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Physiological response of grapevine (cv. Shiraz) to drought, light exposure and heat stress

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CORRIGENDUM

ABSTRACT

The increased intensity and frequency of heatwaves, coupled with prolonged periods of drought, poses a significant threat to viticulture worldwide. Under these conditions, greater damage may occur when the leaf is also exposed to high radiation intensity. To better understand the impact of drought and high radiation exposure during heatwaves on grapevine physiology, we established a factorial experiment using well-watered or water-deficit Shiraz grapevines with different radiation exposure due to the row orientation. Given the East-West row orientation, the two sides faced directly north or south, receiving different radiation intensities. To monitor the impact of irrigation and radiation exposure on PSII functionality, leaf chlorophyll fluorescence was continuously monitored over a 20-day period on leaves on the north side and on the south side of the canopy of each plant, while leaf gas exchange measurements were performed on adjacent leaves. Water-deficit vines were maintained at a midday stem water potential (SWP) of –1.4 MPa, while well-watered plants had SWP of –0.8 MPa during the experiment. High radiation exposure was the dominant factor impairing PSII performance rather than heat or water stress alone. The north side leaves (N) showed lower maximum efficiency of PSII than the south side leaves (S) on hot days, especially when plants were water-stressed. S leaves had higher photochemical (Y(II)) and lower non-photochemical yields (Y(NPQ)) than N leaves, predominantly at midday. Water stress further decreased Y(II) and increased Y(NPQ) in N leaves, but not in S leaves. Leaf net assimilation, stomatal conductance, and transpiration were higher in N leaves compared to S leaves, notably pronounced in the well-watered plants than in the water-deficit ones. The coupling between stomatal conductance and assimilation showed similar pattern in water-deficit and well-watered vines in N leaves, while in S leaves, water-deficit plants showed lower changes in stomatal conductance compared to well-watered ones for the same increase in assimilation. These findings suggest that despite the positive impact of irrigation to sustain the canopy during heatwaves, additional management strategies (such as shade netting) may be required to reduce radiation exposure and to maintain leaf function during and following heatwaves.

KEYWORDS: gas exchange, chlorophyll fluorescence, heat stress, water stress, energy partitioning, heat dissipation, stomatal optimality

INTRODUCTION

The expected increase in the frequency and intensity of the heatwaves due to climate change is likely to exacerbate the negative impacts of the drought events when concurrent, and to intensify the susceptibility of the vineyard to these extreme weather events.

Climate change has affected viticulture in different ways on both large and small scales. These effects range from altering the viticultural suitability regions, to shifting the phenological stages and adversely affecting fruit quality and plant performance, especially in warm areas (Venios *et al.*, 2020). Dry conditions have already shifted the southern limits of grapevine growing areas from 34°N to 35°N, with an expected shift of the northern expansions up to 51–55°N in the future, according to Guiot *et al.* (2023). Warmer areas that are traditionally suitable for viticulture may become less favourable due to rising temperatures, while cooler regions that were once marginal for grape growing may benefit from a warming climate (Santos *et al.*, 2020). Even though these shifts may allow viticulture to expand to new production areas, they can also impose vulnerability on currently productive regions under heat and drought stress (Devot *et al.*, 2023). The concurrency of the heatwaves and drought events accelerates soil water loss due to the increased plant evaporative demand and consequently causes high economic damage (Devot *et al.*, 2023). A better understanding of the plant function during heatwaves and drought periods is fundamental to improve plant resilience and productivity in the context of climate change.

Grapevines are mainly established in arid and semi-arid areas characterized by warm and dry summers. The interaction of other environmental factors in these areas, such as excess heat and radiation, with drought exacerbates water stress and causes multiple stresses (Carvalho *et al.*, 2016). The combination between high temperatures and water deficit can negatively affect key physiological functions such as stomatal conductance, gas exchange and the photochemical efficiency of PSII (Flexas & Medrano, 2002), in addition to increased cell death rates and berry shrivelling at harvest (Bonada *et al.*, 2013).

To overcome the adverse environmental stress, photosystem II (PSII) developed protective mechanisms to mitigate the damage and to maintain high performance efficiency (Bussotti & Pollastrini, 2021). Such mechanisms involve down-regulating the photochemical processes and dissipating the excess absorbed energy non-photochemically as heat. Once photochemical processes and non-photochemical energy dissipation are insufficient, the plants become susceptible to photodamage upon further exposure to irradiation (Wang *et al.*, 2009).

Since the plant's exposure to multiple stress might result in synergistic or antagonistic responses (Carvalho *et al.*, 2016), experiments under controlled conditions are widely conducted to distinguish the effects of each single stressor from those of combined stresses. In such experiments, the plants are subjected to one and/or more stressors at different intensities to draw a clear conclusion of the plant response to the applied stress (Kalaji *et al.*, 2018). Pou *et al.* (2008) showed that grapevine exposure to water stress decreased leaf photosynthesis mainly due to stomatal and mesophyll limitations, while photoinhibition was triggered under high light conditions. This suggests that maintaining an equilibrium between light availability and water supply is critical for the PSII performance. When drought stress is combined with excess light intensity, the risk of photoinhibition increases (Bacelar *et al.*, 2007) and might result in harmful reactive oxygen species production in the photosynthetic apparatus (Mullineaux *et al.*, 2006). Ju *et al.* (2021), suggested that combined heat and water stress can intensify the damage of PSII, as indicated by the lower values of maximum PSII efficiency, compared to that when stresses were applied individually revealing more damages to the photosystem when exposing contemporarily to both stresses.

While the results of controlled environment experiments can be used to disentangle the mechanisms of plant responses to individual or combined stressors , these often fail to represent the complexity of real field conditions where multiple environmental factors interact simultaneously, although such interactions can significantly influence the extent and the duration of the plant response to the stress (Swoczyna *et al.*, 2022). This creates challenges to extrapolate the findings of these experiments to realistic field conditions and draw definitive conclusions regarding plant responses to stress. Field experiments usually allow for more accurate incorporation of the variable environmental factors providing relevant understanding of the plant response to the stressors under dynamic, heterogeneous environmental conditions. Therefore, the integration between *in situ* and controlled environment studies is crucial for developing effective management strategies under climate stress scenarios.

Plant response to the changes in their surroundings is also relatively slow and it requires time to stabilize. Conventional instantaneous measurements capture the plant's immediate reaction to a stressor at a specific pre-chosen time. Such measurements may not offer a comprehensive perspective on how plants acclimate to stressors, potentially resulting in biased or incomplete understanding of how plants adapt to stress over time. Continuous monitoring of the plant responses to stress over time under realistic field conditions provides a wide range of data which are difficult to obtain using instantaneous measurements (Porcar-Castell *et al.*, 2008). For this purpose, we conducted our study to continuously monitor the grapevines response to two irrigation treatments, well-watered and water-deficit, during hot summer days on high radiation exposed leaves on the north side of the canopy and low radiation exposed leaves on the south side of the canopy. The objective of this research was to test the validity of two hypotheses for field grown grapevines: i) water availability can mitigate the negative effects of heat stress on the functionality of PSII, and ii) photoinhibition of PSII is intensified when high light conditions coincide with low water availability and/or high temperature.

CORRIGENDUM

As climate change is likely to drive the increased simultaneous occurrence of high temperatures and water stress, this study aims to investigate the interaction between these two stressors with high radiation to provide insights into the mechanisms that allow grapevines to cope with the extreme conditions and to better understand the conditions where damage to the photosynthetic system occurs. This information can support decisions on vineyard management to improve the resilience of the production system in response to climate change.

MATERIALS AND METHODS

1. Site description

A two-factor (irrigation × side of the canopy) experiment was carried out during summer 2022–2023 in a vineyard in Barossa Valley in South Australia using own-rooted Shiraz vines (clone BVRC3). vines were planted in 1998 on red brown soil, with an east-west row orientation. Vine spacing was 2.25 m between plants and 3 m between rows. Vines were spur-pruned to 40–50 buds per vine, trained to a single-wire trellis system, and the canopy was allowed to sprawl. The experimental filed settings are further described in Bonada *et al.*, (2020). Two rows of the experimental field, separated by three guard rows, were selected and 6 plants on the first row and 4 plants on the second row were used for the trial. Half of the plants on each row were subjected to water-deficit (D) and the other half were well-watered (W), (N = 5 per each irrigation treatment). To avoid interference 3 plants were used as buffers between irrigation treatments on each row. At each irrigation level, the light exposure of the leaves was also considered and it was differentiated based on the side of the row where the measured leaves were located. The north side (N) of the canopy corresponded to high light exposure as it received direct sun for most of the day (peak values ca. 1500–2000 µmol m^{-2} s^{-1}) and the south side (S) of the canopy corresponded to low light exposure as it was shaded by the remainder of the canopy (peak values ca. 500–700 µmol m^{-2} s^{-1}).

2. Irrigation treatments

Vines were drip irrigated at a flow rate of 4.6 L h^{-1} during each irrigation event that ran for approximately 12 h. Each row had one lateral with compensated button drippers spaced at one meter intervals. During the experimental period, well-watered vines were irrigated on five occasions and received 473 L/vine of irrigation in total to maintain stem water potential values at –0.8 to –1 MPa in comparison with their deficit counterparts that were irrigated on two occasions and received 164 L/vine in total to maintain stem water potential of –1.3 to –1.5 MPa; there was also 6 mm of rainfall during the monitored period (Figure 1).

To monitor the water status of the vines during the experimental period, mid-day stem water potential was measured fortnightly on one leaf per plant (Table 1) using a Scholander pressure chamber (PMS Instruments, Model 600, Albany, OR, USA) following the method described by Hsiao (1990).

TABLE 1. Measured stem water potential values during the experiment.

DOY	W	D
51	–0.96 ± 0.04	–1.38 ± 0.02
60	–0.94 ± 0.03	–1.3 ± 0.03

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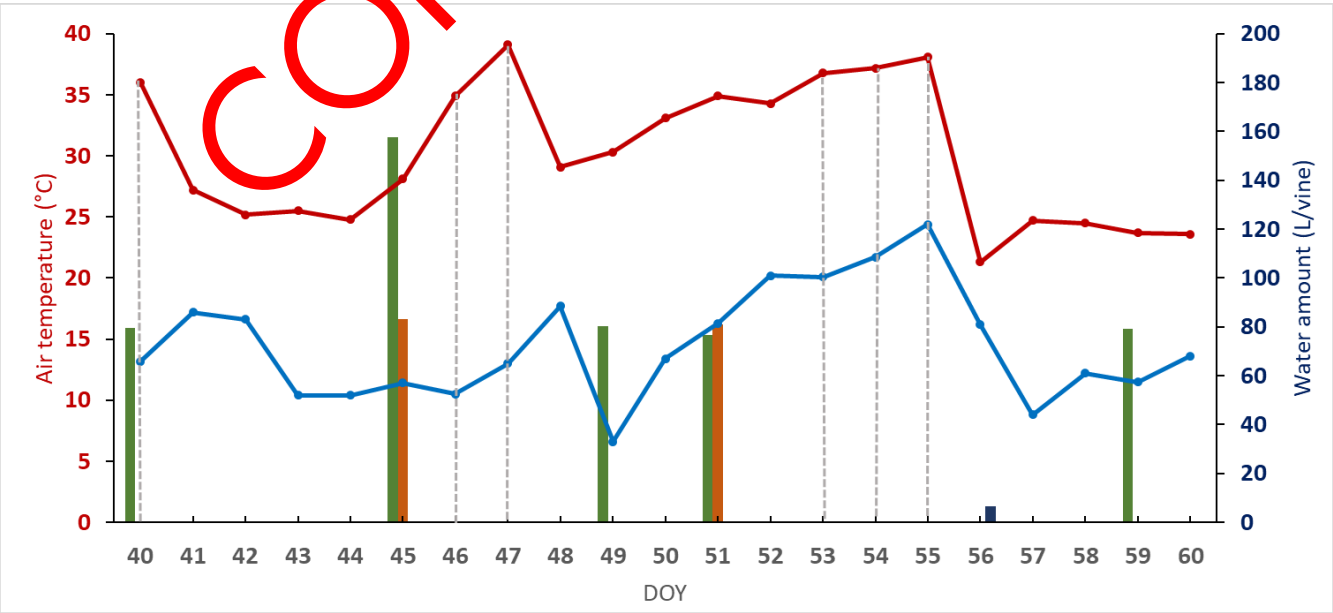


FIGURE 1. Maximum and minimum daily air temperature (°C, red and blue lines, respectively), precipitation (L, blue bar) and irrigation amounts (L/vine) for the well-watered (green bars) and water-deficit (orange bars) treatments, dotted grey lines indicate DOYs with Tmax > 35 °C.

3. Meteorological data

Weather observations including air temperature and precipitation were collected by the Australian Bureau of Meteorology station – Nuriootpa PIRSA at 60 minutes intervals. This station is located approximately 750 m from the experimental site. A heatwave occurrence was considered whenever Tmax exceeded 35 °C for 3 consecutive days (according to The South Australian Regional Office of the Bureau of Meteorology).

4. Chlorophyll fluorescence and gas exchange measurements

On each side of the selected plants, three fully expanded, consecutive leaves, grown on a fruit bearing shoot (between the 8th and 10th nodes) were used for chlorophyll fluorescence and gas exchange measurements. Leaves were assigned the following treatments abbreviations: (NW) well-watered on the north side, (ND) water-deficit on the north side, (SW) well-watered on the south side, and (SD) water-deficit on the south side.

Continuous readings of chlorophyll fluorescence were recorded using 12 heads of two MONI-PAM units and 8 heads of a MICRO-PAM unit (Heinz Walz, Eichenring, Effeltrich, Germany) starting from DOY 40 until DOY 60 on one leaf on each side of every plant. Day and night fluorescence measurements were recorded at 30 and 60 min intervals, respectively. Day measurements started when PAR values measured by the heads were higher than 2 µmol m^{-2} s^{-1}. The measuring and actinic light intensities were set at 190 µmol m^{-2} s^{-1}, and saturating pulse intensity was 6000 µmol m^{-2} s^{-1}. In order to minimize light exposure, the measuring light was turned off during night measurements.

Complimentary measurements of gas exchange were performed on DOYs 44, 48, 51, 55, and 58 in the morning between 10–12 am (Australian Central Daylight Time) on two leaves per each side of every plant adjacent to the leaf that was used for chlorophyll fluorescence measurements. Gas exchange measurements were recorded using a portable photosynthesis system CIRAS-3 version 2.00 (PP Systems, Amesbury, MA, USA) connected to PLC3 universal leaf cuvette with a 70 × 25 mm window. Conditions inside the cuvette were as follows: CO_2 reference at 450 µmol mol^{-1}, H_2O reference at 80 % relative humidity, cuvette flow at 300 cc min^{-1}, analyser flow at 100 cc min^{-1}, light source LED at 2000 µmol $m^{-2}s^{-1}$ intensity, and cuvette temperature was set to match the ambient temperature.

Coupling between stomatal conductance and assimilation (normalized to VPD and CO_2) was performed using the unified model according to Medlyn *et al.* (2011).

5. Statistical analysis

The effect of the irrigation treatment and the side of the canopy over the experimental period (DOY) was tested using repeated measurements ANOVA analysis with irrigation, side, and DOY as fixed factors. Differences between the slopes of the linear models used for the coupling between stomatal conductance and assimilation were tested using a pairwise Tukey test. As there were no significant row effects on the measured variables, these analyses were not reported here. Statistical analyses were performed with R software (RStudio v 4.0.5, R v 4.0.5) and the effect of the treatment was considered significant at *p-value* < 0.05. Data were averaged over three hours of measurements between 2:00–5:00 am for Fv/Fm, and between 8:00–11:00 (morning), 11:00–14:00 (midday), and 14:00–18:00 (afternoon) for Y(II) and Y(NPQ) (Australian Central Daylight Time). Data represent mean ± SE. Chlorophyl fluorescence parameters were calculated according to the standard formulas described by Genty *et al.* (1989).

RESULTS

1. Meteorological conditions

Maximum air temperatures (Tmax) higher than 35 °C were recorded on 6 days during the experimental period, namely: DOYs 40, 46, and 47, which will be referred to as "hot days", and on the consecutive DOYs 53, 54, and 55, which will be referred to as a "heatwave". Following the hot days and the heatwave, there was a sharp drop in Tmax by 8 °C and 10 °C on DOYs 49 and 48, respectively, and by 16 °C after the heatwave, which coincided with a rainfall event of 6 mm (Figure 1).

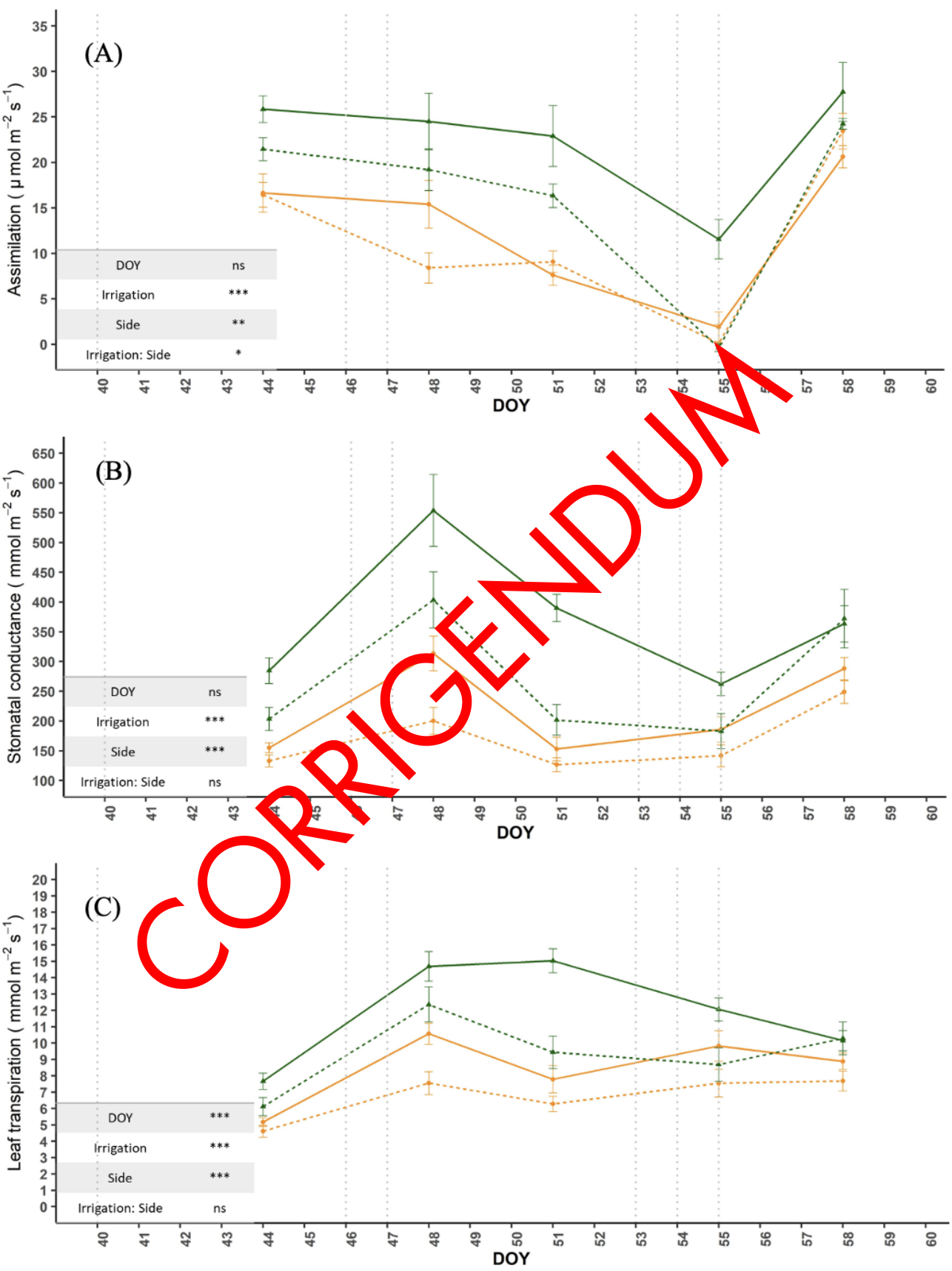
2. Leaf gas exchange

The irrigation treatment significantly affected leaf assimilation regardless of Tmax (Figure 2A). The well-watered vines showed a higher assimilation rate compared to water-deficit ones. The side of the canopy also had a significant effect on leaf assimilation, although it was more pronounced in well-watered plants (NW > SW) than in water-deficit plants.

Stomatal conductance and leaf transpiration were affected by both irrigation treatment and side of the canopy (Figure 2B and 2C, respectively). In general, well-watered plants had higher values of stomatal conductance and leaf transpiration than water-deficit ones, and the north side leaves showed higher values than south side ones, especially in well-watered plants.

The coupling between stomatal conductance and leaf assimilation (normalized to VPD and CO_2) revealed similar patterns between well-watered and water-deficit vines in the north side leaves (Figure 3, N). Although the north side leaves in the well-watered plants showed higher stomatal conductance than the water-deficit ones for the same rate of normalized assimilation, the change in stomatal conductance per unit change in normalized assimilation was not significantly different between the two irrigation treatments (no significant differences between the slopes). South side leaves, instead, showed significant differences between the slopes of the two irrigation treatments (Figure 3, S). South side leaves in the water-deficit plants showed significantly lower changes in stomatal conductance compared to well-watered ones for the same increase in the normalized assimilation (*p-value* = 0.03).

CORRIGENDUM



CORRIGENDUM

FIGURE 2. Leaf assimilation (A), stomatal conductance (B), and leaf transpiration (C) in well-watered vines (green lines) and water-deficit vines (orange lines) on the north side (continuous lines) and on the south side (dashed lines) of the canopy. Asterisks in the tables represent significant effects of the treatment and ns indicate no significant effect across all sample dates from the repeated measurements ANOVA. Dotted grey lines indicate days with Tmax > 35 °C.

3. Chlorophyll fluorescence measurements

On the hot days, the maximum efficiency of PSII (Fv/Fm) was significantly affected by both the irrigation and the side of the canopy (Figure 4). North side leaves showed lower Fv/Fm values than the south side leaves. Water stress on the hot days further decreased Fv/Fm in the ND compared to NW ones. During the heatwave, the irrigation treatment significantly affected Fv/Fm in the north side leaves. Fv/Fm was the lowest in the ND leaves, while other treatments showed similar Fv/Fm values. Apart from the ND leaves, the sudden drop in Tmax following the hot days caused a decline in Fv/Fm in all the vines, followed by a gradual increase when Tmax increased again. After the heatwave, Fv/Fm in all the vines dropped sharply and remained low for the last 5 days of the experiment during which Tmax was between 21 and 24 °C.

The effective yield of PSII (Y(II)) was more influenced by the side of the canopy than by the irrigation treatment (Figure 5). Moreover, leaves showed a different response to the irrigation treatment depending on the side of the canopy where they were located. North side leaves showed lower Y(II) values than south side ones. This effect was the most evident at midday compared to morning and afternoon. Water stress further decreased Y(II) in the north side leaves compared to the equivalent leaves on well-watered vines, especially when Tmax was higher than 30 °C. Following the hot days, Y(II) did not show any recovery from heat stress in any of the treatments. After the heatwave, north side leaves showed a sharp increase followed by a sharp decrease in Y(II) in the morning and at midday in both irrigation treatments.

The yield of regulated heat dissipation (Y(NPQ)) was mostly affected by the side of the canopy rather than the irrigation treatment (Figure 6). Generally, north side leaves showed higher Y(NPQ) than the south side leaves, while the effect of irrigation was observed on the morning as ND leaves had higher values of Y(NPQ) when Tmax was higher than 30 °C. The temperature drops after the hot day 47 caused a decrease followed by a sudden increase in Y(NPQ) in ND leaves in the morning. While the temperature drops after the heatwave triggered a sharp decrease followed by a sharp increase in Y(NPQ) observed on the morning and at midday in the sun-exposed leaves for the three days following the rain event.

DISCUSSION

The findings of this study confirm our initial hypotheses regarding the beneficial impact of irrigation in mitigating the adverse effects of heat stress on the efficiency and the functionality of PSII. The results also confirm that greater exposure to high radiation further increases the vulnerability of PSII caused by heat and water stress.

This research complements the results from controlled environment studies by considering field conditions where other factors, such as the heterogeneous exposure of leaves to sunlight, interact with the different sources of stresses. It provides insights into the adaptive mechanisms employed by grapevines to withstand stressful conditions and enhances our comprehension of the circumstances that lead to increased vulnerability in the photosystem, such as temperatures higher than 35 °C accompanied by midday stem water potential around –1.4 MPa and light exposure around 1500–2000 µmol m^{-2} s^{-1}, experienced by the plants in our experiment. The knowledge of these critical values can assist in making strategic decisions to support vineyard management – such as optimizing irrigation scheduling, implementing canopy management and shading techniques (*e.g.*, kaolin sprays or shade nets), and re-considering row orientation (Garcia-Tejera *et al.*, 2023) and to make the production system more resilient in the face of an increasing occurrence of heatwaves and water scarcity.

Grapevine leaves showed resistance in terms of maximum efficiency of PSII to temperatures higher than 35 °C and maintained high photochemical performance when soil water was available and/or radiation was lower than 1500 µmol m^{-2} s^{-1}. When temperatures exceeding 35 °C were accompanied by water stress and/or high light conditions (< –1.4 MPa midday stem water potential and/or < 1500 µmol m^{-2} s^{-1} radiation), increased sensitivity of PSII was observed resulting in a negative impact on leaf photochemical performance. This highlights the importance of providing increased soil moisture or reduced direct sunlight exposure as part of vineyard management strategies during heatwaves.

Despite the observed changes in PSII efficiency (Fv/Fm), gas exchange measurements (Figure 2) did not reveal consistent detrimental effects on photosynthetic rates under stress conditions. This suggests that the leaves were able to maintain sufficient photochemical functionality under the conditions of our experiment, and that the applied stress did not reach the physiological threshold of damage (Chaves *et al.*, 2009; Flexas & Medrano, 2002).

Irrigation treatment had the primary impact on the leaf gas exchange parameters (Figure 2). Regardless of the temperature, well-watered plants maintained higher stomatal conductance allowing more efficient evaporative cooling and higher leaf net uptake of CO_2 compared to water-deficit plants (Figure 2). This aligns with the findings of other studies that reported higher stomatal conductance and lower leaf temperature in grapevines leaves subjected to heat stress when well irrigated due to the efficient stomatal regulation and cooling mechanisms (Tan *et al.*, 2023). Kriedemann (1968) also observed that sultana grapevine leaves exhibited no significant decrease in their photosynthesis rate when exposed to temperatures between 35–40 °C, provided the plants were adequately hydrated. Although the positive effect of irrigation on leaf gas exchange parameters was observed on both sides of the canopy, the higher exposure to sunlight on the north side resulted in higher stomatal conductance, leaf transpiration and consequently net assimilation compared to the leaves on the south side of the canopy (Figure 2). This suggests that the combination between water availability and high radiation promoted the CO_2 assimilation in north side leaves compared to the south side leaves.

CORRIGENDUM

Leaves of water-deficit plants showed lower levels of transpiration due to stomatal closure which reduced leaf net assimilation. In contrast to the well-watered plants, light exposure in water-deficit plants had a relatively small impact on gas exchange parameters (Figure 2), suggesting that water status, rather than light exposure, was the predominant factor influencing leaf net assimilation. These findings align with previous studies that reported limited variations in stomatal conductance in water-stressed grapevines under different light intensities (Chaves *et al.*, 2010; Flexas *et al.*, 2009).

The coupling between stomatal conductance and leaf assimilation normalized to VPD and CO_2 showed quite similar behaviour in both irrigation treatments in the north side leaves indicating similar stomatal control of the trade-off between carbon assimilation and transpiration under high light conditions (Figure 3). Well-watered vines

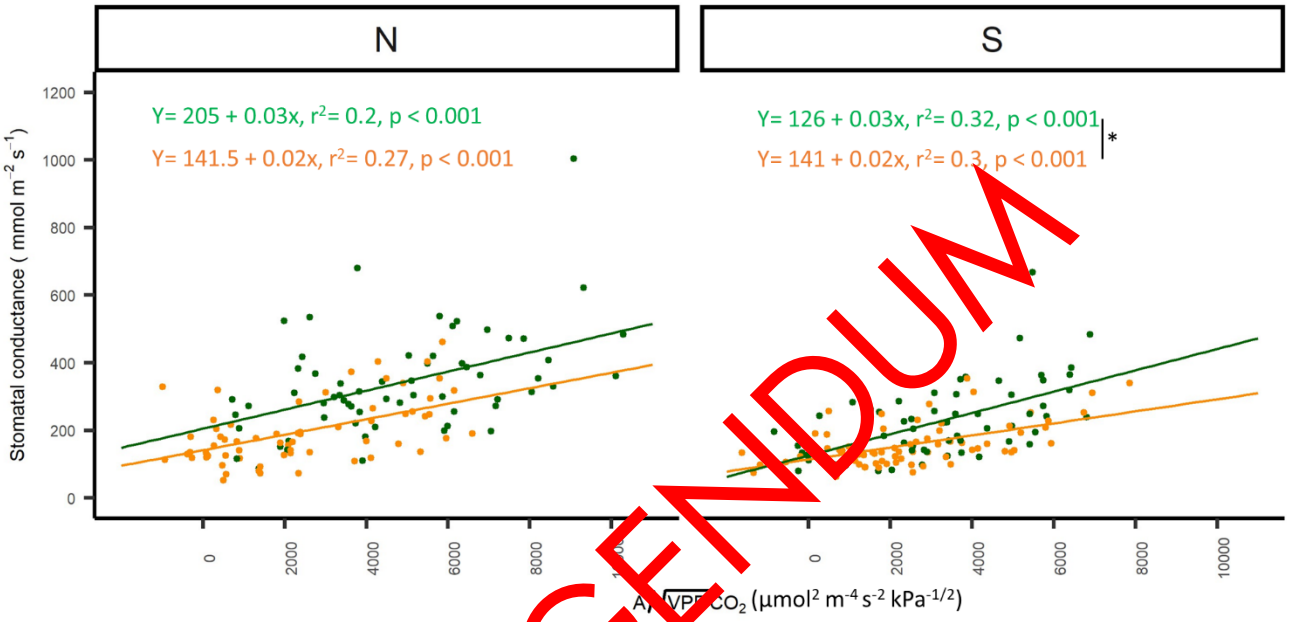


FIGURE 3. Coupling between stomatal conductance and leaf assimilation normalized for air VPD and CO2 in well-watered vines (green dots) and water-deficit vines (orange dots) on the north side (N) and on the south side (S) of the canopy. Asterisk represents significant differences between the slopes of well-watered and water-deficit vines on the south side of the canopy, *n* = 62.

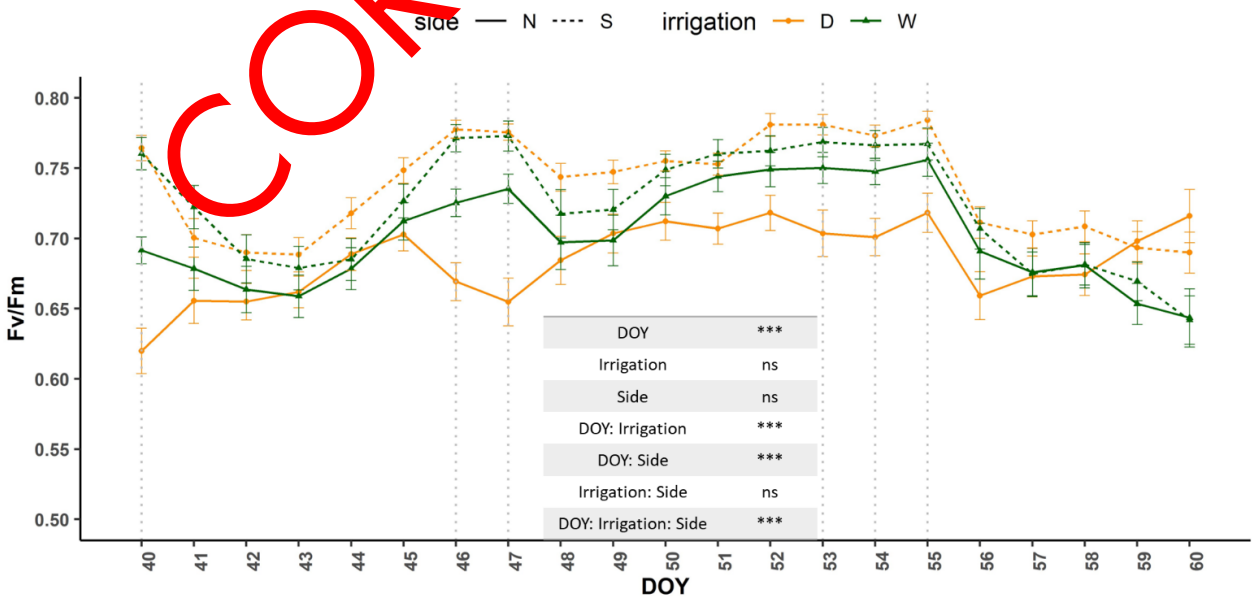


FIGURE 4. Maximum efficiency of PSII (Fv/Fm) in well-watered vines (green lines) and water-deficit vines (orange lines) on the north side (continuous lines) and on the south side (dashed lines) of the canopy. Asterisks in the table represent significant effects of the treatment and ns indicates no significant effect across all sample dates from the repeated measurements ANOVA. Dotted grey lines indicate days with Tmax > 35 °C.

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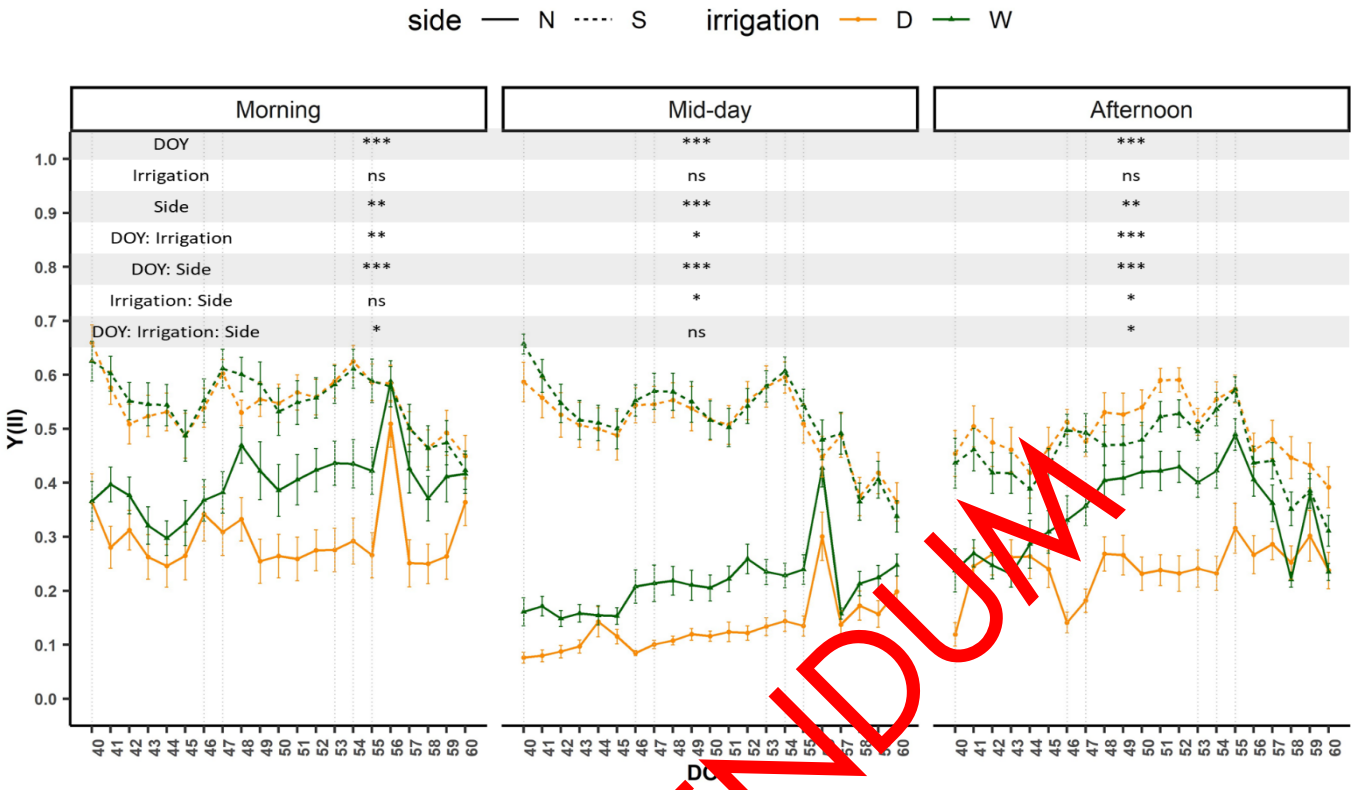


FIGURE 5. Effective photochemical yield of PSII (Y(II)) in well-watered vines (green lines) and water-deficit vines (orange lines) on the north side (continuous lines) and on the south side (dashed lines) of the canopy. Asterisks in the tables represent significant effects of the treatment and ns indicates no significant effect across all sample dates from the repeated measurements ANOVA. Dotted grey lines indicate days with Tmax > 35 °C.

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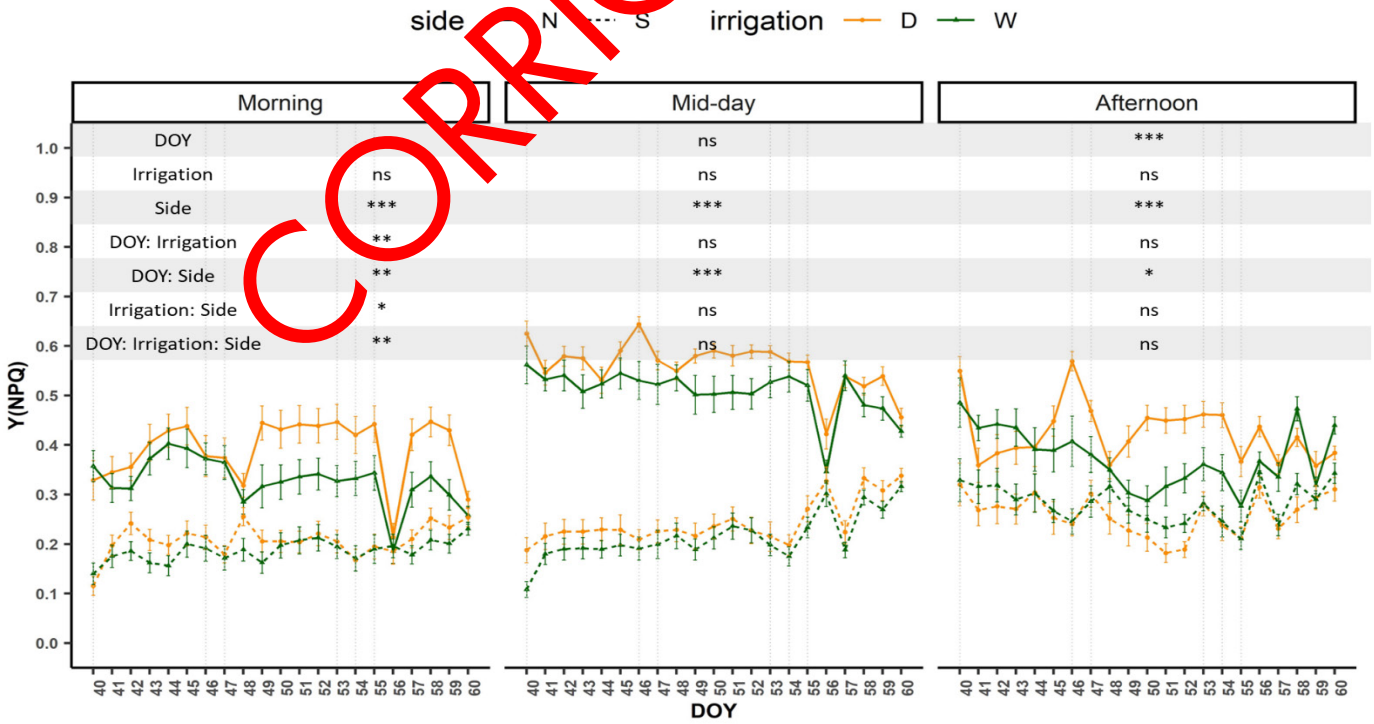


FIGURE 6. Regulated energy partitioning as heat in PSII (Y(NPQ)) in well-watered vines (green lines) and water-deficit vines (orange lines) on the north side (continuous lines) and on the south side (dashed lines) of the canopy. Asterisks in the table represent significant effects of the treatment and ns indicates no significant effect across all sample dates from the repeated measurements ANOVA. Dotted grey lines indicate days with Tmax > 35 °C.

showed ca. 45 % higher intercept than water-deficit vines suggesting that the well-watered vines did not follow a water conservative behaviour in the presence of high light and soil water availability, while water-deficit vines were more water conservative, leading to a higher intrinsic water use efficiency. Similar responses have been observed in grapevines by Flexas and Medrano (2002), who reported increased water use efficiency under drought conditions through tighter stomatal regulation.

Under lower light conditions on the south side leaves, the significantly lower slope in water-deficit vines compared to that in well-watered vines indicates an increased constraint of stomatal aperture due to hydraulic limitations resulting in smaller increase in gs for a given rise is A. In contrast, the hydraulic relieve in well-watered vines on the south side contributed to more open stomata in response to increased assimilation demand producing steeper slope (Medlyn *et al.*, 2011). Furthermore, the differences in leaf microclimate conditions under high radiation and low radiation, such as lower leaf temperature, may further reduce evaporative demand and accentuate the contrast in stomatal strategy between irrigation regimes. This hydraulic regulation complements previous findings of heat-induced downregulation of Photosystem I redox state in grapevine leaves (Qiu *et al.*, 2025), highlighting that both drought and heat stress impose distinct but convergent limitations on photosynthesis with drought restricting CO_2 diffusion through stomatal closure, and heat constraining electron transport capacity.

Continuous chlorophyll fluorescence measurements allowed us to track the changes in the leaf response to the environmental condition during different times of the day as well as under naturally leaf dark adaptation, and the leaf response to the changed environmental conditions due to the heat stress. Chlorophyll fluorescence measurements showed that direct sunlight exposure on the north side leaves negatively affected leaf performance in terms of the efficiency of photosystem II and redirected the energy allocation between photochemical and non-photochemical pathways, especially when high temperature and water stress were concurrently present (Figures 4, 5, and 6). Temperatures higher than 35 °C increased the sensitivity of PSII when leaves were directly exposed to sunlight in the north side leaves, whereas the lower sunlight exposure in the south side leaves helped the leaves to maintain higher PSII efficiency (Figure 4). This suggests that the increased energy absorption exacerbates the effect of heat stress on north side leaves potentially resulting in damage in the thylakoid membranes of PSII. These results are consistent with the findings of Peña-Olmos and Casierra-Posada (2013) who observed that exposure to elevated direct radiation in defoliated Chardonnay vines resulted in higher leaf temperature and consequent damage to the PSII indicated by low values of Fv/Fm. These results are also in line with Greer (2019) who reported high thermal sensitivity of PSII when temperature exceeded 35 °C in Shiraz grapevines under field conditions.

In the present study, the coincidence of high temperature along with water stress led to a further decrease in Fv/Fm values in the north side leaves. This response was not observed in the south side water-deficit leaves (Figure 4) suggesting that the high radiation intensified the impact of the combined heat and water-stress on PSII and resulted in lack of sinks of the excess absorbed energy which might potentially cause a production of reactive oxygen species (ROS) (Savitch *et al.*, 2009). When PSII is photodamaged under severe stress conditions, plants activate alternative electron dissipation mechanisms, such as Mehler reaction, to dissipate the excess energy resulting in overproduction of the ROS and consequently damage in PSII reaction centers (Savitch *et al.*, 2009). Carvalho *et al.* (2015) reported that grapevine exposure to water stress together with high light and/or high temperature results in reduction in the antioxidants, such as L-Ascorbic acid and Glutathione, that are necessary to eliminate ROS through the ascorbate-glutathione cycle indicating difficulty in maintaining the cellular redox state and consequently causing photoinhibition of PSII. These findings imply that photoinhibition can be amplified when there is an imbalance between light and water availability for photosynthetic performance (Bacelar *et al.*, 2007).

Absorbed energy partitioning within PSII between photochemical and non-photochemical quenching was mainly driven by the side of the canopy where leaves were located regardless of temperature and irrigation treatments (Figures 5 and 6). This effect was most pronounced at midday during the peak of the radiation intensity. When leaves were more exposed to sunlight on the north side of the canopy, most of the absorbed light was allocated to non-photochemical quenching, with less light being utilized for photochemistry. This energy rechannelling towards non-photochemistry serves to dissipate excess energy harmlessly as heat; and consequently helping to safeguard PSII from photoinhibition caused by the excessive absorption of excitation energy (Wang *et al.*, 2009). In fact, under our field conditions, these regulatory responses occurred without an immediate decline in carbon assimilation indicating functional constraints and energy reallocation within PSII, rather than irreversible damage or oxidative stress.

Under low light exposure, high temperature and water-stress had no effects on the photochemical (Y(II)) and non-photochemical yield (Y(NPQ)) in the south side leaves (Figures 5 and 6). Nevertheless, when the leaves were exposed to high levels of direct sunlight on the north side of the canopy (above 1500 µmol m^{-2} s^{-1}), water stress further decreased Y(II) and increased Y(NPQ) in the leaves of water-deficit plants, especially at midday, regardless the temperature (Figures 5 and 6). This energy relocation under water-stress was also reported by Prieto *et al.* (2010) who observed more energy allocation towards protective pathways in grapevines to avoid photoinhibition at the expense of photochemistry, particularly under high light exposure.

Chaves *et al.* (2009) also reported that when water-stress impairs CO_2 fixation, the consumption of energy by Calvin cycle occurs at a slower rate than its production. This results

CORRIGENDUM

in an excess of energy available for the use in photochemical processes and necessitates protective mechanisms to dissipate the energy beyond what is used in photosynthesis (Chaves *et al.*, 2009). These protective mechanisms compete with photochemical processes for the absorbed light and consequently, when the efficiency of non-photochemical processes increases, there is a corresponding decrease in the quantum yield of PSII, and vice versa (Genty *et al.*, 1989).

CONCLUSIONS

This experiment reinforces the critical role of water availability in maintaining higher photosynthetic performance when plants are exposed to high temperatures. In addition, our results confirm that leaf exposure to high radiation together with heat stress intensifies the sensitivity of the photosynthetic system, especially when plants are experiencing water stress.

In the context of climate change and increasing water scarcity, our findings suggest that reducing excessive net solar radiation—through the use of kaolin-based 'sunscreens' or shading nets—could represent practical strategies to help grapevines cope with heat stress while maintaining high leaf physiological performance during hot summer days.

REFERENCES

Bacelar, E. A., Santos, D. L., Moutinho-Pereira, J. M., Lopes, J. I., Gonçalves, B. C., Ferreira, T. C., & Correia, C. M. (2007). Physiological behaviour, oxidative damage and antioxidative protection of olive trees grown under different irrigation regimes. *Plant and Soil, 292*(1-2), 1-12. https://doi.org/10.1007/s11104-006-9088-1

Bonada, M., Edwards, E. J., McCarthy, M. G., Sepúlveda, G. C., & Petrie, P. R. (2020). Impact of low winter chilling during dormancy on vine productivity and development. *Australian Journal of Grape and Wine Research, 26*(4), 325-342. https://doi.org/10.1111/ajgw.12445

Bonada, M., Sadras, V., Moran, M., & Fuentes, S. (2013). Elevated temperature and water stress accelerate mesocarp cell death and shrivelling, and decouple sensory traits in shiraz berries. *Irrigation Science, 31*, 1317-1331. https://doi.org/10.1007/s00271-013-0407-z

Bussotti, F., & Pollastrini, M. (2021). Revisiting the concept of stress in forest trees at the time of global change and issues for stress monitoring. *Plant Stress, 2*, 100013. https://doi.org/10.1016/j.stress.2021.100013

Carvalho, L. C., Coito, J. L., Colaço, S., Sangiogo, M., & Amâncio, S. (2015). Heat stress in grapevine: The pros and cons of acclimation. *Plant, Cell & Environment, 38*(4), 777-789. https://doi.org/10.1111/pce.12445

Carvalho, L. C., Coito, J. L., Gonçalves, E. F., Chaves, M. M., & Amancio, S. (2016). Differential physiological response of the grapevine varieties touriga nacional and trincadeira to combined heat, drought and light stresses. *Plant Biology, 18*, 101-111. https://doi.org/10.1111/plb.12410

Chaves, M. M., Flexas, J., & Pinheiro, C. (2009). Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell. *Annals of Botany, 103*(4), 551-560. https://doi.org/10.1093/aob/mcn125

Chaves, M. M., Zarrouk, O., Francisco, R., Costa, J. M., Santos, T., Regalado, A. P., Rodrigues, M. L., & Lopes, C. M. (2010). Grapevine under deficit irrigation: Hints from physiological and molecular data. *Annals of Botany, 105*(5), 661–676. https://doi.org/10.1093/aob/mcq030

Devot, A., Royer, L., Caron Giauffret, E., Ayral, V., Deryn, D., Arvis, B., & Giraud, L. (2023). *The impact of extreme climate events on agricultural production in the EU policy department for structural and cohesion policies directorate-general for internal policies PE 733.115 -april 2023 EN STUDY*. Policy Department for Structural and Cohesion Policies.

Flexas, J., & Medrano, H. (2002). Drought-inhibition of photosynthesis in C3 plants: Stomatal and non-stomatal limitations revisited. *Annals of Botany, 89*, 183–189. https://doi.org/10.1093/aob/mcf027

Garcia-Tejera, O., Bonada, M., Petrie, P. R., Nieto, H., Bellvert, J., & Sadras, V. O. (2023). Viticulture adaptation to global warming: Modelling gas exchange, water status and leaf temperature to probe for practices manipulating water supply, canopy reflectance and radiation load. *Agricultural and Forest Meteorology, 331*, 109351. https://doi.org/10.1016/j.agrformet.2023.109351

Genty, B., Briantais, J., & Baker, N. R. (1989). The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica Et Biophysica Acta (BBA)-General Subjects, 990*(1), 87-92. https://doi.org/10.1016/S0304-4165(89)80016-9

Greer, D. H. (2019). Short-term temperature responses of photosynthesis and PSII photochemistry in field-grown Shiraz vines with and without fruit. *Australian Journal of Grape and Wine Research, 25*(4), 412–421.

Guiot, J., Bernigaud, N., Bondeau, A., Bouby, L., & Cramer, W. (2023). *Viticulture extension in response to global climate change drivers – lessons from the past and future projections*. Copernicus GmbH. https://doi.org/10.5194/egusphere-2022-1451

Hsiao, T. C. (1990). Measurements of plant water status. *Agronomy,* (30), 243-279.

Ju, Y., Min, Z., Zhang, Y., Zhang, K., Liu, M., & Fang, Y. (2021). Transcriptome profiling provide new insights into the molecular mechanism of grapevine response to heat, drought, and combined stress. *Scientia Horticulturae, 286.* https://doi.org/10.1016/j.scienta.2021.110076

Kalaji, H. M., Račková, L., Paganová, V., Swoczyna, T., Rusinowski, S., & Sitko, K. (2018). Can chlorophyll-a fluorescence parameters be used as bio-indicators to distinguish between drought and salinity stress in tilia cordata mill? *Environmental and Experimental Botany, 152*, 149-157. https://doi.org/10.1016/j.envexpbot.2017.11.001

Kriedemann, P. E. (1968). Photosynthesis in vine leaves as a function of light intensity, temperature, and leaf age. *VITIS-Journal of Grapevine Research, 7*(3), 213.

Medlyn, B. E., Duursma, R. A., Eamus, D., Ellsworth, D. S., Prentice, I. C., Barton, C. V., Crous, K. Y., De Angelis, P., Freeman, M., & Wingate, L. (2011). Reconciling the optimal and empirical approaches to modelling stomatal conductance. *Global Change Biology, 17*(6), 2134-2144. https://doi.org/10.1111/j.1365-2486.2010.02375.x

Mullineaux, P. M., Karpinski, S., & Baker, N. R. (2006). Spatial dependence for hydrogen peroxide-directed signaling in light-stressed plants. *Plant Physiology, 141*(2), 346-350. https://doi.org/10.1104/pp.106.078162

Peña-Olmos, J. E., & Casierra-Posada, F. (2013). Chlorophyll fluorescence in partially defoliated grape plants (vitis vinifera L. cv. chardonnay). *Revista Facultad Nacional De Agronomía Medellín, 66*(1), 6881-6889.

CORRIGENDUM

Porcar-Castell, A., Pfündel, E., Korhonen, J. F., & Juurola, E. (2008). A new monitoring PAM fluorometer (MONI-PAM) to study the short-and long-term acclimation of photosystem II in field conditions. *Photosynthesis Research, 96*, 173-179. https://doi.org/10.1007/s11120-008-9292-3

Pou, A., Medrano, H., Tomás, M., Martorell, S., Ribas-Carbó, M., & Flexas, J. (2008). Anisohydric behaviour in grapevines under water stress: Changes in photosynthesis and stomatal conductance are associated with differential stomatal and mesophyll limitations. Plant and Cell Physiology, 49(9), 1426–1436.

Prieto, J. A., Louarn, G., Pérez Peña, J., Ojeda, H., & Lebon, E. (2010). FABA, a dynamic model of carbon assimilation and partitioning to simulate grapevine response to elevated CO_2 and water stress. Agricultural and Forest Meteorology, 150(3), 349–369.

Qiu, Q., Sun, Y., Guo, D., Wang, L., Pagay, V., & Wang, S. (2025). Heat stress downregulates photosystem I redox state on leaf photosynthesis in grapevine. *Agronomy, 15*(4), Article 948. https://doi.org/10.3390/agronomy15040948

Santos, J. A., Fraga, H., Malheiro, A. C., Moutinho-Pereira, J., Dinis, L., Correia, C., Moriondo, M., Leolini, L., Dibari, C., & Costafreda-Aumedes, S. (2020). A review of the potential climate change impacts and adaptation options for european viticulture. *Applied Sciences, 10*(9), 3092. https://doi.org/10.3390/app10093092

Savitch, L. V., Ivanov, A. G., Gudynaite-Savitch, L., Huner, N. P. A., & Simmonds, J. (2009). Effects of low temperature stress on excitation energy partitioning and photoprotection in zea mays. *Functional Plant Biology, 36*(1), 37-49. https://doi.org/10.1071/FP08093

Swoczyna, T., Kalaji, H. M., Bussotti, F., Mojski, J., & Pollastrini, M. (2022). *Environmental stress - what can we learn from chlorophyll a fluorescence analysis in woody plants? A review*. Frontiers Media SA. https://doi.org/10.3389/fpls.2022.1048582

Tan, J. W., Shinde, H., Tesfamicael, K., Hu, Y., Fruzangohar, M., Tricker, P., Baumann, U., Edwards, E. J., & Rodríguez López, C. M. (2023). Global transcriptome and gene co-expression network analyses reveal regulatory and non-additive effects of drought and heat stress in grapevine. *Frontiers in Plant Science, 14*, 1096225. https://doi.org/10.3389/fpls.2023.1096225

Venios, X., Korkas, E., Nisiotou, A., & Banilas, G. (2020). Grapevine responses to heat stress and global warming. *Plants (Basel), 9*(12), 1754. https://doi.org/10.3390/plants9121754

Wang, L., Loescher, W., Duan, W., Li, W., Yang, S., & Li, S. (2009). Heat acclimation induced acquired heat tolerance and cross adaptation in different grape cultivars: Relationships to photosynthetic energy partitioning. *Functional Plant Biology, 36*(6), 516-526. https://doi.org/10.1071/FP09008

CORRIGENDUM