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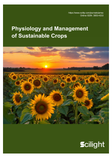

Article

Canopy Management Effects on Temperature and CO_2 Dynamics in Garnacha Grapes Under Mediterranean Conditions

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Abstract: Grape (*Vitis vinifera* L.) production is increasingly challenged by rising temperatures and drought conditions due to climate change, especially in Mediterranean regions. These conditions affect grapevine photosynthesis and berry metabolism, ultimately impacting yield and wine quality. This study aimed to quantify the dynamics of CO_2 fluxes from Garnacha grapes in response to temperature, radiation, and ripening stage. An empirical model was developed to estimate the impact of canopy management on fruit carbon balance using data from vineyards in Majorca, where defoliation and grape cluster shading were applied. Our model accurately predicted CO_2 release across ripening stages and environmental conditions. CO_2 release under darkness increased during early ripening stages but declined as berries matured, while light conditions substantially reduced respiratory losses. Temperature significantly influenced CO_2 release, with defoliation raising berry temperatures by over 4 °C and increasing maximum daytime carbon losses by approximately 17% compared to controls. Shading berries from defoliated plants mitigated these effects, lowering temperature and carbon losses to control levels. The study underscores the risks of heatwaves and elevated nighttime temperatures, which most drive respiratory carbon losses that shading cannot offset. These findings highlight the importance of adaptive canopy management, combining defoliation and shading, to sustain grape quality and yield under warming climates.

Keywords: canopy management; carbon balance; fruit; radiation; respiration; temperature; *Vitis vinifera*

1. Introduction

Grapevine (*Vitis vinifera* L.) is a valuable and versatile fruit crop worldwide, with 7.2 million of cultivated hectares and a total grape production of 74.7 million tonnes according to the International Organisation of Vine and Wine [1], mainly produced in temperate regions characterized by warm and dry summers. Climate change imposes increasingly warm and dry conditions in Mediterranean regions [2], including frequent and severe heat events during the growing season, which pose challenges for high quality wine grape production [3].

An increase in temperatures provokes inhibition of the photosynthetic capacity of grapevines, mainly due to stomatal closure [4], affecting to the stock of soluble carbohydrates in cane and trunks [5]. Also, high temperatures can significantly affect fruit quality throughout the fruit maturation stages. High temperatures generally accelerate respiration and gluconeogenesis processes and increase malate degradation in grapes during postveraison stages [6–10]. However, respiration sensitivity to temperature could be dependent on the berry developmental and ripening stage [11]. Additionally, respiration losses can be compensated in part by CO_2 fixation in the fruit during the green stages of the berry [12,13], so that unripe sun-adapted berries show better adaptation to high light conditions due to their higher capacity of photosynthetic energy consumption and thermal energy dissipation [14]. Consequently, an adequate exposure of the fruit to sunlight will be crucial in the current scenario of climate change with high temperatures causing a reduction on grape quality [15,16], including a general reduction of organic acids [10] and anthocyanins [17], and an increase in sugars [18], leading to high alcohol content and lower acidity in wines [19].

Many management practices have been proposed to increase resilience of grapevines to climate change and to alleviate its negative effects on grape quality [3,20], including alternative cultivars and rootstocks, changing geographic location, irrigation, soil amendments, canopy manipulation, and shading, among others. Specifically, to mitigate the negative effects of high temperatures at the cluster level, shading techniques have been tested to lower the temperature and radiation during grape ripening stages. In fact, these shading practices can be especially interesting in regions with high air relative humidity, where defoliation is a common practice to control pests and diseases [21], by modifying the canopy microclimate, more exposed and, therefore, more subjective to higher temperatures. Vineyards shading (at plant level) and hydrocooling have been explored in order to reduce canopy temperatures and delaying maturation, although with no clear effects on berry size and sugar concentration in berries [22–25], probably interfering with water availability. However, shade nets at plant level have installation costs and can interfere with various practices in the vineyards, making their application difficult in many winegrowing areas.

Therefore, the combination of defoliation and shading at different developmental and ripening stages could help to regulate and adapt the fruit quality parameters to the seasonal environmental conditions. In fact, this combination of techniques at the cluster level from the green stages of the berry to the completed ripen stages have proved to modify grape quality parameters [26], resulting in higher concentrations of malic and tartaric acids and °Brix in shaded defoliated berries compared to non-shaded defoliated ones. Grape berry is able to respire either sugars (mainly glucose and fructose) or organic acids, depending on the phenological stage and maturation stage [27,28]. Therefore, an increase in respiration due to rises in temperature can affect both alcohol and the acidity of wines. Defoliation, although useful for balancing resources-sinks and pest control, can be detrimental if excessive radiation results in rises of temperature. In order to properly balance the positive and negative aspects of this practice, it is necessary to quantify the effect that temperature and light exposure have on grape metabolism taking into account the different developmental and ripening stages.

The aim of this study was to quantify the dynamics of CO_2 fluxes from Garnacha grapes in response to radiation and temperature. Possible acclimation or changes in carbon metabolism in response to long-term light exposure treatments were evaluated. Based on the data obtained, a model was developed to calculate CO_2 release according to fruit ripening and the temperature and radiation to which it is exposed, using real climate data from a vineyard in Majorca (Bodegas Ribas), where the practice of defoliation and grape berry shading was applied.

2. Materials and Methods

2.1. Study Site, Plant Material and Shading Treatments

Two study sites were involved: the experimental field at the University of the Balearic Islands, where grapes of Garnacha vines were collected, and the commercial vineyard of Bodegas Ribas, where data on temperature and radiation of Garnacha grape berries were collected (both in Majorca, Spain). In both vineyards, plants had been grafted on 110-Richter rootstocks and planted with a 1-m separation between plants and 2.4–2.5 m between rows. The direction of the vineyard rows was NE-SW in both cases. Grapes of Garnacha and data of temperature and radiation were collected simultaneously at both study sites during summer 2020 (from 9 July to 18 August). Berries were collected following the stratified sampling method described in Hernández-Montes et al. [26] based on tactile and visual features of grapes, which lead to the next homogeneous categories regarding the developmental stages: green hard (GH), green soft (GS), blush/pink (Pink), red/purple (Red) and blue (Blue). Only Pink and Red stages overlapped over time (Supplementary Materials Figure S1). Two kinds of grapes were identified: sun exposed and naturally shaded grapes from morning until midday.

2.2. Gas Exchange Measurements

CO_2 fluxes of the grape berries of different plants (n = 3) were determined by gas exchange measurements using a GFS-3000 system (Heinz Walz, Effeltrich, Germany). Each sample consisted of 3–4 detached berries collected from the same plant. The berries were introduced in the cuvette for Petri-Dish 3010-P (Supplementary

Materials Figure S2). Temperature of chamber remained at 25, 35 or 45 °C (maximum oscillation of 1 °C), and a relative humidity of 40–60% was set during the measurements. A flow of 600 μmol s^{-1} was used. Photosynthetic photon flux density (PPFD) was initially set to 750 μmol m^{-2} s^{-1} and CO_2 release under light conditions (CR_L) was measured after 10 min of stabilization after sample location. Then, the response of CO_2 release under a light curve (750, 570, 340, 170, 80, 40, 13 μmol m^{-2} s^{-1}, intervals of 3 min) was measured. After 5 min under darkness, the CO_2 release under dark conditions (CR_D) was recorded. All measurements (CR_L, CR_D and CO_2 release during light curve) were the result of averaged three technical replicates measured with 1 min of difference. CO_2 release was normalized to the fresh weight (FW) of the sample.

2.3. Modeling CO_2 Release in Response to Light, Temperature and Ripening

The response of CO_2 release to radiation and temperature was fitted to a non-linear model using the R statistical software (1.4.2.3 version) [29] through ordinary nonlinear least squares regression techniques using *nlme* package [30]. The semiempirical model was based on light response of photosynthesis and exponential response of respiration as a base for carbon fluxes [31–34], with some modifications. The light response equation of Smith [35] was adapted:

$$CO_2release = \left(CR_D - \frac{(CR_D - CR_L) \cdot PPFD \cdot AQE}{\sqrt{(AQE \cdot PPFD)^2 + (CR_D - CR_{LD})^2}} - 0.9296\right)1.2301 \tag{1}$$

where CR_D and CR_L are the CO_2 release under dark conditions and light saturation, respectively, and *AQE* is the apparent quantum efficiency (initial slope of the light curve). Values of 0.9296 and 1.2301 are the final intercept and slope corrections of the model to force a 1:1 relationship between observed and modelled CO_2 release (see Statistical analysis section). Seeing the variable exponential response of CR_D along ripening (Supplementary Materials Figure S3) [11], CR_D was expressed as a function of temperature (*T*) and day of year (*DOY*, ranged from 190 to 230, equivalent to 9 July and 18 August) following the empirical model of Heskel et al. [36] with modifications:

$$CR_D = e^{(aDOY^2 + bDOY + c) + 0.1012T - 0.0005T^2} \tag{2}$$

where *a*, *b* and *c* are fitted parameters. CR_L was expressed as a sigmoid function of *DOY* with an intercept depending on *T*:

$$CR_L = \frac{Y_{max}}{1 + e^{(-\sigma(DOY - DOY_{max})}} + CR_{L,min} + dT \tag{3}$$

where Y_{max}, σ, DOY_{max}, $CR_{L,min}$ and *d* are fitted parameters. Y_{max} represents the theoretical maximum of CR_L as DOY tends to infinity, DOY_{max} is the theoretical day of the year at which the inflection point of the sigmoid curve occurs, and σ denotes the steepness (or shape) of the sigmoid curve. It is important to note that these parameters serve primarily to mathematically describe the curve's behaviour at its extremes or points of inflection, but they do not necessarily have a direct biological meaning, as they often refer to values outside the range of *DOY* measured in the field. Equations (2) and (3) were solved independently from the gas exchange dataset obtained under dark conditions or with saturated radiation (750 μmol m^{-2} s^{-1}). *AQE* was expressed as a polynomic relation of CR_D-CR_L with different slopes depending on *T*:

$$AQE = (eT + f)(CR_D - CR_L)^2 + (gT + h)(CR_D - CR_L) \tag{4}$$

where *e*, *f*, *g* and *h* are fitted parameters. Equation (4) was solved using *AQE* values of each light curve (initial slope of the CO_2 release-PPFD relationship) and CR_D and CR_L values of the same sample.

2.4. Estimation of Carbon Losses of Grape Berries According to Crop Management

Temperature and radiation of grape berries were collected from an experiment in commercial crop (Bodegas Ribas, Majorca) developed in 2022 [26], where different exposure treatments were applied: (1) grape berries shaded by the plant leaves (Control); (2) exposed grape berries after defoliation (D); and (3) shaded grape berries after defoliation and covering using the plant's own shoots (D + S). Defoliation was carried out by removing all the leaves from the base of the shoot up to the second cluster. Temperature and radiation sensors (HOBO Pendant® modelo UA-002-64, Bourne, MA, USA) were installed at the cluster level and programmed to measure each 10 min. CO_2 release was estimated with the same frequency from Equations (1)–(4) and previously fitted parameters *a*, *b*, *c*, Y_{max}, σ, DOY_{max}, $CR_{L,min}$, *d e*,*f*, *g*, and *h* using temperature and radiation data from each exposure treatment applied in Bodegas Ribas. For each day, the maximum and minimum CO_2 release (CR_{max} and CR_{min}, respectively) was obtained. Only data from 9 July to 18 August were considered.

2.5. Statistical Analysis

Statistical analysis was done using R statistical software (1.4.2.3 version) [29]. The effect of shading treatment in the CO_2 release of grape berries was tested by a *t*-test comparing shaded and sun exposed values for each measuring temperature and ripening stage. The accuracy of the proposed model and the parameters obtained was estimated by comparison of measured vs modelled values by linear regression. The relationship between the obtained AQE and the difference between measured CR_D and CR_L was also tested by linear regression. CR_D, CR_L and AQE models (Equations (2)–(4)) were fitted and tested first with 11.2% of data (83 entries, those measured under dark conditions or under saturating light of 750 μmol m^{-2} s^{-1}). Then, the entire CO_2 release model (Equation (1)) with all estimated parameters (a, b, c, Y_{max}, σ, DOY_{max}, $CR_{L,min}$, d e, f, g, and h) was used for calculating the estimated CO_2 release, and full dataset (739 entries) was used for testing the accuracy of the model by linear regression. Additional intercept of −0.9296 and slope of 1.2301 was used for correcting the Equation (1) in order to obtain a relationship as close as possible to 1:1. Finally, the differences between defoliation treatments of Bodegas Ribas in CR_{max} and CR_{min} and maximum, mean and minimum temperature (T_{max}, T_{mean}, T_{min}, respectively) was tested by a one-way ANOVA considering the same DOY of the 2020 experiment (from 9 July to 18 August). Additional R packages used for data analysis were *plyr* [37], *ggplot2* [38], and *agricolae* [39].

3. Results

3.1. Carbon Fluxes of Grape Berries Response to Radiation, Temperature and Ripening

In all temperatures and long-term light exposure treatments, CO_2 release under dark conditions (CR_D) increased initially at the first stages of grape berries ripening (from GH to GS) but start decreasing from Pink to Blue stage (Figure 1A). When berries were measured under light conditions, CO_2 release decreased considerably in all cases, especially in high temperature measurements (averaged decrease of 48%, 62% and 64% for 25, 35 and 45 °C, respectively) and early stages of ripening (60%, 80%, 70%, 54% and 23% of average decrease for GH, GS, Pink, Red and Blue stages) (Figure 1B). In both dark and light conditions, temperature of berries during measurements affected considerably their CO_2 release, achieving to an average of 38 μmol CO_2 g^{-1} FW h^{-1} under dark conditions and 16 μmol CO_2 g^{-1} FW h^{-1} under light conditions along the full ripening stage. Although significant differences were observed in CR_D between long-term shaded and sun exposed grape berries, those were not consistent along the study (only in berries at Pink stage measured at 35 and 45 °C, with opposite directions).

The apparent quantum efficiency (*AQE*) obtained from the light curves oscilated from 0.03 to 0.53 (Figure 2A), without clear tendencies between temperatures and shade treatments. AQE varied along ripening stages with a similar pattern as CR_D, it is, increasing its values from GH to GS and decreasing from Pink to Blue. The relationship between AQE and the difference between CR_D and CR_L was significant ($R^2 = 0.464$, $p < 0.001$) (Figure 2B).

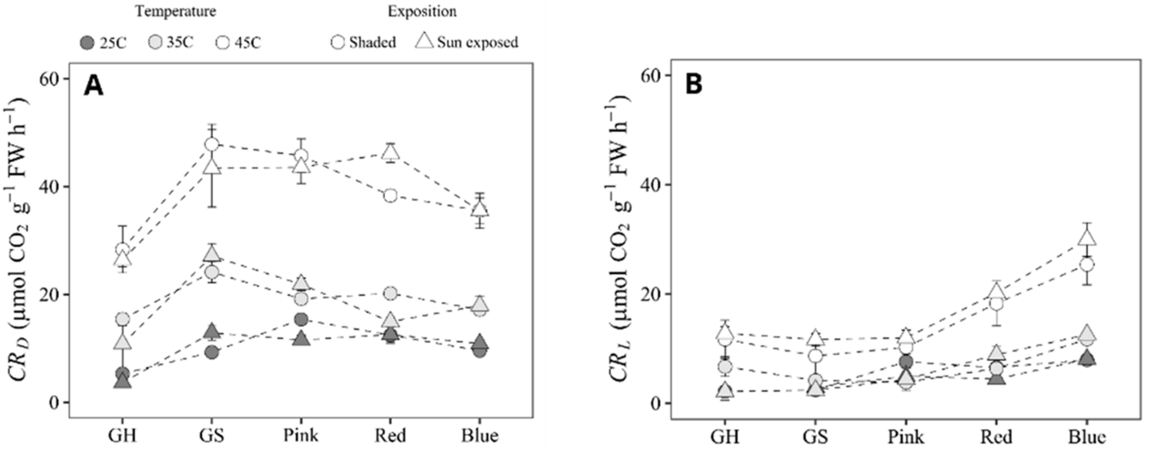

Figure 1. Variation of CO_2 release per dry weight of detached Garnacha grapes under dark conditions (CR_D) (**A**) and light conditions (CR_L); (**B**) with the development of grapes according to temperature of measurement and prior exposure treatment.

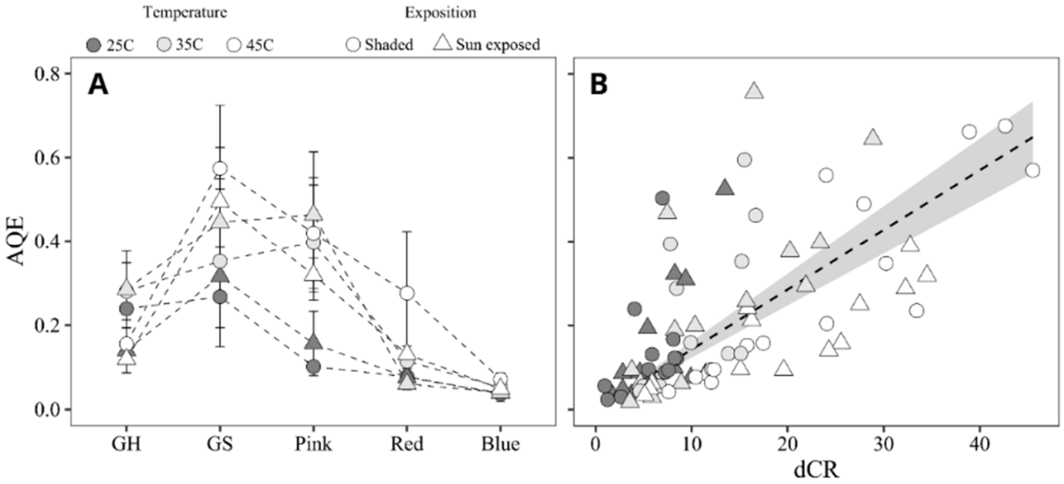

Figure 2. (**A**) Variation of the apparent quantum efficiency (AQE, it is, the initial slope of the CO_2 release-radiation relationship) of detached Garnacha grapes with the ripening of grapes accordign to temperature of measurement and prior long-term shading treatment of grapes; (**B**) Relationship between AQE and the difference between CO_2 release under dark and light conditions (dCR) ($R^2 = 0.464$, $p < 0.001$).

Measured CR_D, CR_L and AQE values were fitted to the Equations (2)–(4), respectively, for obtaining the parameters a, b, c, Y_{max}, σ, DOY_{max}, $CR_{L,min}$, d e, f, g, and h (Table S1). A good fit was obtained for the observed vs modelled values of CR_D (Figure 3A, $R^2 = 0.875$), CR_L (Figure 3B, $R^2 = 0.764$) and AQE (Figure 3C, $R^2 = 0.796$). The fitted parameters were applied to the described CO_2 release model (Equation (1)). The full CO_2 release dataset (light curves at 3 different temperatures, shaded and sun exposed berries at all the stages of ripening) was used to test the accuracy of this model, resulting in a coefficient of correlation of 0.847 (Figure 4).

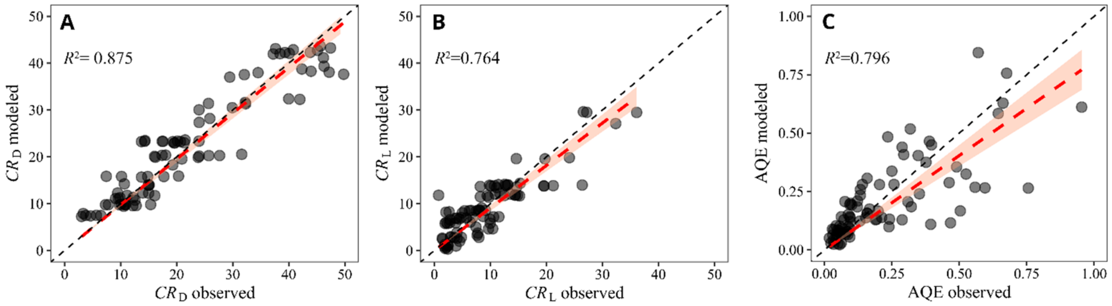

Figure 3. Linear regression between modeled and observed CO_2 release under dark conditions (CR_D, (**A**)), and light conditions (CR_L, (**B**)) and apparent quantum efficiency of the efflux light response (AQE, (**C**)), it is, the initial slope of the CO_2 release-PPFD relationship.

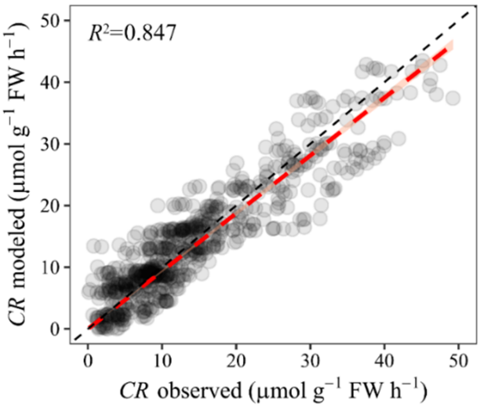

Figure 4. Linear relationship between measured CO_2 release (CR) of all Garnacha grapes and the estimated CR according to their maturity (DOY) and temperature as detailed in the models (1)–(4). All fitted parameters are detailed in Supplementary Materials Table S1.

3.2. Carbon Losses of Grape Berries Resulting from Exposure Treatments

Along the period of grape ripening of Bodegas Ribas (from 9 July to 18 August 2020), grape berries of control plants experienced averaged maximum temperatures of 44.5 ± 0.5 °C (mean ± SE) with mean radiations of light hours of 654 ± 22 μmol m^{-2} s^{-1}, and only during night temperatures decreased to minimum temperatures of 19.2 ± 0.3 °C (Supplementary Materials Figures S5 and S6). Defoliated plants resulted in a significant increase of 4.2 °C in maximum temperature of berries (Figure 5A). Daily mean temperature also increased from 29.7 ± 0.2 °C in berries of control plants to 31.4 ± 0.3 °C in defoliated plants. Those changes in temperature were accompanied by significant increases in average radiation of light hours, duplicated in defoliated plants with exposed berries (Figure 5B). However, shading defoliated plants effectively avoided the heating effect of sun exposure, decreasing berry temperatures and radiation even at lower levels than in control plants. The exposure treatment did not affect minimum temperature of berries.

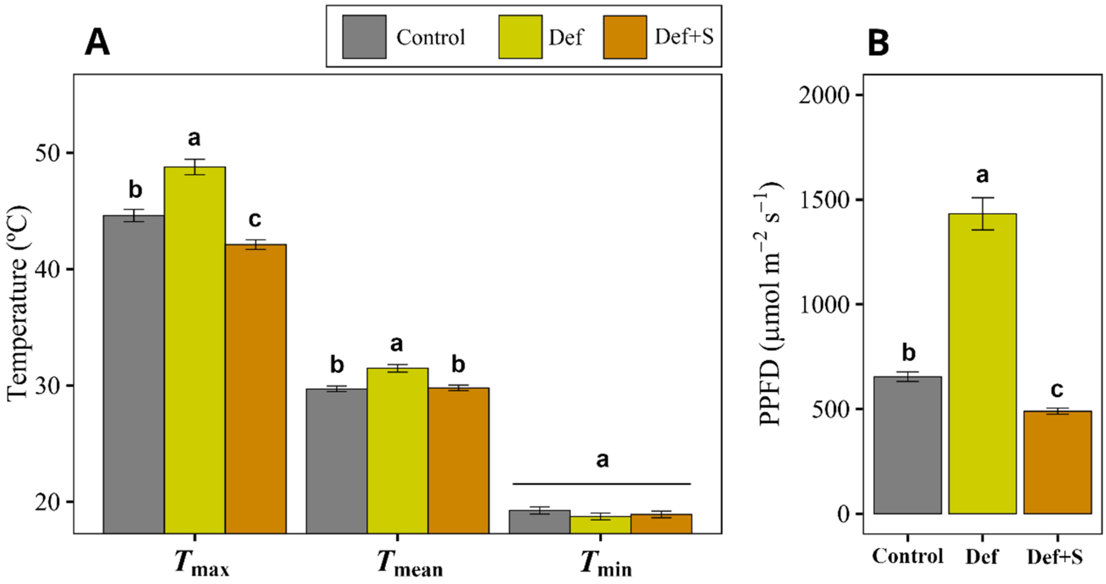

Figure 5. Differences between exposure treatments in grape temperature (**A**) and incident radiation (**B**) along the period of grape ripening of Bodegas Ribas (from 9 July to 18 August 2020, 41 days). Exposure treatments consisted in: grape berries shaded by the plant leaves (Control), exposed grape berries after defoliation (Def), and shaded grape berries after defoliation and covering using the plant's own shoots (Def + S). Bars are mean±SE of daily maximum temperature (T_{max}), daily averaged temperature (T_{mean}), daily minimum temperature (T_{min}) and daylight daily averaged radiation (expressed as mean photosynthetic photon flux radiation, $\text{PPFD}_{\text{mean}}$). Different lower case letters indicate significantly differences between exposure treatments (Tukey HSD *posthoc*, $p < 0.001$).

Those differences in temperature and radiation of berries resulted in variations of rates of CO_2 release. Berries of defoliated plants showed significantly higher daily maximum CO_2 release (32.4 ± 6.0 μmol g^{-1} FW h^{-1}, mean ± SD) than control plants (26.9 ± 4.7 μmol g^{-1} FW h^{-1}) (Figure 6A,B). Such increases in carbon losses did reverse when berries of defoliated plants were artificially shaded. Averaged minimum daily CO_2 release of berries did not differ between exposure treatments (Figure 6C,D).

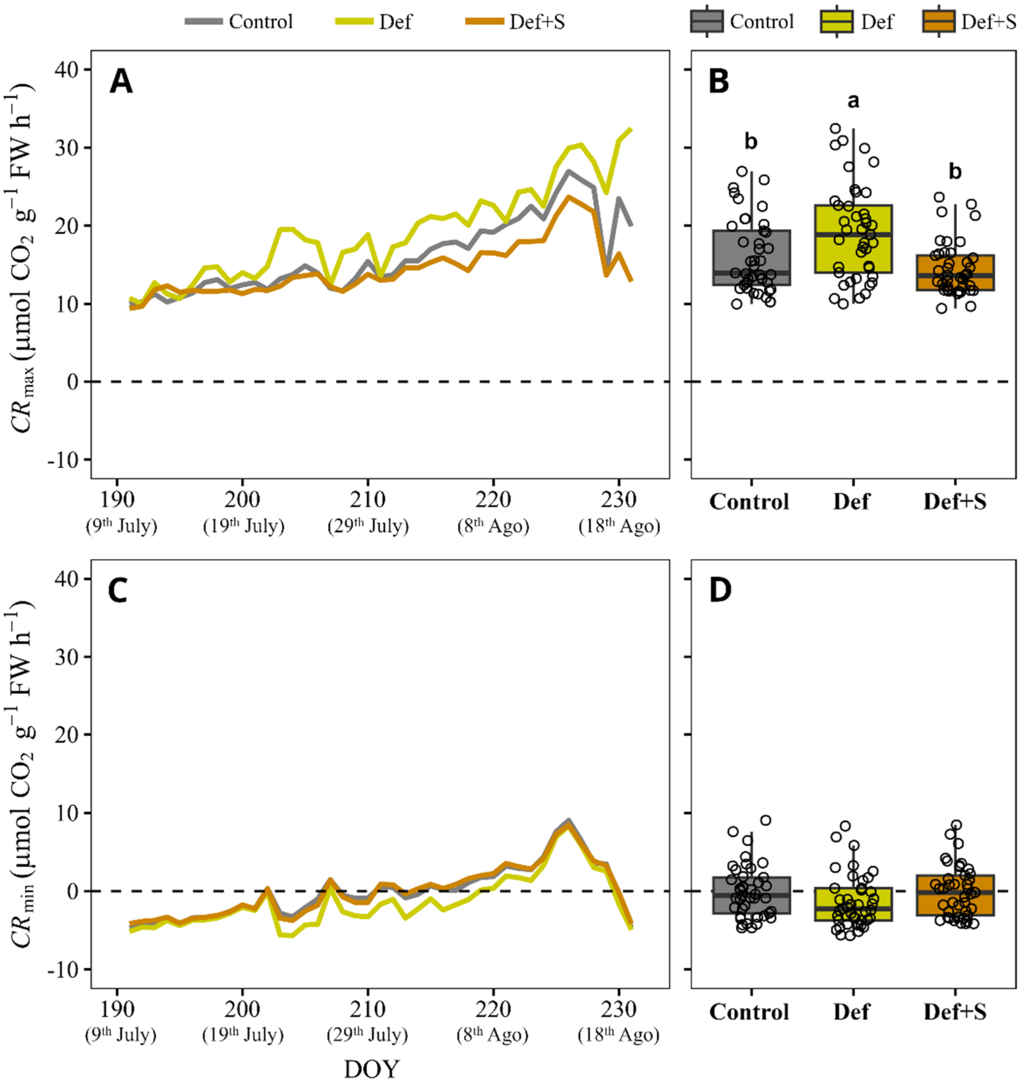

Figure 6. Variation of averaged daily maximum (**A**,**B**) and minimum (**C**,**D**) CO_2 release of grape berries of Bodegas Ribas along ripening period (from 9 July to 18 August 2020, 41 days) and exposure treatments. Exposure treatments consisted in: grape berries shaded by the plant leaves (Control), exposed grape berries after defoliation (Def), and shaded grape berries after defoliation and covering using the plant's own shoots (Def + S). Different lower case letters indicate significantly differences between exposure treatments (Tukey HSD *posthoc*, $p < 0.001$).

4. Discussion

The empirical model developed in this study provides an estimate of the net CO_2 release rate from grapes using grape temperature, radiation, and the ripening stage (DOY) as inputs. The absence of an effect from prior grape exposure on its temperature response throughout ripening suggests that our model can be applied across different grape shading treatments without concern for any imprinting effects influencing the grape's immediate response. Immediate light (as opposed to imprinting) and temperature are important factor in determining respiratory losses in grapes. Similar patterns of temperature-sensitive respiration have been reported in other fruit crops such as cherries and apples [40,41], evidencing that the interplay between respiration, temperature, and photosynthetic compensation may be a broader physiological trait among fleshy fruits. However, the extent of compensation via photosynthesis in grape berries is particularly notable given their semi-autotrophic nature during ripening [42].

The large increases in grape respiration observed during the early ripening stages (GS-Pink, Figure 1), commonly reported in the literature [13,43,44], are offset by photosynthesis activated under radiation. This reduces respiratory losses by 53–87% during these early stages, and by 21–55% during the later Red and Blue stages. It is not possible to determine the metabolic origin of this respiration due to the lack of information on the respiratory quotient (amount of CO_2 produced per O_2 consumed, identifying sugars or organic acids as the substrate for respiration and/or ethanolic fermentation, [45,46]) and, therefore, the actual impact that this compensation by photosynthesis may have on the grape (°Brix or acidity) cannot be accurately assessed either. The respiratory quotient is typically high at the beginning of the ripening phase (veraison) and then decreases throughout ripening, indicating a progressively lower percentage of CO_2 release potentially arising from the oxidation of stored malate [28]; but see also [27,47]. Therefore, it is likely that under radiation, photosynthesis contributes to a shift between respired organic acids to accumulated sugars resulting from the fixation of recaptured CO_2—An effect that gradually slows down with ripening, as evidenced by the decreasing difference in CO_2 release between darkness and light.

The greatest respiratory losses correspond to the measurements taken in darkness, reaching rates of 1.9 μmol CO_2 g^{-1} FW h^{-1} at temperatures of 25 °C—slightly lower than those reported for Tempranillo varieties [47] but apparently higher than other varieties [11,48,49]. It is precisely during the nighttime period that the temperature difference between shaded and unshaded grapes disappears (Figure 5A). Even so, there is a significant effect of defoliation on maximum carbon losses, driven by increased temperatures (Figure 6B), indicating that the increase in daytime carbon release alone is sufficient to cause those changes in total carbon losses when integrated over time. This temperature increase becomes more pronounced toward the end of the harvest period, precisely when the compensatory effects of photosynthesis on daytime CO_2 release are at their lowest (Figure 1B). An increase in temperatures due to a defoliation treatment—mainly during the day as a result of radiation—will primarily affect the later ripening stages, where sugars are likely driving the respiratory response, as suggested by Farmiani et al. [28]. Although there were no significant differences in °Brix between grapes from defoliated plants and the non-defoliated control, a clear effect of defoliation was observed in the reduction of berry weight in the vineyards of Bodegas Ribas [26], with the consequent reduction in yield. If the grapes from defoliated plants are shaded, the effect on CO_2 release reverts to control conditions, in line with berry weight and organic acid values [26].

Our model also highlights the risks posed by heatwaves and rising nighttime temperatures, which are when the greatest respiratory losses occur—losses that cannot be compensated for by any shading treatment. The increase in nighttime temperatures and its negative effects on crop yield is a growing concern [50]. Garnacha is one of the studied varieties that exhibits lower nighttime transpiration rates [51,52], suggesting poorer nocturnal leaf thermal regulation in exchange for maintaining higher water use efficiency (WUE). Elevated nighttime temperatures could not only promote higher respiratory losses in the grape but also impair the translocation of carbohydrates from the grapevine leaf, leading to their accumulation in the leaf and negatively affecting photosynthetic activity through a mechanism of end-product feedback downregulation [53]. Since our plants were not water stressed, our model does not currently incorporate vapor pressure deficit around grapes or grape water status—all factors known to influence grape metabolism and respiration [12,54] and also increasingly common under climate change scenarios.

5. Conclusions

Modeling grape berries CO_2 release in response to light, temperature, and ripening stage allowed for the integration of carbon losses over time and quantified the benefits of combining defoliation and shading techniques after berry softening. The reduction in maximum carbon loss rates due to shading, and therefore, refreshing of berries from defoliated plants was estimated at 17%, returning to the maximum loss rates observed in non-defoliated control plants (26.9 μmol g^{-1} FW h^{-1}). These results underscore the importance of adaptive canopy management under warming climates.

Supplementary Materials

The additional data and information can be downloaded at: https://media.sciltp.com/articles/others/2509231111453063/PMSC-1484-r1-Supplementary-Material-layout.pdf. Figure S1: Progression of color change during veraison of Garnacha over successive days of year. Figure S2: Setup of the GFS-3000 system for gas exchange measurements in grape berries. Figure S3: Exponential increase of CO_2 release under dark conditions in response to temperature rise. Figure S4: CO_2 release in response to photosynthetic photon flux density according to berry temperature. Figure S5: Progression of temperature of Garnacha berries along the period of grape ripening. Figure S6: Progression of photosynthetic photon flux density of Garnacha berries along the period of ripening. Table S1: Fitted parameters.

Author Contributions

E.H.-M.: conceptualization, methodology; E.H.-M. and A.V.P.-C.: data curation; A.V.P.-C.: writing—original draft preparation. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

All data supporting the findings of this study are available at Zenodo https://doi.org/ 10.5281/zenodo.17099406; Perera-Castro and Hernández-Montes (2025).

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Conflicts of Interest

The authors declare no conflict of interest.

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