} equivalent of 0.76 ± 0.02 W m^{-2} s^{-1}) followed an on/off 15 min/15 min cycle repeated during each daily 6 h period of UV-B irradiation, and (2: cFUV) its no UV-B radiation control treatment; (3: SUV) steady UV-B radiation treatment (0.98 ± 0.06 μmol photons m^{-2} s^{-1} equivalent of 0.38 ± 0.02 W m^{-2} s^{-1}), and

(4: cSUV) its no UV-B radiation control treatment. The 15 min on/off cycle falls within the documented range of natural sun/shade patterns and is ecologically relevant (Smith and Berry, 2013). The total unweighted daily UV-B treatments under FUV and SUV were respectively 21.17 ± 0.54 and 21.17 ± 1.30 mmol m^{-2} day^{-1} photon irradiance. This is equivalent to biologically effective doses of UV-B radiation of 4.10 ± 0.11 and 4.10 ± 0.22 kJ m^{-2} day^{-1} weighted according to Caldwell's Generalized Plant Action Spectrum normalized at 300 nm as formulated by Green et al. (1974).

Three plants were grown under each of four light treatments in two replicate compartments (i.e., 3 plants × 4 treatments × 2 replicate blocks, giving a total of 24 plants for each grapevine cultivar and likewise for each *Arabidopsis* genotype). The spectral irradiance was recorded (Fig. S1 and Table S1) with a calibrated array spectroradiometer (Maya, 2000 Pro, Ocean Optics Inc., Dunedin, FL) using a protocol devised for this purpose and detailed in Robson and Aphalo (2019). The greenhouse air temperature was maintained at 25 °C/16 °C day/night and relative humidity at 45 %/75 % day/night.

Plants were grown under LED lamps (AP67 and AP3, GreenLux Oy, Helsinki, Finland; https://www.valoya.com/) giving steady PAR (270 μmol m^{-2} s^{-1}) from 05:00 to 21:00 for grapevines and from 06:00 to 18:00 for *Arabidopsis* (local time). The photoperiods of 16 h for grapevine and 12 h for *Arabidopsis* were selected based on their respective photoperiodic requirements (Rai et al., 2020; Wang et al., 2014).

2.2. Measurements of photosynthetic parameters

The operating efficiency of photosystem II (ϕ_{PSII}) was measured by mini-PAM (Walz GmbH, Effeltrich, Germany) under the light treatments at which the plants were grown, and repeated three times at 08:30 (morning), 12:00 (midday) and 15:30 (afternoon) on each measurement day. For grapevine, the measurements were performed on a mature healthy leaf of each plant (on the fourth to sixth leaf from the base to the apex) five times over 25 days, at five-day intervals, when the eighth distal leaf (counting from the base to the apex) of every plant from each grapevine cultivar was mature. This happened on November 3rd for Tempranillo and on November 23rd for Viura (21 and 51 days, respectively, after the UV-B treatments commenced). For *Arabidopsis*, the measurements were performed on a mature healthy leaf from each plant on the 1st (i.e., the day after transferring plants to the greenhouse), 4th, and 7th day after the UV-B radiation treatment commenced.

The same leaf of grapevine as for ϕ_{PSII} measurement was used to measure maximum quantum yield of PSII (F_v/F_m), net photosynthetic rate (P_n) and stomatal conductance (g_s). F_v/F_m was measured by mini-PAM after 30 min of dark adaption before the daily UV-B radiation began on every measurement day. The P_n and g_s were measured by a total photosynthesis system LI6400XT infra-red gas analyser (LI-COR Biosciences, Lincoln, NE, USA) with a transparent top window made of cellulose diacetate film to measure under each light treatment. The settings for LI6400XT were as follows: flow at 500 μmol s^{-1}, block temperature at 22 °C, leaf fan on fast, and reference CO_2 at 400 μmol mol^{-1}. The measurement of P_n and g_s for both grapevine cultivars was carried out between 09:30 to 11:00 a.m. on the fifth measurement day.

2.3. Measurements of leaf pigments

Optical indices of epidermal flavonols and chlorophyll content were measured by Dualex Scientific + (FORCE-A, Paris, France; Cerovic et al., 2012) on the same leaf used to obtain ϕ_{PSII}.Measurements were repeated three times at 08:30 (morning), 12:00 (midday) and 15:30 (afternoon) on each measurement day for both grapevines and *Arabidopsis*.

2.4. Analysis of photoassimilates

Glucose, fructose, sucrose, and starch were analyzed from *Arabidopsis* leaves harvested after the measurements of ϕ_{PSII} and pigments on the third measurement day (at 15:30 the end of the daily UV-B treatment period). The same leaf chosen for ϕ_{PSII} measurements was harvested, frozen immediately in liquid nitrogen and then freeze-dried. Sugars and starch were extracted and measured as described in Stitt et al. (1989). The supernatants of ethanolic extracts were used to analyze glucose, fructose and sucrose using a Megazyme Sucrose, D-Fructose and D-Glucose kit (Megazyme, County Wicklow, Ireland). The insoluble pellets were used to analyze starch (Stitt et al., 1989). Soluble sugars (glucose, fructose and sucrose) were quantified and expressed on a dry weight basis (μmol g^{-1} DW). Starch content was converted to glucose equivalents and expressed μmol glucose equivalents per gram dry weight [μmol (Glu) g^{-1} DW].

2.5. Data analysis

Statistical analyses were conducted in R version 4.1.3 (R Core Team, 2022). Linear mixed-effects models were used with the packages *lme4* (Bates et al., 2015) and *lmerTest* (Kuznetsova et al., 2017). The two replicate compartments were considered as a random-effect factor. A Type II ANOVA was used to investigate the specific effects on measured parameters of treatments, *Arabidopsis* genotype or grapevine cultivar, the time course (as measurement day), and their interactions. For pigments and ϕ_{PSII}, the effects of time of day and its interactions with other factors were also investigated. The residuals of all linear mixed-effects models were visually inspected for normality using Q-Q plots (Fig. S2). Since the untransformed flavonol data in both grapevine and *Arabidopsis* did not meet the normality criteria, a square-root transformation was applied which improved the fit to normality. We were interested in the difference between steady and fluctuating UV-B treatments, and between UV-B treatments and controls, thus the adjusted *P*-values (adj. *P*) were calculated for the following contrasts: FUV-SUV, FUV-cFUV, SUV-cSUV, and cFUV-cSUV.

Relationships between metabolite contents and photosynthetic parameters were examined using linear regression models. In grapevine leaves, the daily averages of flavonol and chlorophyll content, F_v/F_m and ϕ_{PSII} of each replicate block were used for linear regression analysis. Analysis of photoassimilates of *Arabidopsis* was performed in the leaves sampled at the end of the daily UV-B treatment on the final measurement day. This was compared against the last records of ϕ_{PSII} taken on the same day, and the average of each replicate block was calculated. Differences were considered statistically significant when $P < 0.05$. Hierarchical clustering analysis was conducted in *Arabidopsis* to investigate the regulation of flavonol and chlorophyll accumulation and ϕ_{PSII} mediated by photoreceptors, using the response ratios comparing UV-B treatments to their respective controls.

3. Results

3.1. Comparative response of leaf pigments and photosynthesis to fluctuating and steady UV-B radiation in Tempranillo and Viura grapevines

Flavonol accumulation in grapevine leaves was affected by UV-B treatment ($F = 432.8$, $P < 0.001$) and cultivar ($F = 42.90$, $P < 0.001$), and their interactive effect was significant ($F = 4.24$, $P = 0.006$), but without significant diurnal changes ($F = 1.42$, $P = 0.241$; Table S2A). Considering the effect of fluctuating *vs* steady conditions and their interaction with other factors, there was significantly higher flavonol accumulation under SUV than FUV, especially in Viura (Fig. 1). Under SUV, the relative effect of UV treatment *vs* its control in Tempranillo was 115.7 % higher (adj. $P < 0.001$) and in Viura 158.8 % higher (adj. $P < 0.001$), whereas under FUV the increase due to UV-B radiation was 121.9 % (adj. $P < 0.001$) more in Tempranillo and 92.98 % more (adj. $P < 0.001$) in Viura (Table S2B).

Likewise, leaf chlorophyll content differed with cultivar ($F = 15.07$, $P < 0.001$) and treatment ($F = 7.16$, $P < 0.001$), and their interactive

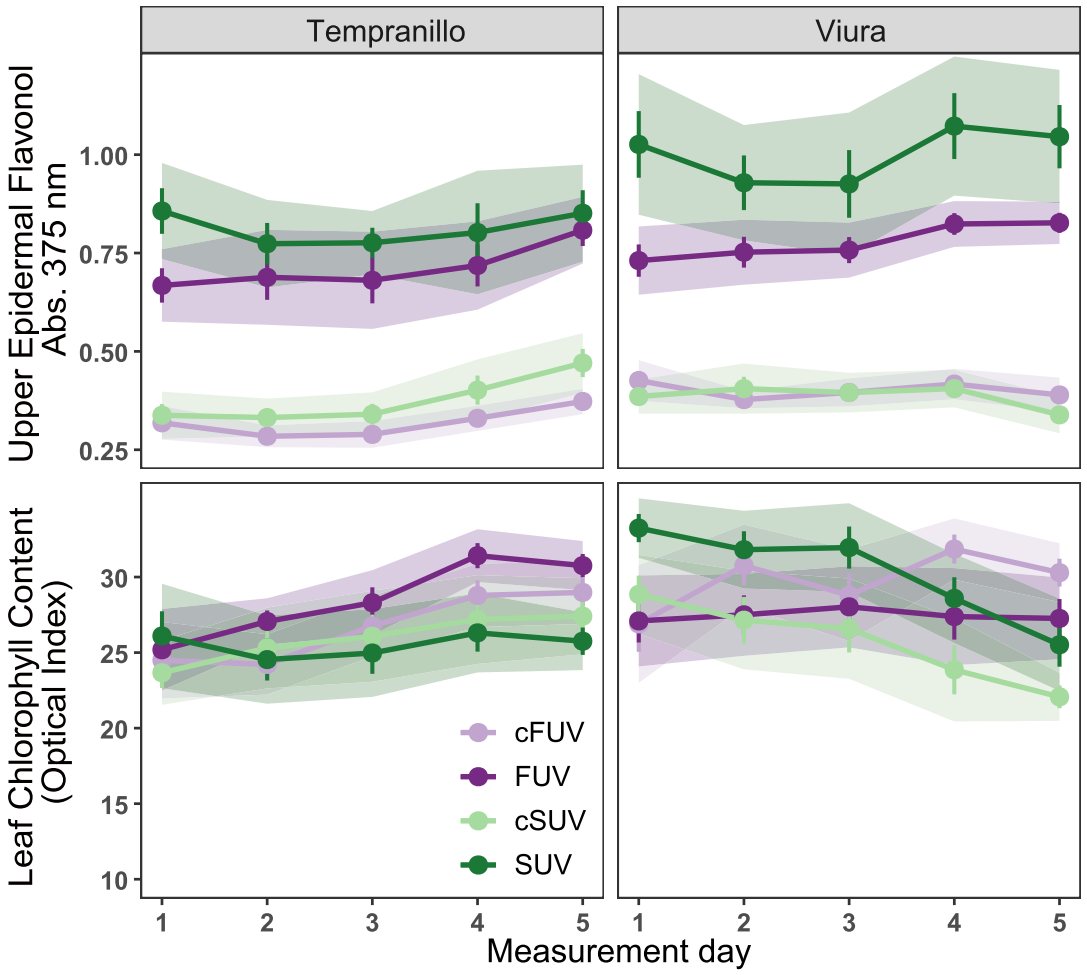

Fig. 1. Epidermal flavonol and chlorophyll contents on a per leaf area basis in grapevine leaves grown under fluctuating and steady UV-B treatments and controls. The *y*-axis scales are optical indices from Dualex Scientific + (arbitrary units). Measurements were taken under fluctuating UV-B radiation (FUV, dark purple) and its attenuated UV-B controls (cFUV, light purple), steady UV-B radiation (SUV, dark green) and its attenuated UV-B controls (cSUV, light green). Data are the daily mean ± SE across replicate blocks ($n = 18$ per panel). Shaded ribbons indicate the 95 % confidence intervals around the fitted line. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

effect was also significant (F = 11.05, $P < 0.001$; Table S3A). In Tempranillo, FUV drove an increase in chlorophyll content, but SUV had no significant effect, as respectively compared to cFUV (adj. $P = 0.027$) and cSUV (adj. $P = 0.662$; Fig. 1). On the other hand, in Viura, the chlorophyll content in FUV was 7.8 % lower than in cFUV (adj. $P = 0.011$), but in SUV chlorophyll content was 17.9 % higher than in cSUV (adj. $P < 0.001$), respectively (Table S3B). Overall, the effects of fluctuating and steady UV on epidermal flavonol content were similar for both cultivars, but the effects on chlorophyll were genotype specific.

There was a very small overall effect of UV-B radiation on the two indicators of PSII function (Fig. 2; Tables S4 and S5A). Especially for F_v/F_m, there was no significant effect of the treatment (F = 0.740, $P = 0.529$; Table S4). And for ϕ_{PSII}, results differed between the two cultivars: in Tempranillo, no significant overall reduction in ϕ_{PSII} was present in the UV-B treatment compared with the controls in both treatments SUV (adj. $P = 0.721$) and FUV (adj. $P = 0.837$); whereas in Viura, SUV and FUV caused near-significant lower ϕ_{PSII} compared to their respective controls; cSUV (adj. $P = 0.053$) and cFUV (adj. $P = 0.053$; Table S5B). To be more specific, in Viura, there was a small decline in ϕ_{PSII} from the second measurement day in both SUV and FUV compared to their controls, meaning that by the fifth day, ϕ_{PSII} was lower in SUV than their controls by 4.53 % (0.76 ± 0.01 *vs* 0.80 ± 0.01) and in FUV by 5.8 % (0.76 ± 0.01 *vs* 0.80 ± 0.01; Fig. 2). In Tempranillo, chlorophyll content was positively correlated with F_v/F_m under FUV and cFUV (Fig. S3a). There were also positive correlations between chlorophyll content and ϕ_{PSII} under FUV, cFUV, and cSUV, but not under SUV (Fig. S3b). In Tempranillo, significant positive correlations between flavonol content and ϕ_{PSII} were found only under the two control treatments, and flavonol content was not related to F_v/F_m (Fig. S3c and d). In contrast, neither chlorophyll nor flavonol content were related to F_v/F_m or ϕ_{PSII} in Viura (Fig. S3).

For photosynthetic rate (P_n), recorded on the last measurement day for each cultivar, there were no significant effects of UV-B treatment (F = 2.39, $P = 0.071$), cultivar (F = 3.79, $P = 0.053$) and their interaction (F = 1.79, $P = 0.150$; Fig. 3a and Table S6A). On the contrary, UV-B treatment (F = 16.05, $P < 0.001$) and cultivar (F = 47.80, $P < 0.001$) both significantly affected stomatal conductance (g_s), and there was a strong interactive effect on g_s between UV-B treatment and cultivar (F = 7.14, $P < 0.001$; Fig. 3b; Table S6A). In Viura, g_s was 142 % higher under SUV (adj. $P < 0.001$) and 105 % higher under FUV (adj. $P < 0.001$) compared to their respective controls (Fig. 3b; Table S6B). In addition, g_s was higher under steady than under fluctuating UV-B radiation in Viura. However, no such differences were found in Tempranillo (Table S6B). Overall, the results indicated that exposure to UV-B enhanced stomatal conductance, but suppressed ϕ_{PSII}, and that the effect was genotype-specific, i.e., there were g_s differences in Viura, but not in Tempranillo.

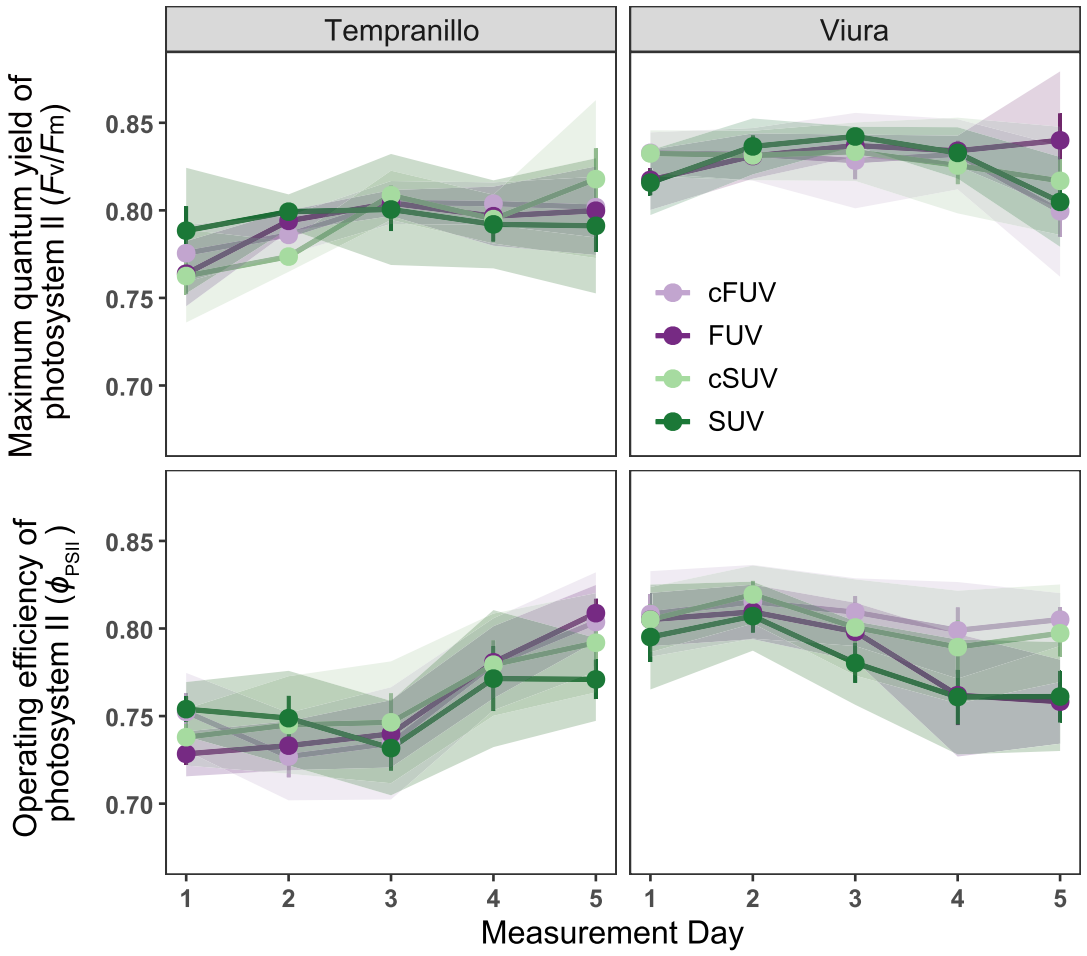

Fig. 2. Maximum quantum yield of photosystem II (F_v/F_m) and operating efficiency of photosystem II (ϕ_{PSII}) in grapevine leaves grown under fluctuating and steady UV-B treatments and controls. Treatments are fluctuating UV-B radiation (FUV, dark purple) and its attenuated UV-B controls (cFUV, light purple), steady UV-B radiation (SUV, dark green) and its attenuated UV-B controls (cSUV, light green). Data are the mean ± SE across replicate blocks ($n = 6$ for F_v/F_m, $n = 18$ for ϕ_{PSII} per panel recorded 3 times per day). Shaded ribbons indicate the 95 % confidence intervals around the fitted line. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

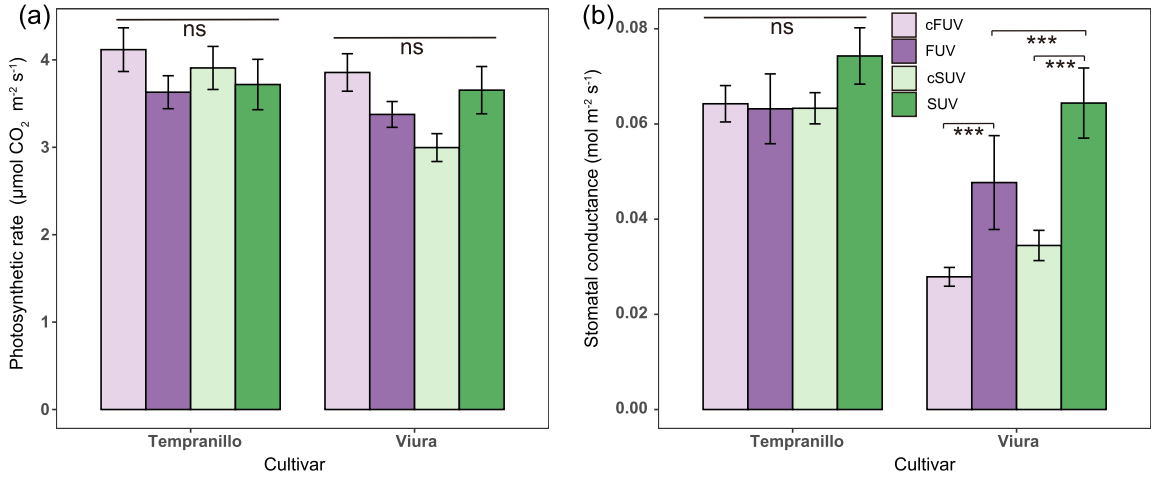

Fig. 3. Gas exchange of grapevine leaves grown under fluctuating and steady UV-B radiation; (a) photosynthetic rate; (b) stomatal conductance. Treatments are fluctuating UV-B radiation (FUV, dark purple) and its attenuated UV-B controls (cFUV, light purple), steady UV-B radiation (SUV, dark green) and its attenuated UV-B controls (cSUV, light green). Data are the mean ± SE across replicate blocks ($n = 6$ per panel). Significant difference for adjusted *P*-values (adj. *P*) *< 0.05, **< 0.01, ***< 0.001 and "ns" indicates non-significant. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2. Photoreceptor-mediated differences in response of leaf pigments and photosynthesis to fluctuating and steady UV-B radiation

Arabidopsis genotypes differed in their epidermal flavonol accumulation ($F = 46.08$, $P < 0.001$; Fig. 4; Table S7A). Under control treatments cFUV and cSUV, flavonol accumulation was lower in *cry1cry2* and *uvr8cry1cry2* than in WT (cFUV: adj. $P < 0.001$, adj. $P < 0.001$; cSUV: adj. $P < 0.001$, adj. $P < 0.001$) and *uvr8* (cFUV: adj. $P < 0.001$, adj. $P < 0.001$; cSUV: adj. $P < 0.001$, adj. $P < 0.001$), and there was no significant difference between WT and *uvr8* (cFUV: adj. $P = 0.868$, cSUV: adj. $P = 0.341$; Table S7B). Considering the effect of UV-B treatment ($F = 8.55$, $P < 0.001$), mean flavonol accumulation was respectively higher by 91 %, 112 % and 119 % in SUV compared to cSUV in WT, *phot1* and *cry1cry2* (Table S7C). The flavonol content was also significantly higher under FUV than cFUV in the same genotypes, it was increased by 57 % and 61 % in WT and *phot1*, and by 91 % in *cry1cry2*. Moreover, epidermal flavonol content was always higher under SUV than FUV in those genotypes. Otherwise, SUV or FUV induced differences in *uvr8* and *uvr8cry1cry2* were less marked relative to their respective no UV-B controls.

The genotypes also differed in their chlorophyll content ($F = 198.4$, $P < 0.001$) and the interactive effect of UV-B treatment and genotype was also significant ($F = 3.06$, $P < 0.001$; Fig. 4; Table S8A). Chlorophyll content increased in FUV and SUV for WT and *cry1cry2* compared to their respective controls. In contrast, the chlorophyll content was 11.9 % lower under SUV compared to cSUV on average in *uvr8* (adj. $P < 0.001$), but there was no significant difference between FUV and cFUV (adj. $P = 0.404$; Table S8B). The chlorophyll content decreased strongly under both FUV and SUV in *uvr8cry1cry2* as compared to their respective controls (cFUV: adj. $P < 0.001$; cSUV: adj. $P < 0.001$).

The genotype ($F = 44.17$, $P < 0.001$), treatment ($F = 5.59$, $P = 0.001$) and their interaction ($F = 5.01$, $P < 0.001$) had significant effects on the ϕ_{PSII} (Fig. 5 and Table S9A). Although the FUV and SUV had no significant effect on ϕ_{PSII} in WT (adj. $P = 0.661$ and adj. $P = 0.750$), *phot1* (adj. $P = 0.750$ and adj. $P = 0.055$) and *cry1cry2* (adj. $P = 0.750$ and $P = 0.750$) compared to their respective controls, for *uvr8*, ϕ_{PSII} was lower by 5.7 % in SUV compared to cSUV (adj. $P = 0.001$; Table S9B). Likewise, compared to each of the control treatments, the FUV and SUV negatively affected ϕ_{PSII} in *uvr8cry1cry2* (adj. $P < 0.001$ and adj. $P < 0.001$).

Generally, the response of flavonol accumulation differed from that of chlorophyll accumulation and ϕ_{PSII} between FUV and SUV among the different photoreceptor mutants. To gain a better understanding of the suite of effects mediated by different photoreceptors, response ratios between UV-B radiation treatments and their respective controls were calculated for flavonol and chlorophyll contents, together with ϕ_{PSII}. These data were then used to create a hierarchical clustering analysis. There were three main clusters of the results for epidermal flavonol response ratios (Fig. 6a). The response ratios of epidermal flavonols in WT and *phot1* under SUV were higher than FUV indicating strong UV-B effects under SUV (two clusters). In *cry1cry2*, the response ratios under FUV and SUV were similarly strong, and could be grouped in the same cluster as WT and *phot1* under SUV. In the third cluster, there were no increases in flavonol accumulation caused by FUV or SUV in the mutants lacking UVR8 (*uvr8* and *uvr8cry1cry2*).

Likewise, there were three main clusters of results of the chlorophyll response ratio to UV treatments (Fig. 6b). Chlorophyll content was not significantly decreased by FUV or SUV in WT, *phot1* and *cry1cry2*, nor by FUV in *uvr8*; these response ratios were in a cluster together. However, the response ratio of chlorophyll was lower in *uvr8* under SUV, forming a distinct cluster. This effect was more pronounced in *uvr8cry1cry2*, where

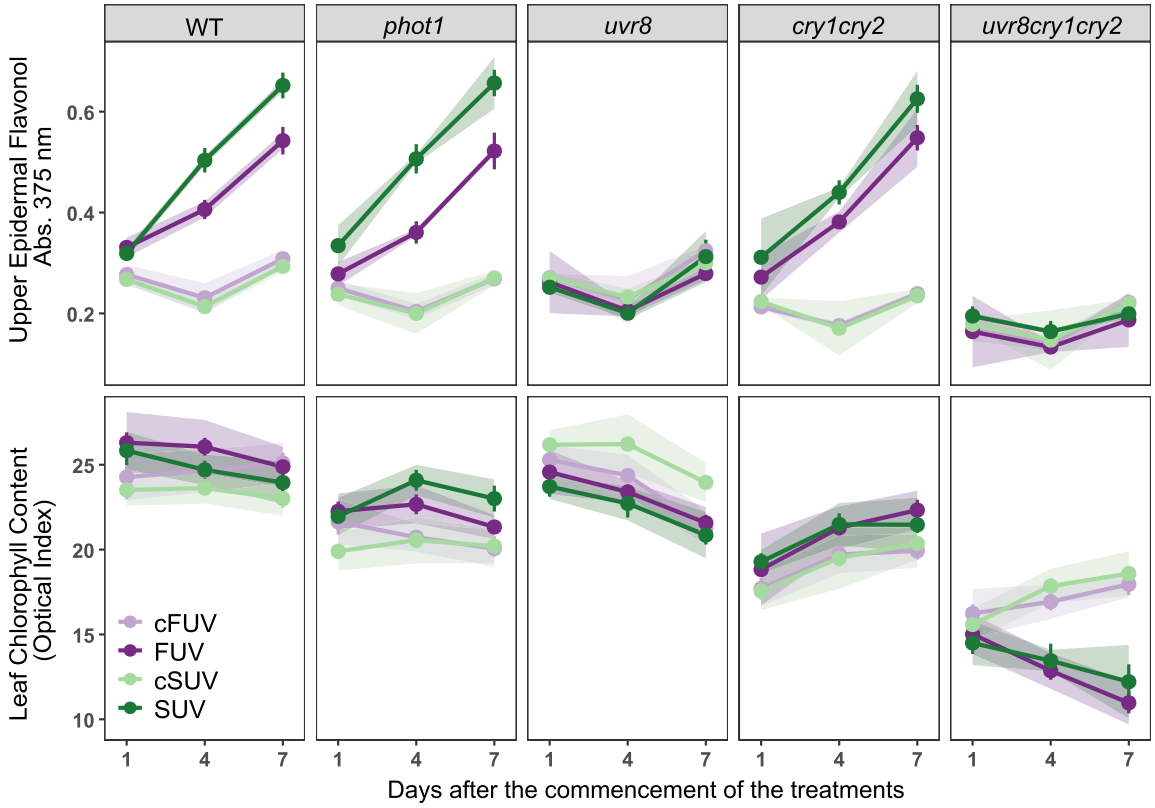

Fig. 4. Epidermal flavonol and chlorophyll contents on a per leaf area basis in *Arabidopsis* leaves grown under fluctuating and steady UV-B radiation. The *y*-axis scales are optical indices from Dualex Scientific + (arbitrary units). Measurements were taken under fluctuating UV-B radiation (FUV, dark purple) and its attenuated UV-B controls (cFUV, light purple), steady UV-B radiation (SUV, dark green) and its attenuated UV-B controls (cSUV, light green). Data are the daily mean ± SE across replicate blocks ($n = 18$ per panel). Shaded ribbons indicate the 95 % confidence intervals around the fitted line. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

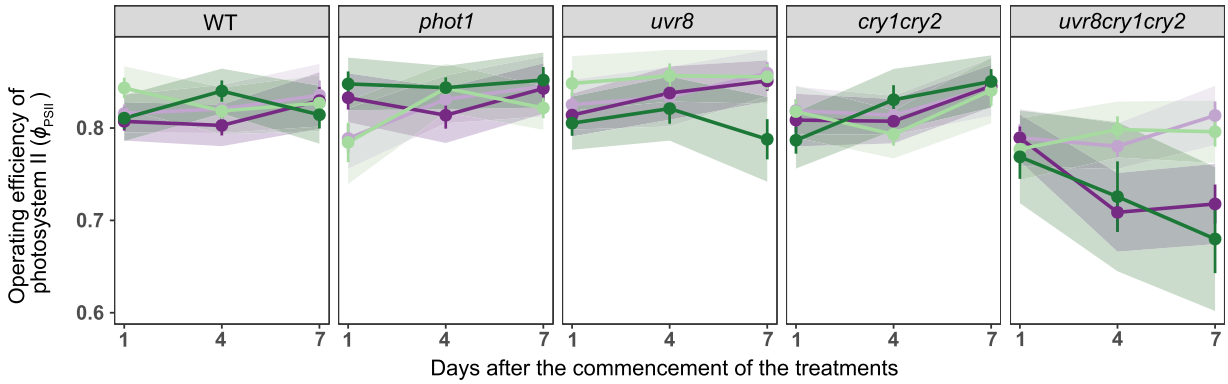

Fig. 5. Operating efficiency of photosystem II (ϕ_{PSII}) of *Arabidopsis* leaves grown under fluctuating and steady UV-B treatments and controls. Treatments are fluctuating UV-B radiation (FUV, dark purple) and its attenuated UV-B controls (cFUV, light purple), steady UV-B radiation (SUV, dark green) and its attenuated UV-B controls (cSUV, light green). Data are the daily mean ± SE across replicate blocks ($n = 18$ per panel). Shaded ribbons indicate the 95 % confidence intervals around the fitted line. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

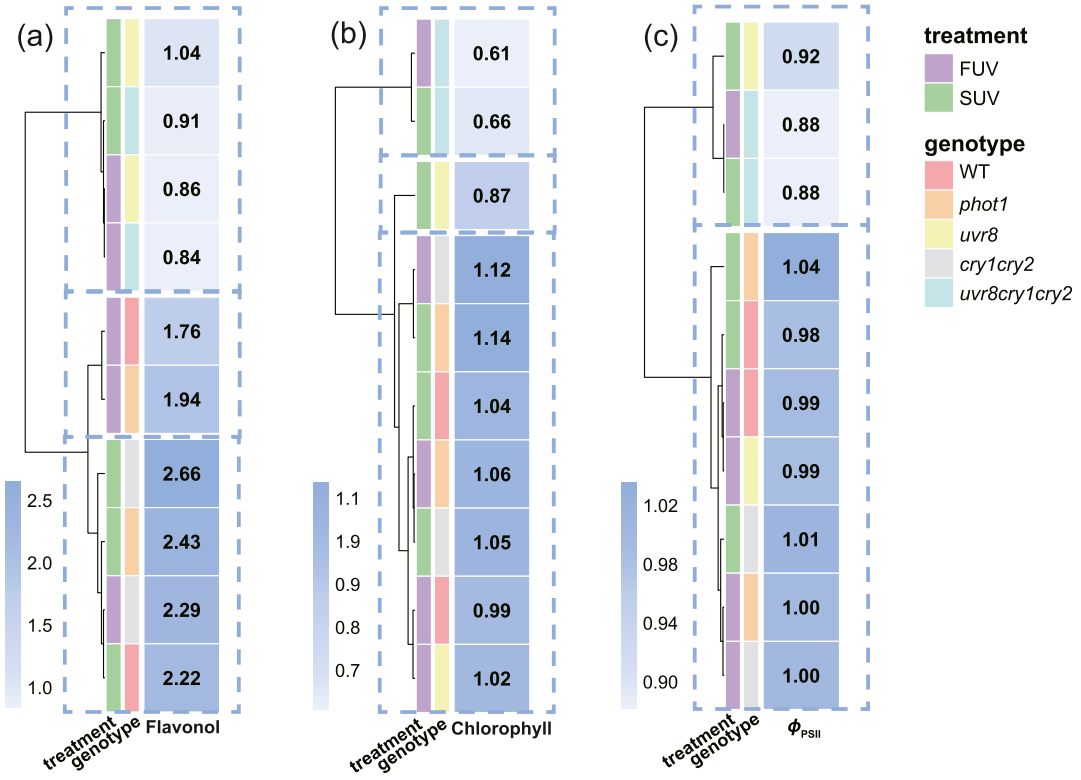

Fig. 6. Hierarchical clustering analysis reveals photoreceptor regulation of (a) flavonol, (b) chlorophyll and (c) photosystem II efficiency (ϕ_{PSII}) in *Arabidopsis*. Clustering was based on the responses to UV-B treatments expressed relative to their respective attenuated UV-B controls.

the ratios were much lower under both FUV and SUV. The results of relative ϕ_{PSII} (Fig. 6c) followed a similar pattern by treatment and genotype to those for chlorophyll content. Among all genotypes, *uvr8-cry1cry2* exhibited the greatest reductions in ϕ_{PSII} under both FUV and SUV. In *uvr8*, relative ϕ_{PSII} was lower under SUV than under FUV, and it was also lower than that of the other genotypes under both UV-B treatments.

3.3. Photoreceptor-mediated response of photoassimilates to fluctuating and steady UV-B radiation

Both the UV-B treatment ($F = 10.76$, $P < 0.001$) and genotype ($F = 6.21$, $P < 0.001$) affected the starch content significantly in *Arabidopsis* plants, and their interactive effect was also significant ($F = 2.69$, $P = 0.004$; Fig. 7a; Table S10A). Although starch content under both SUV and FUV compared to their respective control was not significantly different in WT (adj. $P = 0.919$ and 0.869) nor *phot1* (adj. $P = 0.739$ and 0.657), SUV caused significantly less starch accumulation in *uvr8* (adj. $P = 0.005$) and *cry1cry2* (adj. $P = 0.033$) as compared to cSUV. In SUV and FUV, there was also significantly reduced the starch content in *uvr8-cry1cry2* respectively compared to cSUV (adj. $P = 0.018$) and cFUV (adj. $P < 0.001$; Table S10B). Under control treatments, cFUV and cSUV, starch content was lower in WT compared to *uvr8* (by 20.16 % and 28.08 %), *cry1cry2* (by 18.22 % and 30.08 %) and *uvr8cry1cry2* (by 20.17 % and 21.76 %), while the glucose and fructose contents were higher in WT compared to *cry1cry2* under cFUV (by 14.65 % and 62.36 %) and cSUV (28.85 % and 58.94 %; Fig. 7b and c; Table S11A and B; Table S12A and B). In contrast, glucose decreased significantly in FUV

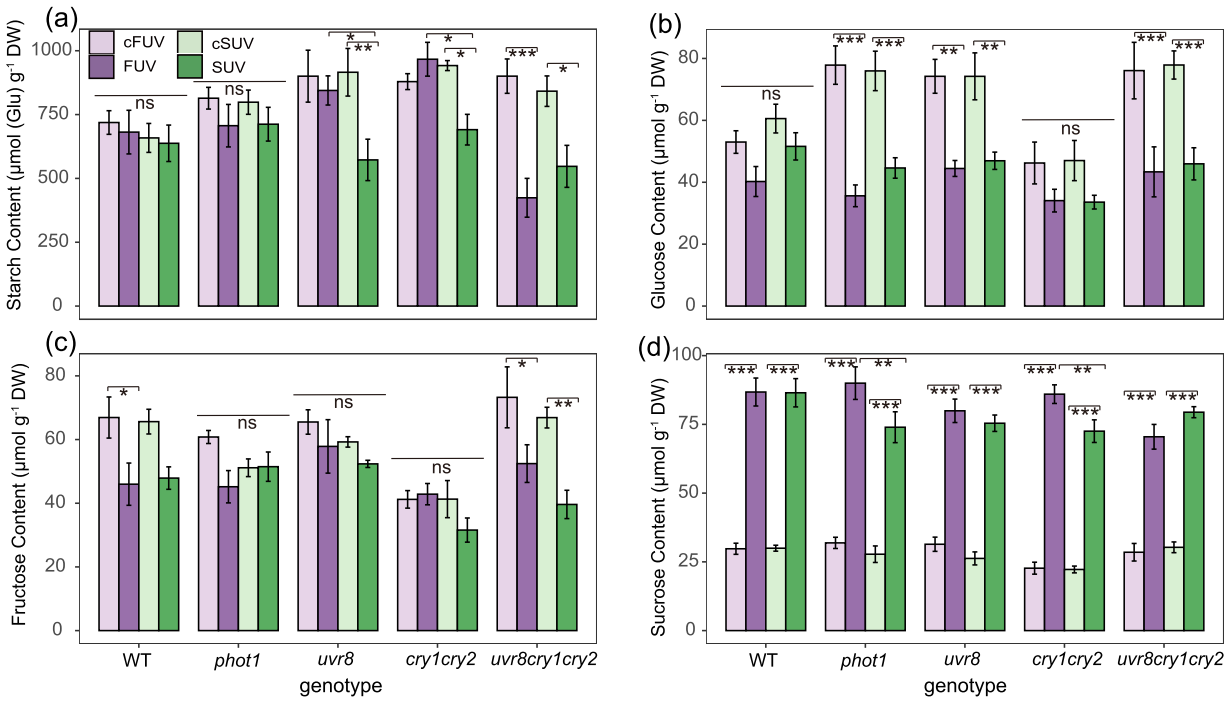

Fig. 7. Photoassimilates contents in *Arabidopsis* leaves grown under fluctuating and steady UV-B treatments and controls. Treatments are fluctuating UV-B radiation (FUV, dark purple) and its attenuated UV-B controls (cFUV, light purple), steady UV-B radiation (SUV, dark green) and its attenuated UV-B controls (cSUV, light green). Leaves were harvested 7 days after UV-B treatments commencement, at the end of the daily UV-B exposure period (15:00). Data are the mean ± SE across replicate blocks ($n = 6$ per panel). Significant difference for adjusted *P*-values (adj. *P*) *< 0.05, **< 0.01, ***< 0.001 and "ns" indicates non-significant. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

and SUV as compared to their respective controls in *phot1* (adj. $P <$ 0.001 and adj. $P < 0.001$), *uvr8* (adj. $P = 0.001$ and adj. $P = 0.002$) and *uvr8cry1cry2* (adj. $P < 0.001$ and adj. $P < 0.001$). Likewise, fructose decreased in WT and *uvr8cry1cry2* under UV-B. On the contrary, increases in sucrose were recorded under UV-B radiation compared to no UV-B control in all genotypes (Fig. 7d). Although there was no significant difference between the sucrose content under FUV and SUV in WT (adj. $P = 0.966$), *uvr8* (adj. $P = 0.466$) and *uvr8cry1cry2* (adj. $P = 0.101$), the increase was smaller in SUV than in FUV for *phot1* (adj. $P = 0.002$) and *cry1cry2* (adj. $P = 0.010$; Table S13A and B).

Concerning the correlation between photosynthesis and photoassimilates, ϕ_{PSII} was positively correlated with starch accumulation in *uvr8* (r = 0.76; $P = 0.030$). Although the relationship was not statistically significant in *uvr8cry1cry2* (r = 0.46; $P = 0.251$), a similarly positive slope was observed (Fig. S4a). Otherwise, there were no significant relationships between ϕ_{PSII} and glucose, fructose, or total sugar content in any of the genotypes of *Arabidopsis* (Figs. S4b,c,d). However, in *uvr8cry1cry2*, there were non-significant positive trends between ϕ_{PSII} and glucose (r = 0.635; $P = 0.091$) and fructose contents (r = 0.670; $P =$ 0.069), and a negative trend between ϕ_{PSII} and sucrose content (r = −0.681; $P = 0.063$).

4. Discussion

4.1. Viura responds to both fluctuating and steady UV-B radiation more strongly than Tempranillo

Flavonol accumulation in the leaf epidermis of both Tempranillo and Viura was increased by our UV-B radiation treatments (Fig. 1). This finding is consistent with previous studies of grapevines under UV-B radiation (Berli et al., 2013; Del-Castillo-Alonso et al., 2016a). Moreover, the response of flavonols to UV-B radiation differed between the two cultivars of grapevine: the increase in flavonol accumulation caused by steady UV-B radiation was greater in Viura than in Tempranillo (Fig. 1). This finding is in agreement with a past comparison of the two cultivars growing outdoors under solar radiation, which found that near-ambient UV-B radiation induced greater flavonol accumulation in Viura than in Tempranillo (Nunez-Olivera et al., 2006).

Notably, we also found that epidermal flavonol content was greater under steady UV-B compared to fluctuating UV-B in both these cultivars. This finding represented a more sensitive response than that found in mature leaves of Cabernet Sauvignon in our previous study, in which no difference in flavonol content between fluctuating and steady UV-B radiation was detected (Su-Zhou et al., 2024). This distinction may be a cultivar-specific response, as our results suggest, but may also be partly explained by the age of the grapevine leaves at the start of the UV-B radiation treatments. Grapevines were grown under UV-B radiation from dormant cuttings throughout bud development and flushing, meaning that grapevine leaves in the present study were younger when first exposed to the UV-B radiation treatments than those in our previous study. We would thus expect that they would be more responsive to UV-B radiation (Majer and Hideg, 2012). In addition, the duration of this experiment was also longer, which may have allowed more opportunity for flavonol accumulation to diverge between the fluctuating and steady UV-B radiation treatments.

Over the course of the experiment, a 5–6 % decline in ϕ_{PSII} was caused by UV-B treatments for Viura but not Tempranillo. This effect size is consistent with effects of solar UV radiation reported in the literature (Jansen et al., 2010). This suggests that ϕ_{PSII} is slightly more sensitive to UV-B radiation in Viura than in Tempranillo (Fig. 2). Although dynamic measurements through the whole experiment period could offer more detailed information, we only selected the final measurement day of each grapevine cultivar for gas exchange measurement, because it reflected the cumulative effects of the treatments. Both Viura and Tempranillo could maintain similar rates of P_n and g_s with and without UV-B radiation, implying that they are able to acclimate effectively to the UV-B doses administered in our treatments (Fig. 2), which were similar to those found under natural conditions where grapevines

are cultivated (Del-Castillo-Alonso et al., 2016b). Given that the UV-B sensitivity of crops may be related to their geographical provenance (Del-Castillo-Alonso et al., 2016a; Rozema et al., 1997), this capacity is consistent with the Mediterranean origin of both cultivars (Anderson and Nelgen, 2020). In addition to screening UV radiation, flavonols quench reactive oxygen species (ROS) produced by high energy photons of UV-B, and as such may help plants to maintain photosynthetic efficiency under oxidative stress conditions (Agati et al., 2012). For example, a positive relationship between F_v/F_m values and flavonoid content has been reported in *Hordeum vulgare* (Klem et al., 2015). We found no evidence of such this general relationship in either Tempranillo or Viura. However, the flavonol content in Tempranillo was positively correlated with ϕ_{PSII} under the control treatments but not under the UV-B treatments (Fig. S3c and d), both cultivars attained high F_v/F_m values under both steady and fluctuating UV-B conditions. This suggests that the photochemical efficiency is robustly protected by a suite of mechanisms, and that the increase in protective capacity that flavonols contributed forms part of an integrated acclimation response under UV-B radiation. Direct measurement of ROS scavenging could validate this assumption. Overall, despite the differences found between the two cultivars, their levels of epidermal UV-absorbing compounds would be expected to confer adequate protection for acclimation to the UV-B radiation conditions imposed in our study. This information may be of use to viticulture practices under changing UV-B conditions associated with climate change. However, while the observed cultivar-specific responses could inform selection in breeding programs, the genetic heritability of these traits requires further validation.

4.2. *Differential flavonol accumulation under fluctuating and steady UV-B radiation is primarily mediated by UVR8 with a minor role for cryptochromes*

The metabolic responses of grapevines to UV-B radiation treatments closely matched those of *Arabidopsis thaliana* Ler wild-type (WT), with steady UV-B driving greater epidermal flavonol accumulation than fluctuating UV-B in both species (Figs. 1 and 4). To provide potentially mechanistic support for the grapevine results, we examined loss-of-function mutants of *Arabidopsis*, which allowed us to assess how specific photoreceptors perceive UV-B radiation and mediate the observed responses. Among photoreceptors, UVR8 mediates the acclimation response to UV-B radiation, including flavonoid accumulation, in a dose-dependent response (Jenkins, 2009; Rizzini et al., 2011; Vanhaelewyn et al., 2019). This has also been found under natural conditions, although the responses did not depend on the UV-B doses received by the plants (Neugart et al., 2024). Consistent with previous findings, our study showed that the absence of functional UVR8 negated any UV-B-induced increase in flavonol accumulation in *uvr8* and *uvr8cry1cry2* under both UV-B treatments (Fig. 4). Higher epidermal flavonol content under fluctuating UV-B compared to steady UV-B was recorded in WT (possessing functional UVR8) but not in *uvr8* or *uvr8cry1cry2* (Fig. 4). This result indicates that, in addition to its dependence on UV-B dose (Jenkins, 2009; Rizzini et al., 2011), the extent of UV-B-dependent regulation of flavonoids *via* UVR8 also differs according to whether UV-B radiation is fluctuating or steady.

Considering blue-light photoreceptors, epidermal flavonol contents in *uvr8cry1cry2* and *cry1cry2* were lower than in WT in controls lacking UV-B radiation (Fig. 4). The LED growth-light spectrum used in our experiment contained blue light, which is perceived by CRYs mediating a flavonoid accumulation response (Brelsford et al., 2019). Previous studies have found particularly weak flavonol accumulation response of *uvr8cry1cry2* under UV-B radiation (Brelsford et al., 2019; Rai et al., 2021), suggesting that CRYs contribute to flavonol accumulation under UV-B radiation through crosstalk with UVR8 even though the CRY action spectrum does not extend to the UV-B region (Rai et al., 2021). Thus, in plants lacking only CRYs (*cry1cry2*), UV-B exposure consistently increased flavonol accumulation under both fluctuating and steady UV-B treatments (Fig. 4). This is consistent with the action spectrum of cryptochromes in stimulating flavonol accumulation under blue light and UV-A radiation, but not UV-B radiation (Brelsford et al., 2019; Rai et al., 2021).

To better identify whether the role of the studied photoreceptors was different under fluctuating and steady UV-B radiation, we inspected the responses of mutants for differences from the WT under these two UV-B treatments. The flavonol accumulation response in *cry1cry2* was more similar to the WT under steady UV-B than under fluctuating UV-B radiation (Fig. 6a). This suggests that CRY-dependent changes in flavonol accumulation are sensitive to fluctuations in UV-B radiation. Photomorphogenic response of UV-B acclimation *via* UVR8 is regulated by the monomerization of homodimeric UVR8 into an activated state under UV-B radiation, after which the negative feedback regulators REPRESSOR OF UV-B PHOTOMORPHOGENESIS 1 (RUP1) and RUP2 facilitate UVR8 ground-state reversion by re-dimerization (Podolec et al., 2021). Accordingly, the absence of either CRY1 or CRY2 suppresses the gene expression of RUP1 and RUP2 (Tissot and Ulm, 2020). Thus, in our study during the fluctuating UV-B radiation treatment, the period with no UV-B between UV-B doses may provide recovery opportunities allowing for the re-dimerization of the active UVR8 monomer. This would potentially explain the lower flavonol accumulation under fluctuating UV-B than steady UV-B (Fig. 8). Alternatively, in plants lacking CRYs the reversion of active UVR8 to the ground state may be suppressed, this would potentially lead to prolonged stimulation of flavonol accumulation as if under steady UV-B radiation. Although few studies have investigated the effects of fluctuating UV-B on flavonol biosynthesis in grapevines, a cultivar-dependent effect of UV-B radiation on flavonol accumulation has been reported (Nunez-Olivera et al., 2006). Our study suggests that grapevine cultivars respond with varying sensitivity to fluctuating *vs* steady UV-B radiation.

UVR8-dependent regulation of photosynthetic capacity and photoassimilate accumulation is stronger under steady UV-B radiation than under fluctuating UV-B radiation.

The UV-B-induced patterns of chlorophyll accumulation and ϕ_{PSII} mediated by the photoreceptors examined here in *Arabidopsis* differed from those of flavonol accumulation (Figs. 4 and 5). There is little experimental evidence that chlorophyll accumulation or ϕ_{PSII} depend on UVR8 under UV-B radiation, although generally inadequate photoprotection or antioxidant defence can lead to chlorophyll degradation (Podolec et al., 2021; Brelsford et al., 2019; Hermanowicz et al., 2019). In plants lacking UVR8, we did find a decline in chlorophyll content (11.9 %) and ϕ_{PSII} (5.7 %) under steady but not under fluctuating UV-B radiation (Figs. 4 and 5). This result suggests that the acclimation to steady UV-B radiation conferred by functional UVR8 can allow a higher chlorophyll content to be maintained. Other mechanisms of photoprotection, such as non-photochemical quenching, partially compensate for the lack of functional UVR8 under moderate UV-B radiation (Leonardelli et al., 2024; Morales et al., 2025), and these may operate during the recovery period in fluctuating UV-B. This would provide plants lacking functional UVR8 the opportunity to alleviate the oxidative stress imposed during the period of UV-B radiation, thus maintaining similar photosynthetic capacities.

We tested whether blue-UV-A photoreceptors CRYs and PHOTs play any role in acclimation to fluctuating UV-B radiation through crosstalk with UVR8. Functional cryptochromes are also important in the acclimation of plants to UV-B radiation under solar radiation, wherein plants typically receive increased UV-A radiation and blue light together with UV-B radiation. Our results corroborated findings that even in the absence of UVR8, CRYs can serve to promote UV-B acclimation (Rai et al., 2019). However, the joint absence of UVR8 and CRYs is lethal in *Arabidopsis* under UV-B radiation (Rai et al., 2019; Morales et al., 2025), as was evident in the reduced chlorophyll content and ϕ_{PSII} in our UV-B treatments in *uvr8cry1cry2* (Figs. 4 and 5). Although phototropins can improve photosynthetic efficiency (Xin et al., 2022) and through chloroplast movements they affect the amount of solar radiation absorbed by

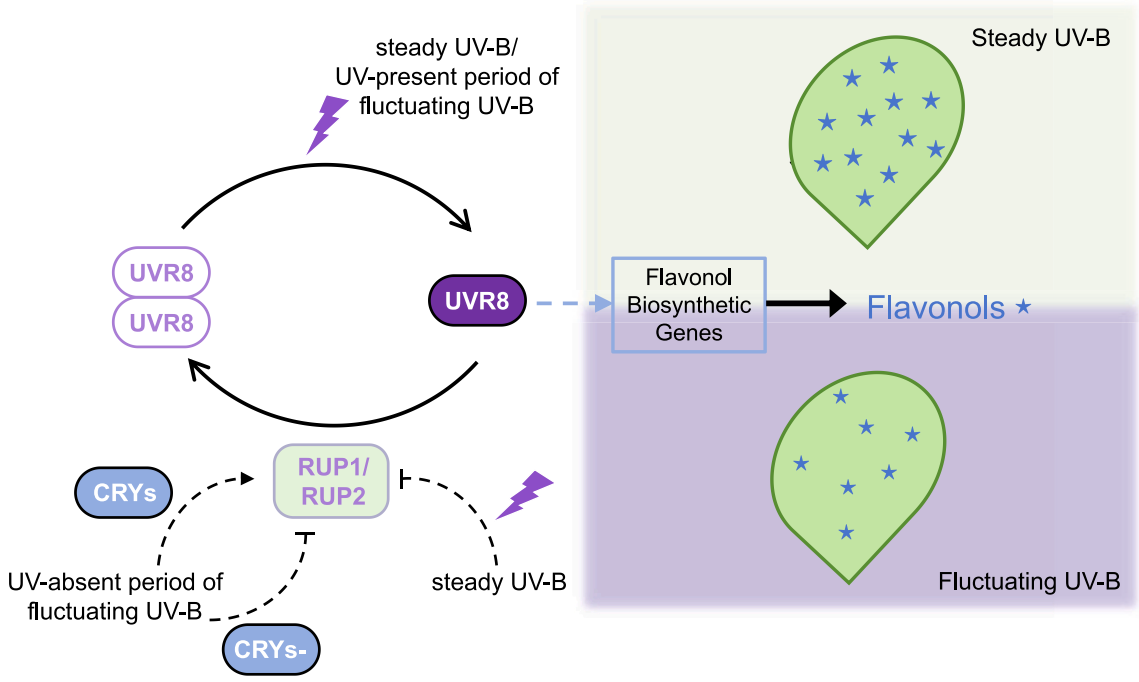

Fig. 8. Schematic suggesting the potential interplay of UVR8 and cryptochromes (CRYs) under steady vs fluctuating UV-B radiation treatments. Long-term effects of UV-B radiation (steady UV-B or during the UV-B-on periods of fluctuating UV-B), homodimeric UVR8 monomerizes into its active form triggering photomorphogenic responses. Negative feedback regulators REPRESSOR OF UV-B PHOTOMORPHOGENESIS 1 (RUP1) and RUP2 subsequently promote UVR8 re-dimerization, returning it to the ground state (Podolec et al., 2021). The absence of CRYs suppresses the expression of RUP1 and RUP2, thereby impeding UVR8 reversion (Tissot and Ulm, 2020). Under fluctuating UV-B radiation, the UV-B-off periods may allow recovery through re-dimerization of UVR8, leading to lower flavonol accumulation in leaves compared with steady UV-B exposure. In contrast, under steady UV-B or in CRY-deficient plants during UV-B-absent periods, limited UVR8 reversion may result in prolonged activation and continuous flavonol accumulation.

the leaf according to its spectral composition (Hermanowicz et al., 2019), functional PHOT1 is reported to only increase ϕ_{PSII} under blue light but not UV-A radiation (Brelsford et al., 2019). Similarly, we did not find evidence of such an effect under either steady or fluctuating UV-B radiation in our experiment.

There is evidence that starch degradation is supported by CRYs in *Solanum lycopersicum* (Dong et al., 2021). Consistent with this finding, we found higher starch content in those mutants lacking CRYs (*cry1cry2* and *uvr8cry1cry2*) compared to WT under no UV-B (control conditions). While previous studies have reported that UV-B radiation can reduce starch accumulation (Fagerberg and Bornman, 1997; Fagerberg, 2007), our UV-B treatments did not significantly decrease starch in either WT or *phot1* mutants (Fig. 7a). However, in the mutants *uvr8* and *cry1cry2*, less starch accumulated under steady UV-B than fluctuating UV-B. This result is consistent with findings in grapevine (*Vitis vinifera* cv Cabernet Sauvignon), where the effect of UV-B radiation in reducing starch concentrations was smaller under fluctuating UV-B compared to steady UV-B (Su-Zhou et al., 2024). These similarities between the response of *Arabidopsis* and grapevine suggest that even without functional UVR8 and CRYs, starch degradation may occur normally under steady UV-B, but less so under fluctuating UV-B. Building on these findings of photoreceptor roles under UV-B radiation in *Arabidopsis*, future studies should specifically examine whether UVR8 and CRYs of grapevine exhibit the differential regulation patterns under steady *vs* fluctuating UV-B radiation as observed in *Arabidopsis*, establishing a mechanistic hypothesis that connects photoreceptor signalling to carbohydrate metabolism, as this knowledge could inform strategies for enhancing UV resilience in grapevine cultivars.

Moreover, in the *uvr8cry1cry2* mutant, the starch concentration was lower (together with ϕ_{PSII}) under both steady and fluctuating UV-B treatments (Fig. S4). Hence the absence of both functional UVR8 and CYRs, not only reduced photosynthetic capacity, but also the storage of carbohydrates under both steady and fluctuating UV-B radiation. Additionally, sucrose, the primary transport carbohydrate, increased across all genotypes under UV-B exposure (Fig. 7). This contrasting response between starch and sucrose suggests that UV-B radiation may alter the balance between storage and transport carbohydrates, potentially influencing source-sink relationships. These findings align with a previous study by Vidović et al. (2015), which reported that UV-B radiation promotes carbon allocation from source to sink tissues. Although it has been established that carbon partitioning is influenced by light (Heuvelink et al., 2025), implying a potential role of photoreceptors in its regulation, the specific functions of relevant photoreceptors remain unclear. The observed reduction in starch accumulation, coupled with increased sucrose levels, may reflect enhanced export of photoassimilates from source to sink (Fig. 7). Both UVR8 and CRYs may play more prominent roles under steady UV-B conditions than under fluctuating regimes.

5. Conclusion

Comparing the response of two grapevine cultivars to fluctuating and steady UV-B radiation, we found that Viura (a white grape cultivar) had a stronger response involving higher epidermal flavonol accumulation and depression of ϕ_{PSII} compared with Tempranillo (a red grape cultivar). There were no large differences in the response to fluctuating and steady UV-B radiation of the same median dose, but slightly greater accumulation of epidermal flavonol sunscreen occurred under steady UV-B treatments, while slightly less inhibition of photosynthetic yield was maintained under fluctuating UV-B treatments. This response in grapevine was consistent with that found in *Arabidopsis*, which was employed to identify the underlying processes behind these patterns of responses. We found that UVR8, and to a lesser extent cryptochromes, mediated reductions of a similar magnitude in flavonol accumulation

under fluctuating and steady UV-B radiation. The regulatory role of cryptochromes in photoassimilate accumulation appeared stronger under steady UV-B than under fluctuating UV-B radiation, since the reduction of starch accumulation in *cry1cry2* was greater under steady UV-B. Understanding the role of UVR8 and CRYs in responses to solar UV-B radiation, which fluctuates natural in plant canopies, can guide the selection and cultivation of grapevine cultivars with a predictable response to variable UV-B conditions. This knowledge is particularly relevant in the context of climate change and changes in aerosol pollution affecting UV radiation exposure, as well as serving to guide viticultural practice such as selective defoliation.

CRediT authorship contribution statement

Chenxing Su-Zhou: Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Maxime Durand:** Writing – review & editing, Supervision, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Javier Martinez-Abaigar:** Writing – review & editing, Methodology, Conceptualization. **Alexey Shapiguzov:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Saijaliisa Kangasjarvi:** Writing – review & editing, Resources, Methodology, Investigation. **Xu Liu:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **T. Matthew Robson:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Data availability statement

All relevant data supporting the findings of this study are available from the corresponding author upon reasonable request.

Funding sources

This work was supported by the Key Research and Development of Shaanxi province (2023-ZDLNY-21, 2025NC-YBXM-025), Agricultural Collaborative Innovation and Promotional Alliance of Shaanxi province (LMZD202105), and Young Elite Scientists Sponsorship Program by Shaanxi Association for Science and Technology (20250620) to Xu Liu; the China Scholarship Council (Grant 202206300065 to Chenxing Su-Zhou). Javier Martinez-Abaigar's contribution is supported by the project PID2023-150695NB-I00, funded by MCIU/AEI/10.13039/501100011033/FEDER, EU. The Research Council of Finland funded Maxime Durand (decision #351008) and Alexey Shapiguzov (decision #346140). Matthew Robson was supported by Research Council of Norway Project QUEST-UV (#324670).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

We thank Pedro J. Aphalo for advice on data analysis and Hirofumi Ishihara for help with the sugar and starch analysis.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.plaphy.2025.110863.

References

Agati, G., Azzarello, E., Pollastri, S., Tattini, M., 2012. Flavonoids as antioxidants in plants: location and functional significance. Plant Sci. 196, 67–76.
Anderson, K., Nelgen, S., 2020. Which winegrape varieties are grown where. A Global Empirical Picture.Revised. University of Adelaide Press, Adelaide, Australia.
Baier, M., Dietz, K.J., 2005. Chloroplasts as source and target of cellular redox regulation: a discussion on chloroplast redox signals in the context of plant physiology. J. Exp. Bot. 56 (416), 1449–1462. https://doi.org/10.1093/jxb/eri161.
Banerjee, R., Batschauer, A., 2005. Plant blue-light receptors. Planta 220, 498–502.
Barnes, P.W., Robson, T.M., Zepp, R.G., Bornman, J.F., Jansen, M.A.K., Ossola, R., Wang, Q.W., Robinson, S.A., Foereid, B., Klekociuk, A.R., Martínez-Abaigar, J., Hou, W.C., Mackenzie, R., Paul, N.D., 2023. Interactive effects of changes in UV radiation and climate on terrestrial ecosystems, biogeochemical cycles, and feedbacks to the climate system. Photochem. Photobiol. Sci. 22 (5), 1049–1091. https://doi.org/10.1007/s43630-023-00376-7.
Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Software 67 (1), 1–48.
Berli, F.J., Alonso, R., Bressan-Smith, R., Bottini, R., 2013. UV-B impairs growth and gas exchange in grapevines grown in high altitude. Physiol. Plantarum 149 (1), 127–140.
Bernhard, G.H., Madronich, S., Lucas, R.M., others, 2023. Linkages between COVID-19, solar UV radiation, and the Montreal protocol. Photochem. Photobiol. Sci. 22, 991–1009. https://doi.org/10.1007/s43630-023-00373-w.
Brelsford, C.C., Morales, L.O., Nezval, J., Kotilainen, T.K., Hartikainen, S.M., Aphalo, P. J., Robson, T.M., 2019. Do UV-A radiation and blue light during growth prime leaves to cope with acute high light in photoreceptor mutants of *arabidopsis thaliana*? Physiol. Plantarum 165 (3), 537–554.
Briggs, W.R., Huala, E., 1999. Blue-light photoreceptors in higher plants. Annu. Rev. Cell Dev. Biol. 15, 33–62.
Carbonell-Bejerano, P., Diago, M.P., Martínez-Abaigar, J., Martínez-Zapater, J.M., Tardáguila, J., Núñez-Olivera, E., 2014. Solar ultraviolet radiation is necessary to enhance grapevine fruit ripening transcriptional and phenolic responses. BMC Plant Biol. 14, 183. https://doi.org/10.1186/1471-2229-14-183.
Cerovic, Z.G., Masdoumier, G., Ghozlen, N.B., Latouche, G., 2012. A new optical leaf-clip meter for simultaneous non-destructive assessment of leaf chlorophyll and epidermal flavonoids. Physiol. Plantarum 146, 251–260.
Chan, K.X., Phua, S.Y., Crisp, P., McQuinn, R., Pogson, B.J., 2016. Learning the languages of the chloroplast: retrograde signaling and beyond. Annu. Rev. Plant Biol. 67, 2553. https://doi.org/10.1146/annurev-arplant-043015-111854.
Del-Castillo-Alonso, M.Á., Diago, M.P., Tomás-Las-Heras, R., Monforte, L., Soriano, G., Martínez-Abaigar, J., Núñez-Olivera, E., 2016a. Effects of ambient solar UV radiation on grapevine leaf physiology and berry phenolic composition along one entire season under Mediterranean field conditions. Plant Physiol. Biochem. 109, 374–386.
Del-Castillo-Alonso, M.Á., Castagna, A., Csepregi, K., Hideg, É., Jakab, G., Jansen, M.A., Jug, T., Llorens, L., Mátai, A., Martínez-Lüscher, J., Monforte, L., Neugart, S., Olejnickova, J., Ranieri, A., Schödl-Hummel, K., Schreiner, M., Soriano, G., Teszlák, P., Tittmann, S., Urban, O., Verdaguer, D., Zipoli, G., Martínez-Abaigar, J., Núñez-Olivera, E., 2016b. Environmental factors correlated with the metabolite profile of *Vitis vinifera* cv. pinot noir berry skins along a European latitudinal gradient. J. Agric. Food Chem. 64 (46), 8722–8734. https://doi.org/10.1021/acs.jafc.6b03272.
Dong, H., Hu, C., Liu, C., Wang, J., Zhou, Y., Yu, J., 2021. ELONGATED HYPOCOTYL 5 mediates blue light-induced starch degradation in tomato. J. Exp. Bot. 72 (7), 2627–2641.
Durand, M., Robson, T.M., 2023. Fields of a thousand shimmers: canopy architecture determines high-frequency light fluctuations. New Phytol. 238 (5), 2000–2015.
Durand, M., Zhuang, X., Salmon, Y., Robson, T.M., 2024. Caught between two states: the compromise in acclimation of photosynthesis, transpiration and mesophyll conductance to different amplitudes of fluctuating irradiance. Plant Cell Environ. 47 (12), 5220–5236.
Fagerberg, W.R., Bornman, J.F., 1997. Ultraviolet-B radiation causes shade-type ultrastructural changes in Brassica napus. Physiol. Plantarum 101, 833–844.
Fagerberg, W.R., 2007. Below-ambient levels of UV induce chloroplast structural change and alter starch metabolism. Protoplasma 230 (1–2), 51–59.
Galvão, V.C., Fankhauser, C., 2015. Sensing the light environment in plants: photoreceptors and early signaling steps. Curr. Opin. Neurobiol. 34, 46–53.
Green, A.E.S., Sawada, T., Shettle, E.P., 1974. The middle ultraviolet reaching the ground. Photochem. Photobiol. 19, 251–259.
Guo, H., Yang, H., Mockler, T.C., Lin, C., 1998. Regulation of flowering time by *arabidopsis* photoreceptors. Science 279, 1360–1363.
Heijde, M., Ulm, R., 2012. UV-B photoreceptor-mediated signalling in plants. Trends Plant Sci. 17, 230–237.
Henry, C., Watson-Lazowski, A., Oszvald, M., Griffiths, C., Paul, M.J., Furbank, R.T., Ghannoum, O., 2020. Sugar sensing responses to low and high light in leaves of the C_4 model grass *setaria viridis*. *Journal of experimental botany*, 71 (3), 1039–1052.
Hermanowicz, P., Banaś, A.K., Sztatelman, O., Gabryś, H., Łabuz, J., 2019. UV-B induces chloroplast movements in a Phototropin-Dependent manner. Front. Plant Sci. 10, 1279. Oct 15.
Heuvelink, E., Acevedo-Siaca, L.G., Van de Poel, B., Van der Jeucht, L., Vialet-Chabrand, S., Steppe, K., Ji, Y., Körner, O., Kusuma, P., Langer, S., Li, T., Van Ieperen, W., Verdonk, J.C., Zepeda, A.C., Zhang, Y., Marcelis, L.F.M., 2025. Tomato in the spotlight: light regulation of whole-plant physiology in tomato. J. Exp. Bot. https://doi.org/10.1093/jxb/eraf315 eraf315.

Hernández-Verdeja, T., Strand, Å., 2018. Retrograde signals navigate the path to chloroplast development. Plant Physiol. 176 (2), 967–976. https://doi.org/10.1104/pp.17.01299.

Jansen, M.A., Martret, B.L., Koornneef, M., 2010. Variations in constitutive and inducible UV-B tolerance; dissecting photosystem II protection in *Arabidopsis thaliana* accessions. Physiol. Plantarum 138, 22–34.

Jenkins, G.I., 2009. Signal transduction in responses to UV-B radiation. Annual review of *plant biology*, 60, 407–431.

Klem, K., Holub, P., Štroch, M., Nezval, J., Špunda, V., Tříska, J., Jansen, M.A., Robson, T.M., Urban, O., 2015. Ultraviolet and photosynthetically active radiation can both induce photoprotective capacity allowing barley to overcome high radiation stress. Plant Physiol. Biochem. 93, 74–83.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. J. Stat. Software 82 (13), 1–26. https://doi.org/10.18637/jss.v082.i13.

Lamy, K., Portafaix, T., Josse, B., Brogniez, C., Godin-Beekmann, S., Bencherif, H., Revell, L., Akiyoshi, H., Bekki, S., Hegglin, M.I., Jöckel, P., Kirner, O., Liley, B., Marecal, V., Morgenstern, O., Stenke, A., Zeng, G., Abraham, N.L., Archibald, A.T., Butchart, N., Chipperfield, M.P., Di Genova, G., Deushi, M., Dhomse, S.S., Hu, R.-M., Kinnison, D., Kotkamp, M., McKenzie, R., Michou, M., O'Connor, F.M., Oman, L.D., Pitari, G., Plummer, D.A., Pyle, J.A., Rozanov, E., Saint-Martin, D., Sudo, K., Tanaka, T.Y., Visioni, D., Yoshida, K., 2019. Clear-sky ultraviolet radiation modelling using output from the chemistry climate model initiative. Atmos. Chem. Phys. 19 (15), 10087–10110. https://doi.org/10.5194/acp-19-10087-2019.

Lastdrager, J., Hanson, J., Smeekens, S., 2014. Sugar signals and the control of plant growth and development. J. Exp. Bot. 65, 799–807.

Leonardelli, M., Tissot, N., Podolec, R., Ares-Orpel, F., Glauser, G., Ulm, R., Demarsy, E., 2024. Photoreceptor-induced sinapate synthesis contributes to photoprotection in arabidopsis. Plant Physiol. 196 (2), 1518–1533.

Liu, L., Kong, J., Fan, P., Wang, Y., Duan, W., Liang, Z., Matus, J.T., Dai, Z., 2024. Supplementing with monochromatic blue LED light during the day, rather than at night, increases anthocyanins in the berry skin of grapevine (*Vitis vinifera* L.). Planta 10 (3), 69. https://doi.org/10.1007/s00425-024-04500-4, 260.

Majer, P., Hideg, E., 2012. Developmental stage is an important factor that determines the antioxidant responses of young and old grapevine leaves under UV irradiation in a green-house. Plant Physiol. Biochem. 50, 15–23.

Mao, J., Zhang, Y.C., Sang, Y., Li, Q.H., Yang, H.Q., 2005. From the cover: a role for *arabidopsis* cryptochromes and COP1 in the regulation of stomatal opening. Proc. Natl. Acad. Sci. U. S. A 102, 12270–12275.

Matus, J.T., Cavallini, E., Loyola, R., Höll, J., Finezzo, L., Dal Santo, S., Vialet, S., Commisso, M., Roman, F., Schubert, A., Alcalde, J.A., Bogs, J., Ageorges, A., Tornielli, G.B., Arce-Johnson, P., 2017. A group of grapevine MYBA transcription factors located in chromosome 14 control anthocyanin synthesis in vegetative organs with different specificities compared with the berry color locus. Plant J. 91 (2), 220–236.

Morales, L.O., Shapiguzov, A., Rai, N., Aphalo, P.J., Brosché, M., 2025. Protection of photosynthesis by UVR8 and cryptochromes in *arabidopsis* under blue and UV radiation. Plant Cell Environ. 48 (8), 6321–6335. https://doi.org/10.1111/pce.15608.

Neugart, S., Steininger, V., Fernandes, C., Martínez-Abaigar, J., Núñez-Olivera, E., Schreiner, M., Strid, Å., Viczián, A., Albert, A., Badenes-Pérez, F.R., Castagna, A., Dáder, B., Fereres, A., Gaberscik, A., Gulyás, Á., Gwynn-Jones, D., Nagy, F., Jones, A., Julkunen-Tiitto, R., Konstantinova, N., Lakkala, K., Llorens, L., Martínez-Lüscher, J., Nybakken, L., Olsen, J., Pascual, I., Ranieri, A., Regier, N., Robson, M., Rosenqvist, E., Santin, M., Turunen, M., Vandenbussche, F., Verdaguer, D., Winkler, B., Witzel, K., Grifoni, D., Zipoli, G., Hideg, É., Jansen, M.A.K., Hauser, M. T., 2024. A synchronized, large-scale field experiment using *Arabidopsis thaliana* reveals the significance of the UV-B photoreceptor UVR8 under natural conditions. Plant Cell Environ. 47 (10), 4031–4047. https://doi.org/10.1111/pce.15008.

Nunez-Olivera, E., Martinez-Abaigar, J., Tomas, R., Otero, S., Arroniz-Crespo, M., 2006. Physiological effects of solar ultraviolet-B exclusion on two cultivars of *Vitis vinifera* L. from La Rioja, Spain. Am. J. Enol. Vitic. 57 (4), 441–448.

Paik, I., Huq, E., 2019. Plant photoreceptors: multi-functional sensory proteins and their signaling networks. Semin. Cell Dev. Biol. 92, 114–121.

Podolec, R., Demarsy, E., Ulm, R., 2021. Perception and signaling of Ultraviolet-B radiation in plants. Annu. Rev. Plant Biol. 72, 793–822.

Quail, P.H., 2002. Phytochrome photosensory signalling networks. Nat. Rev. Mol. Cell Biol. 3, 85–93.

Rai, N., Neugart, S., Yan, Y., Wang, F., Siipola, S.M., Lindfors, A.V., Winkler, J.B., Albert, A., Brosché, M., Lehto, T., Morales, L.O., Aphalo, P.J., 2019. How do cryptochromes and UVR8 interact in natural and simulated sunlight? J. Exp. Bot. 70 (18), 4975–4990.

Rai, N., O'Hara, A., Farkas, D., Safronov, O., Ratanasopa, K., Wang, F., Lindfors, A.V., Jenkins, G.I., Lehto, T., Salojärvi, J., Brosché, M., Strid, Å., Aphalo, P.J., Morales, L. O., 2020. The photoreceptor UVR8 mediates the perception of both UV-B and UV-A wavelengths up to 350nm of sunlight with responsivity moderated by cryptochromes. Plant Cell Environ. 43 (6), 1513–1527.

Rai, N., Morales, L.O., Aphalo, P.J., 2021. Perception of solar UV radiation by plants: photoreceptors and mechanisms. Plant Physiol. 186 (3), 1382–1396. Jul 6.

R Core Team, 2022. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rizzini, L., Favory, J.J., Cloix, C., Faggionato, D., O'Hara, A., Kaiserli, E., Ulm, R., 2011. Perception of UV-B by the *Arabidopsis* UVR8 protein. Science 332, 103–106.

Robson, T.M., Aphalo, P.J., 2019. Transmission of ultraviolet, visible and near-infrared solar radiation to plants within a seasonal snow pack. Photochem. Photobiol. Sci. 18 (8), 1963–1971.

Robson, T.M., Klem, K., Urban, O., Jansen, M.A., 2015. Re-interpreting plant morphological responses to UV-B radiation. Plant Cell Environ. 38 (5), 856–866.

Rozema, J., Van de Staaij, J.W.M., Tosserams, M., 1997. Effects of UV-B radiation on plants from agro- and natural ecosystems. In: Lumsden, P.J. (Ed.), Plants and UV-B. Responses to Environmental Change, 232. Cambridge University Press, UK, p. 213.

Smith, W.K., Berry, Z.C., 2013. Sunflecks? Tree Physiol. 33, 233–237.

Stitt, M., Lilley, R.M., Gerhardt, R., Heldt, H.W., 1989. Metabolite levels in specific cells and subcellular compartments of plant-leaves. Methods Enzymol. 174, 518–552.

Su-Zhou, C., Durand, M., Aphalo, P.J., Martinez-Abaigar, J., Shapiguzov, A., Ishihara, H., Liu, X., Robson, T.M., 2024. Weaker photosynthetic acclimation to fluctuating than to corresponding steady UVB radiation treatments in grapevines. Physiol. Plantarum 176 (3), e14383. https://doi.org/10.1111/ppl.14383.

Tissot, N., Ulm, R., 2020. Cryptochrome-mediated blue-light signalling modulates UVR8 photoreceptor activity and contributes to UV-B tolerance in *Arabidopsis*. Nat. Commun. 11 (1), 1323.

Vanhaelewyn, L., Viczián, A., Prinsen, E., Bernula, P., Serrano, A.M., Arana, M.V., Ballaré, C.L., Nagy, F., Van Der Straeten, D., Vandenbussche, F., 2019. Differential UVR8 signal across the stem controls UV-B-Induced inflorescence phototropism. Plant Cell 31 (9), 2070–2088.

Vialet-Chabrand, S., Matthews, J.S., Simkin, A.J., Raines, C.A., Lawson, T., 2017. Importance of fluctuations in light on plant photosynthetic acclimation. Plant Physiol. 173 (4), 2163–2179.

Vidović, M., Morina, F., Milić, S., Albert, A., Zechmann, B., Tosti, T., Winkler, J.B., Jovanović, S.V., 2015. Carbon allocation from source to sink leaf tissue in relation to flavonoid biosynthesis in variegated *Pelargonium zonale* under UV-B radiation and high PAR intensity. Plant Physiol. Biochem. 93, 44–55.

Wang, M., Vannozzi, A., Wang, G., Liang, Y.H., Tornielli, G.B., Zenoni, S., Cavallini, E., Pezzotti, M., Cheng, Z.M., 2014. Genome and transcriptome analysis of the grapevine (*Vitis vinifera* L.) WRKY gene family. Horticulture Research 26 (1), 14016.

Xin, G.Y., Li, L.P., Wang, P.T., Li, X.Y., Han, Y.J., Zhao, X., 2022. The action of enhancing weak light capture via phototropic growth and chloroplast movement in plants. Stress biology 2 (1), 50.