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Impact of leaf removal on recovery of young grapevines under heatwave conditions: A study in an ecotron environment

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ABSTRACT

One of the primary challenges of climate change faced by viticulture is the rising frequency of extreme weather events, including heatwaves. The aim of this study was to test apical leaf removal as a mitigation strategy during heatwaves based on the hypothesis that reducing total leaf area translates to lower transpirational water losses, thereby improving the water status of young grapevine plants under multiple stress conditions. Two-year-old Sauvignon blanc vines were subjected to progressive severe drought stress in combination with a heatwave (max air temperature 40 °C), which were simulated in a controlled environment. Key physiological parameters, such as pre-dawn water potential, stomatal conductance, Fv/Fm and net assimilation were measured before (acclimation), during and after (recovery) the heatwave. Drought stressed plants reached a maximum pre-dawn water potential of –1.4 MPa. Drought stress negatively affected all physiological parameters, especially stomatal conductance, which was reduced to almost zero for the duration of the stress.

As a consequence, leaf temperatures during the heatwave reached up to 48.8 °C in drought stressed (WS) plants in contrast to well-watered (WW) plants, which reached a recorded maximum of 43.2 °C. Leaf removal had contrasting effects depending on water availability: in WW vines, it reduced cumulative transpiration by 15 %, whereas under drought stress, it had no impact due to near-complete stomatal closure. However, leaf removal positively influenced recovery, since WS leaf removal vines regained stomatal conductance values comparable to WW vines three days after rewatering. By the end of the 5-day recovery period, all physiological parameters in WS plants, whether leaf removal or control, returned to levels comparable to WW vines.

Overall, this work proved that the success of apical leaf removal is highly dependent on water stress level. The practical relevance of this research lies in the necessity of finding ways to mitigate the effects of extreme weather events, especially in a context where irrigation water may be not available and with young vines that are characterised by a still undeveloped root system.

KEYWORDS: drought stress, heat stress, climate change adaptation, Sauvignon blanc, transpiration

INTRODUCTION

Grapevine *(Vitis vinifera)* is a crop of global economic relevance, with total worldwide exports representing up to 36 billion euros in value in 2023 (OIV, 2023). Climate change and the increasing frequency of extreme weather events, such as heatwaves, are threatening grapevine health and productivity (Jones *et al.*, 2005; Schultz, 2000). Heatwaves, defined by the IPCC as a period of at least two consecutive days with abnormally hot weather (IPCC, 2022), are a particular threat to viticulture, as they often involve multiple stresses at the same time – mainly drought, heat and radiation. This becomes evident in the physiological responses observed during heatwaves, with cellular damage and negative consequences to photosynthesis and water status (Shtai *et al.*, 2024; Venios *et al.*, 2020). However, grapevines have shown remarkable recovery capabilities following heatwave and drought stress, although this depends on several factors including stress intensity, cultivar and phenological stage (Bondada & Shutthanandan, 2012; Dayer *et al.*, 2019; Flexas *et al.*, 1999; Hernández-Montes *et al.*, 2019; Pou *et al.*, 2010). Hernández-Montes *et al.* (2019) studied the effect and recovery of heat and drought on potted Cabernet-Sauvignon and Riesling vines and showed that physiological parameters such as transpiration and net photosynthesis can fully recover within 1-5 days after a stress event, depending on the timing during the growing season. Similarly, in Flexas *et al.* (1999) drought stressed plants recovered water potential and net assimilation on the first day of recovery. However, recovery duration is also dependent on stress intensity since, in addition to stomatal conductance, metabolic limitation (*e.g.*, a decrease in the enzymes involved in the Calvin cycle) also plays a role (Flexas & Medrano, 2002; Quick *et al.*, 1992).

Previous studies have highlighted different ways to agronomically manage these stresses. The application of antitranspirants and kaolin proved to be particularly effective (Gutiérrez-Gamboa *et al.*, 2021; Rogiers *et al.*, 2018). Kaolin increases canopy reflectance, thus acting as a sunscreen and thereby maintaining the grapes and canopy at a lower temperature (Palliotti *et al.*, 2014). Antitranspirants, on the other hand, form a thin layer that reduces water loss (Gutiérrez-Gamboa *et al.*, 2021). An interesting secondary effect of antitranspirants is reduced stomatal functionality, lowering transpiration and assimilation. which in turn is associated with delayed berry ripening (Andreotti *et al.*, 2024). Apical leaf removal is another promising canopy management strategy for delaying ripening and mitigating increased temperatures during berry development (Palliotti *et al.*, 2013). In field trials in which leaf area was reduced by between 30 and 40 % during veraison (at approximately 16 °Brix), it was possible to harvest with a reduction in total soluble solids of between 1.1 and 1.4 °Brix compared to the non-defoliated control (Gatti *et al.*, 2019; Palliotti *et al.*, 2013). In Poni *et al.* (2013), apical leaf removal was performed on potted vines, with a particular focus on net photosynthesis; the results pointed to the presence of a compensation mechanism involving a reduction in leaf area that had a temporary effect on gas exchange, which was at a later timepoint recovered by the increase in efficiency of the remaining leaves. In contrast to kaolin or antitranspirant applications, leaf removal is not vulnerable to wash-off and can also be performed manually, reducing CO_2 emissions and the need for machinery. While the impact on berry quality and leaf gas exchanges has been extensively researched, the potential of applying apical leaf removal just before a heatwave to alleviate stress has not yet been investigated.

This study tested the hypothesis that removing the apical leaves of shoots before subjecting grapevine to combined heat and drought stress can help mitigate the anticipated negative effects on grapevine physiology; it aimed to highlight the importance of canopy management as a tool for increasing vineyard resilience in the context of a changing climate.

MATERIALS AND METHODS

1. Plant material and experimental design

The experiment was performed on two-year-old Sauvignon blanc vines grafted on SO4. Vines were grown in 24 L pots containing sandy loam soil (64 % sand, 25 % silt, 11 % clay). In winter, the plants were pruned to five buds. The plants were grown in an open-sided glasshouse (a ransparent shelter with no lateral walls) located at the Laimburg Research Centre (Pfatten, Italy), shoot thinning was performed at about BBCH 15, leaving three shoots per plant. In mid-July, they were transferred to the experimental chambers at the terraXcube extreme climate simulation centre in Bolzano, Italy (https://terraxcube.eurac.edu/). Three chambers that were 2.8 m × 3 m × 2.8 m in size were used for the experiment, each chamber being a replicate. Controlled parameters inside the chambers were air temperature, relative humidity, light daylength and radiation intensity (Figure 1). The total duration of the experiment was three weeks. The first week served as an acclimation period, allowing plants to adapt to the ecotron chambers. During this phase, daily minimum and maximum air temperatures were maintained at 15 °C and 30 °C, respectively. The heatwave took place in the second week and was followed by a one-week recovery period. In the two days before the onset of the heatwave, the air temperature range was increased in two steps (Increase day 1 and 2) of 3 °C until daily minimum and maximum temperatures of 24 and 40 °C were reached. These temperatures were maintained throughout the 5-day heatwave, a duration typical for the area according to Zanotelli *et al.* (2022). After the heatwave, temperatures were restored to 15 °C (daily minimum) and 30 °C (daily maximum) and all pots were irrigated to field capacity on the afternoon of the final day of the heatwave, marking the start of recovery. This approach mimicked conditions typically observed in the field during a precipitation event. Photosynthetic active radiation was maximum at midday with approximately 1,130 μmol m^{-2} s^{-1} (with lights gradually turning on at 05:00 and fading out at 20:00) and achieved through LED lights simulating the solar spectrum from 280 to 900 nm. Relative humidity was kept inversely proportional

to the temperature curve at between 30 and 60 %. VPD had a respective daily minimum and maximum of 0.7 and 3 kPa during acclimation and ranged from 1.2 to 5.2 kPa during the heatwave. Daily cycles of the climate chamber parameters are summarised in Figure 1.

2. Treatments

This experiment followed a factorial design based on two experimental factors: i) apical leaf removal at two levels: control/no leaf removal (C), and leaf removal (LR), and ii) drought stress at two levels: well-watered (WW) and water stress (WS). The trial was conducted in three separate chambers, each containing four vines, with one vine assigned to each of the four treatment combinations: C + WW, C + WS, LR + WW, and LR + WS.

2.1. Apical leaf removal

Before leaf removal, the leaf area of each plant was estimated. To do this in a non-destructive way, the following protocol was followed: three shoots from extra plants (vines belonging to the same group of the ones used for the experiment) were sampled, after which an image of each leaf of each shoot was obtained separately using a scanner (Seiko Epson Corporation, Japan) and a precision ruler as reference. Subsequently, single leaf area and the length of the midvein were measured with ImageJ (https://imagej.net/) using the analyse particles and the straight line function. Then, a linear regression between leaf area and midvein length was calculated according to Junges and Anzanello (2021) ($y = –48.6 + 16.9x$ with $R^2 = 0.92$, Figure S1).

The midvein of each leaf of the experimental plants was then measured by hand and the individual values were fitted within the regression. This served two purposes: firstly, the sum of the individual leaf areas of a plant allowed the whole plant leaf area to be determined in order to assess the homogeneity of the plants (Figure S2); secondly, by calculating the cumulative leaf area of the shoot, the exact number of leaves to remove to achieve 40 % of leaf area reduction could be determined at a precision of ±1 %. Each vine had approximately 60 leaves, and an average of 25 leaves per plant were removed. Leaf removal was carried out manually (Figure 2) early in the morning of day of experiment (DoE) 5.

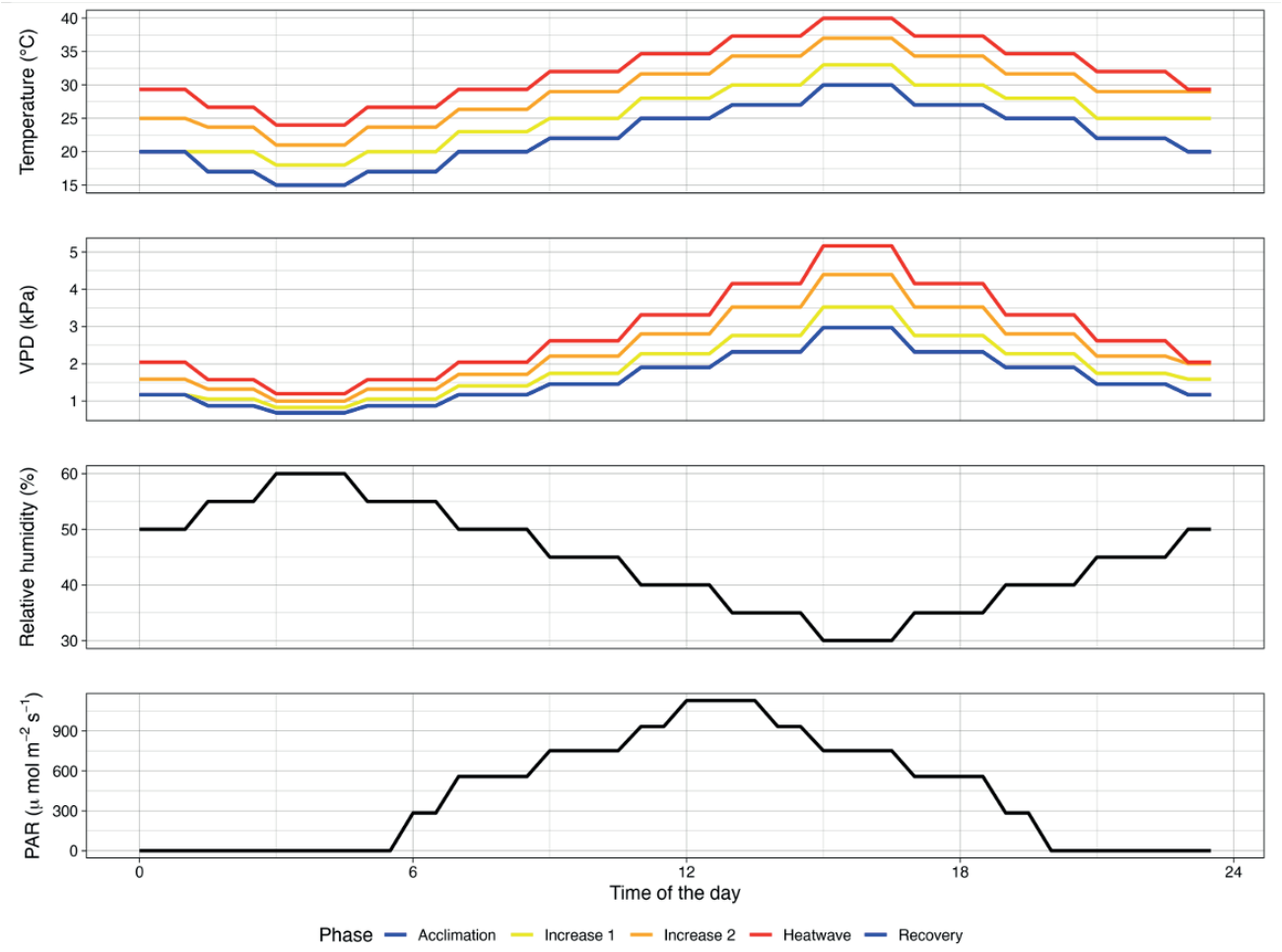


FIGURE 1. Daily air temperature, VPD, humidity and PAR set inside the chambers during the experiment. While daily cycles of relative humidity and PAR remained constant during the course of the experiment, the air temperature was determined by the experimental phases (in chronological order): acclimation (8 days, blue line), temperature increase (Increase 1 and 2, lasting one day each, yellow and orange lines, respectively), heatwave (5 days, red line) and recovery (5 days, blue line).



FIGURE 2. Grapevine plants before (left) and after (right) 40 % leaf removal in the apical shoot zone.

2.2. Drought stress

The two water regimes that were maintained during the experiment were intended to resemble irrigation at company level and severe drought stress. The irrigated treatment was kept at a pre-dawn water potential of between 0 and –0.3 MPa, whereas the severely stressed treatment was maintained at a pre-dawn water potential of below –0.8 MPa. Irrigation in WS treatments was stopped on DoE 2. When target water potential was reached, the water status was maintained by watering the vines daily with a volume of water equal to that lost during the day *via* transpiration (see section 3.2. and Table S1).

3. Measured parameters

3.1. Leaf physiological parameters

The following physiological and biophysical parameters were measured at leaf level: i) maximum quantum yield of PSII (Fv/Fm), ii) stomatal conductance to water vapour (hereafter referred to simply as stomatal conductance) (mmol m^{-2} s^{-1}), iii) leaf temperature (°C), and iv) net assimilation (μmol m^{-2} s^{-1}). For each vine, three fully developed leaves between the third and sixth node of the shoots were chosen and tagged, and the aforementioned parameters were measured consistently throughout the experiment.

Fv/Fm was measured every second day using a portable fluorometer (Handy PEA+, Hansatech Instruments Ltd., England) with clips left on the leaves for 20 min for dark adaptation. Stomatal conductance (g_s) was measured every second day (every day during the heatwave) using a Decagon SC-1 leaf porometer (Decagon Devices, Inc., USA). Leaf surface temperature (T_{leaf}) was measured every second day using a Extech 42512 (Teledyne FLIR LLC) infrared thermometer on the central lobe of each tagged leaf. Assimilation (A) was measured at the beginning of the experiment (DoE 2), at the beginning and end of the heatwave (DoE 11 and 15, respectively) and on the first and last day of recovery (DoE 16 and 20). For these measurements, a Walz GFS-3000 infrared gas analyser (Heinz Walz GmbH, Germany) was used and the following conditions in the leaf cuvette were set: a photosynthetic photon flux density (PPFD) of 1,000 μmol m^{-2} s^{-1}, a CO_2 mole fraction of 450 μmol mol^{-1}, an airflow rate of 750 μmol s^{-1}, and a cuvette temperature based on ambient values (Shtai *et al.*, 2024).

Pre-dawn water potential (Ψ_{pd}, in MPa) was measured every second day using a Scholander pressure chamber (Plant Water Status Console Series 3000, Soilmoisture Equipment Corp., USA), following the methodology described in Deloire *et al.* (2020). Pre-dawn measurements were performed on one non-tagged mature leaf per vine from the centre of the canopy (*i.e.*, between the third and the tenth node).

3.2. Whole-plant transpiration and soil water potential

Each pot was placed on a customised lysimeter (Umwelt-Geräte-Technik GmbH, Germany) equipped with a WZ 1042 load cell (MessTechnik Sauerland GmbH, Germany) to measure weight differences over time (one measurement per minute). The weight loss was considered to be equal to total vine transpiration, since the pots were covered with

aluminum foil to ensure the evaporation component from the soil was negligible. Daily transpiration was calculated as difference between the weight at sunrise and the weight at sunset. The calculation of this difference accounted for the exact volume of irrigation water applied to each plant per day (Table S1). Further, the cumulative water loss during the course of the experiment was calculated by summing the daily transpiration volume over time to assess the total water loss of the different treatments.

Soil water potential (MPa) was measured with three FRT 15D full range tensiometers (Umwelt-GeräteTechnik GmbH, Germany) per pot. All three sensors were placed at a depth of approximately 15 cm around the stem of the vine, and the measurements were made every five minutes.

4. Statistical analysis

Data was analysed using R (R Core Team, 2021). To test for differences between treatments, linear mixed-effects models were created for each parameter using the nlme package (Pinheiro *et al.*, 2024). The fixed effects included leaf removal, water status and time as independent variables, while the measured parameter was treated as the dependent variable. To avoid pseudoreplication, the three measurements taken from each plant were averaged. Plants were set as a random factor. Models were checked for normality, homoscedacity and autocorrelation. Subsequently, the estimated marginal means were calculated using the emmeans package (Lenth, 2024). Based on this, pairwise comparisons were performed using Tukey's Honestly Significant Difference (HSD) post-hoc test within the multcomp package (Hothorn *et al.*, 2008). Significance of interactions between the experimental factors was tested by performing a two-way ANOVA. Subsequently, two sets of pairwise comparisons (with $\alpha = 0.05$) were made to distinguish between the experimental factors: i) effect of water status within each leaf removal treatment, and ii) effect of leaf removal within each water treatment.

RESULTS

1. Soil and vine water status

The water potential dynamics were similar in terms of pre-dawn water potential and soil water potential (Figure 3). In the water stress (WS) treatments, irrigation was stopped on the second day of the experiment, with soil water potential decreasing to approximately –0.15 MPa by day 5, and pre-dawn water potential decreasing to approximately –0.6 MPa by day 7. Both types of water potential decreased progressively until day 12. The decrease in soil water potential in WS nondefoliated vines appeared to be greater than in WS leaf removal vines, reaching –1.1 MPa and –0.84 MPa on DoE 11, respectively. On day 12, due to the onset of basal leaf senescence in WS treatments at a pre-dawn water potential of approximately –1 MPa and a soil water potential of between –0.9 and –1 MPa, "emergency irrigation" was carried out. This irrigation event resulted in a temporary increase in the respective pre-dawn and soil water potential values on day 13 (Figure 3). In contrast to soil water potential, pre-dawn water potential subsequently decreased further, reaching a maximum stress level of about –1.4 MPa in the morning of the last day of the heatwave. Finally, all the pots were watered to field capacity for the recovery period and the water potentials of WS plants returned to WW levels. No significant differences were found between the different leaf removal treatments of the same irrigation regime.

2. Leaf physiological parameters

Stomatal conductance decreased drastically with decreasing water availability (Figure 4). At the onset of the heatwave (DoE 11), the water-stressed plants reached a minimum of approximately 30 mmol m^{-2} s^{-1}, which was maintained until recovery, with the exception of a slight peak on day 13 due to the aforementioned emergency irrigation event. In comparison, WW treatments had a mean g_s of approximately 460 mmol m^{-2} s^{-1} during the heatwave. During the recovery period, the g_s values of water-stressed plants increased steadily and were back on par with the WW plants by the end of the experiment. Though only statistically significant on day 12, defoliated vines in the WW treatments generally showed higher g_s values when compared with those from non-defoliated control vines in the first 10 days after leaf removal (Figure 4). Mean g_s during the heatwave was about 497 mmol m^{-2} s^{-1} in WW leaf removal and 412 mmol m^{-2} s^{-1} in WW control. In WS vines, on the other hand, no differences between the leaf removal treatments were observed due to drought-related stomatal closure (*i.e.*, the interaction between drought stress and leaf removal was not significant). However, WS leaf removal vines recovered stomatal conductance more quickly than WS control vines. On the third day of recovery (DoE 18), there were no significant differences in g_s between WS leaf removal and WW leaf removal, whereas WS control vines still showed a significantly lower g_s value as compared to the other treatments). On the last day of recovery no significant differences were found between treatments.

As expected, leaf temperature was also severely impacted by water status, which was especially visible during the heatwave (Figure 5). With a daily maximum air temperature of 40 °C, leaf surface temperature was on average 39 °C in the well-watered plants and 44 °C in the water-stressed ones. During the heatwave, the highest single recorded leaf temperature in the water-stressed plants was 48.8 °C, whereas the maximum recorded leaf temperature in the well-watered plants was 43.2 °C. No significant differences were observed between the leaf removal treatments and their respective non-defoliated control, and the interaction between drought stress and leaf removal was not significant.

Similar to stomatal conductance, measured net assimilation was drastically reduced by water stress (mean leaf assimilation of WS vines during the heatwave was 0.4 µmol m^{-2} s^{-1}). In WW vines, mean leaf assimilation during the heatwave was 11.5 µmol m^{-2} s^{-1} and 9.3 µmol m^{-2} s^{-1} for leaf removal and the control, respectively. It worth noting that assimilation almost doubled with temperature increase and high water availability (Figure 6). On the first day of recovery, net

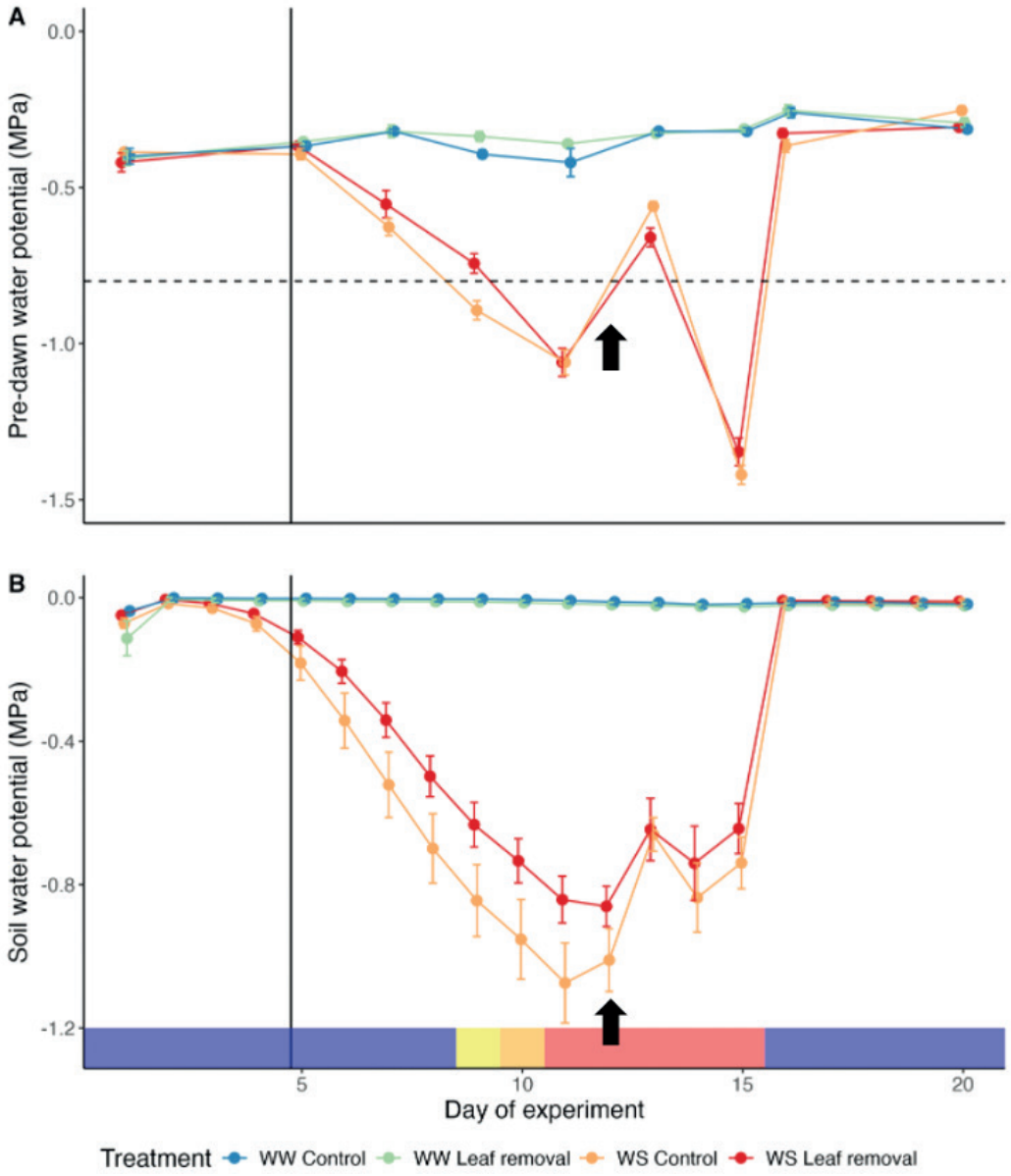


FIGURE 3. Pre-dawn (A)and soil water potential (B) during the course of the experiment (n = 3 ± standard error). Different colours indicate treatments: the black vertical line at DoE 5 indicates the moment of leaf removal, whereas the dashed horizontal line in Panel A indicates the threshold for what is considered severe water stress for grapevine (Deloire *et al.*, 2020). The black arrows indicate the emergency irrigation event on day 12. The colours along the x-axis indicate the phases of the experiment: acclimation (blue), temperature increase (yellow and orange) heatwave (red) and recovery (blue).

assimilation in WS vines returned to 35 % of values measured in WW vines. By the end of the recovery period, net assimilation rate in WS vines recovered to about 76 % of values measured in WW vines. No significant effect of leaf removal and on net assimilation was recorded. Similarly, the interaction between drought stress and leaf removal was not significant.

Fv/Fm in well-watered plants remained at about 0.80 during the course of the experiment with no differences between leaf removal and control. Fv/Fm in water-stressed plants deteriorated significantly when in combination with heat stress (Figure 7). Water stress significantly lowered Fv/Fm in both leaf removal and control vines. However, the effect of leaf removal in the WS treatments was also significant, with defoliated vines showing higher values than the non-defoliated control, and with observed mean Fv/Fm values of 0.76 and 0.71 for the leaf removal and control, respectively, on the last day of the heatwave. The day following rewatering, the values for Fv/Fm in WS vines were back on a par with those measured in the WW treatments.

3. Whole-plant transpiration

Daily transpiration per vine was greatly influenced by air temperature and water availability. During the acclimation phase before leaf removal, all treatments showed an average transpiration of about 500 g water per day per vine.

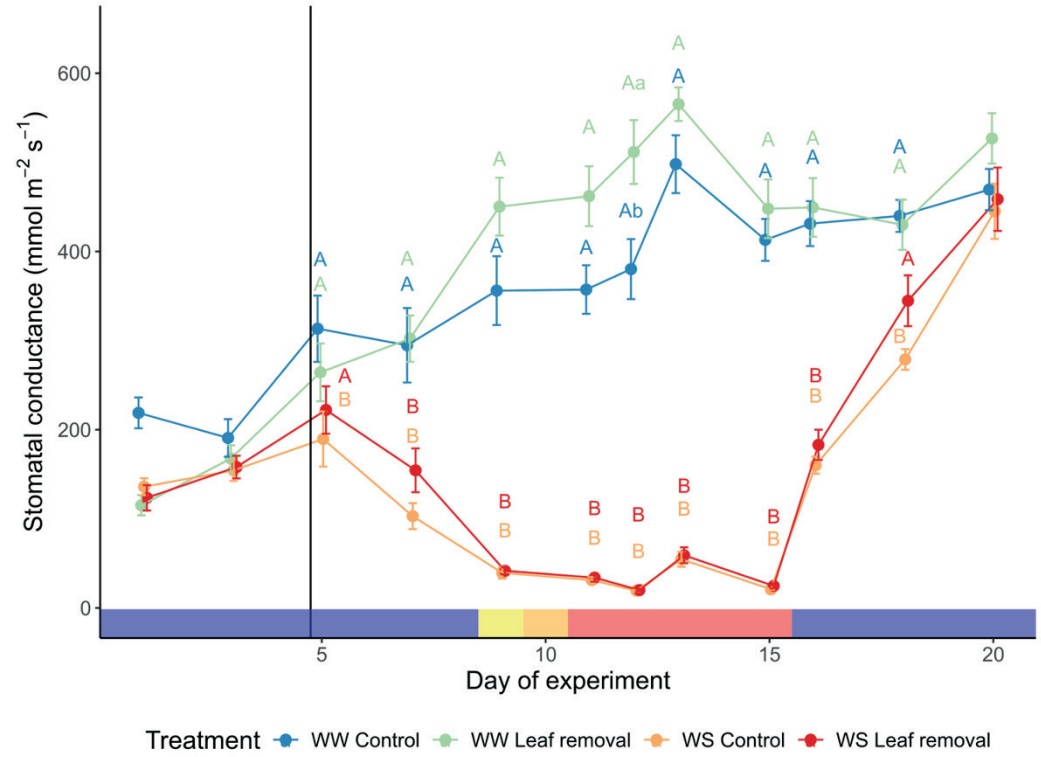


FIGURE 4. Stomatal conductance during the course of the experiment (n = 3 ± standard error). The black vertical line at DoE 5 indicates the moment of leaf removal, the colours along the x-axis indicate the phases of the experiment: acclimation (blue), temperature increase (yellow and orange) heatwave (red) and recovery (blue). Uppercase letters indicate a significant effect of water status within each leaf removal treatment (leaf removal or control); lowercase letters indicate significant effect of leaf removal depending on water status (WW or WS).

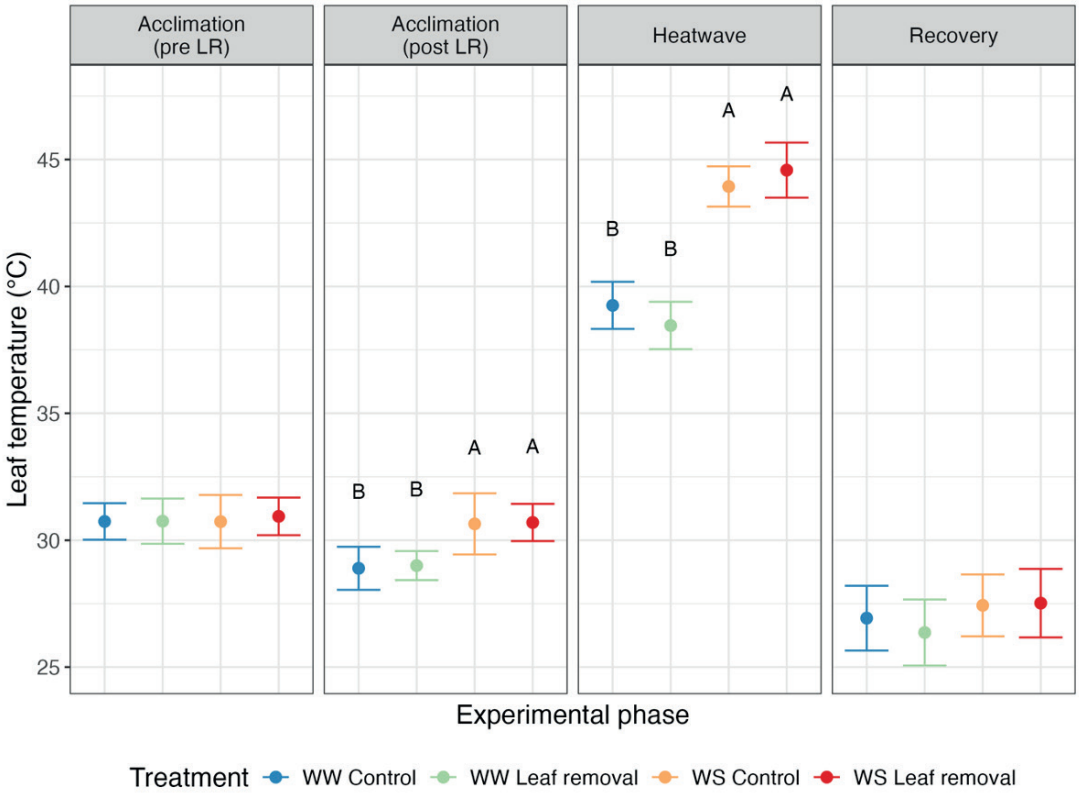


FIGURE 5. Leaf temperature in the main experimental phases (mean ± standard error, n = 3): acclimation (pre-leaf removal) DoE 1-4, acclimation (post-leaf removal) DoE 5-8, heatwave DoE 11-15, recovery DoE 16-20. Uppercase letters indicate a significant effect of water status within each leaf removal treatment (leaf removal or control).

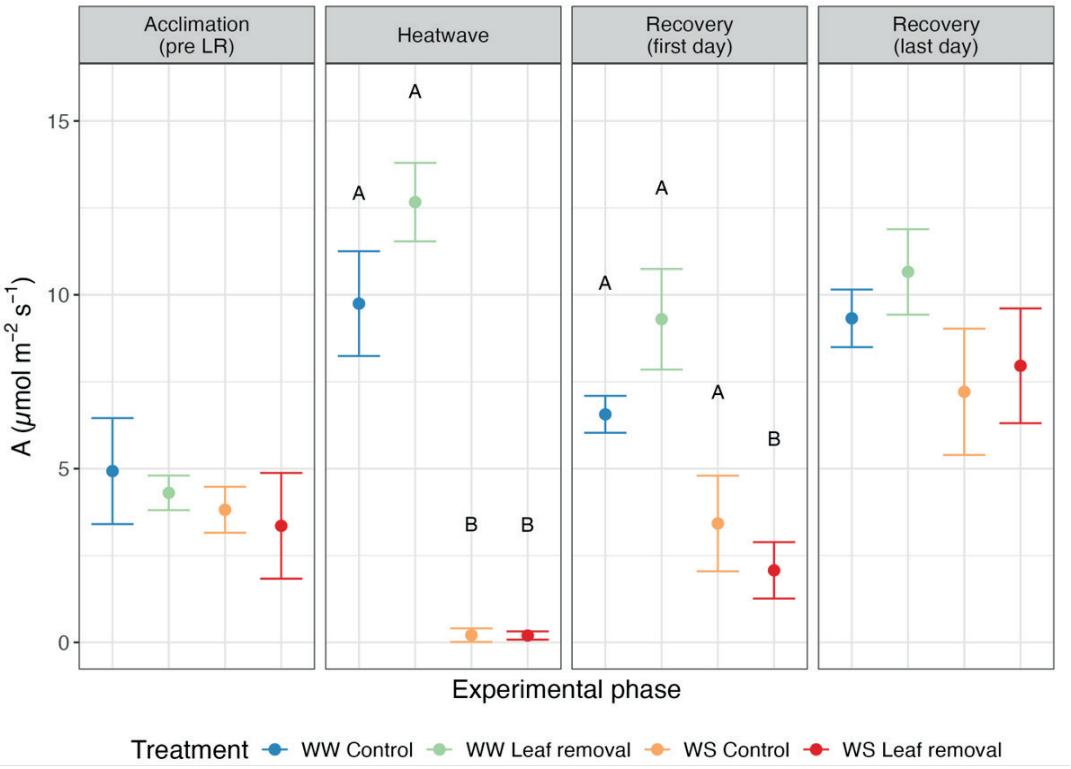


FIGURE 6. Leaf net assimilation rate measured with an infrared gas analyser in the main experimental phases (mean ± standard error, *n* = 3): acclimation (pre-leaf removal) DoE 2, heatwave DoE 12 and 15, recovery DoE 16 and 20. Uppercase letters indicate a significant effect of water status within each leaf removal treatment (leaf removal or control).

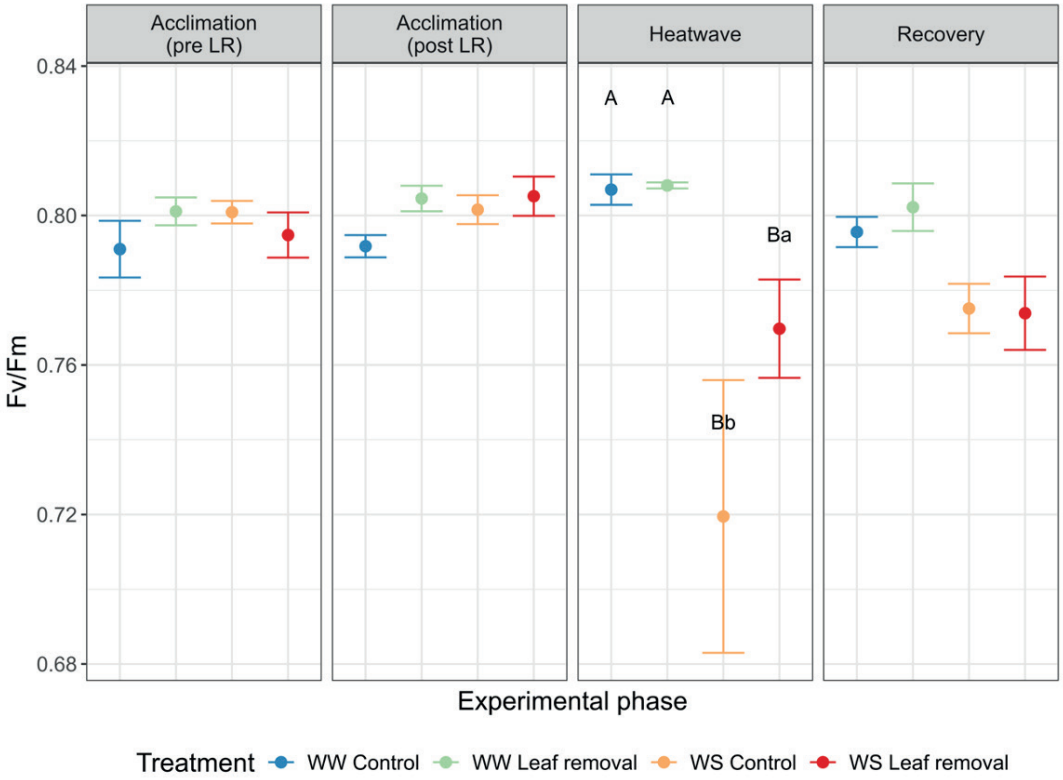


FIGURE 7. Fv/Fm in the main experimental phases (mean ± standard error, *n* = 3): acclimation (pre-leaf removal) DoE 1-4, acclimation (post-leaf removal) DoE 5-8, heatwave DoE 11-15, recovery DoE 16-20. Uppercase letters indicate a significant effect of water status within each leaf removal treatment (leaf removal or control), lowercase letters indicate significant effect of leaf removal within each water status (WW or WS).

With progressing drought stress, daily transpiration of WS treatments decreased until a plateau of about 100 g per day was reached, which was maintained until recovery. In WW plants on the other hand, daily transpiration increased to about 1,100 g during the heatwave (Figure 8A). The effect of leaf removal was significant in WW treatments with mean daily transpirational water losses being lower in leaf removal vines than the non-defoliated control. However, in WS treatments, no significant differences were observed between the leaf removal and control vines. Although the interaction between water treatment and leaf removal did not reach levels of statistical significance ($p = 0.0603$), the trend suggests a potential interaction that may support these observations. During the acclimation period following leaf removal, mean daily transpirational water losses in WW defoliated vines were 36 % lower than in the non-defoliated controls. During the heatwave, transpirational water losses were 16 % lower in WW defoliated vines compared to the controls. Similarly, the cumulative water loss was significantly lower in WW leaf removal plants than in WW control in the heatwave and recovery phase (Figure 8B). Leaf removal in WW plants was responsible for a decrease in 14.6 % in transpirational water losses during the course of the whole experiment.

DISCUSSION

This study focused on two experimental factors (vine water status and leaf removal) in the face of a 5-day heatwave. Key physiological parameters were monitored before, during and after the heatwave. Drought stress significantly lowered water potential, stomatal conductance and photosynthesis. Apical leaf removal, on the other hand, showed potential as a short-term measure to reduce water use under well-watered conditions but was less effective under drought stress because of stomatal closure. Due to the complexity of the influence of the treatments on the measured parameters, the discussion will focus on each of the two experimental factors separately.

1. Drought stress

In the present study, drought stress had a significant effect on all measured physiological parameters. Both the leaf pre-dawn and soil water potentials confirmed that severe water stress occurred during the heatwave (Deloire *et al.*, 2020), with the pre-dawn water potential reaching values as low as –1.01 MPa. The pre-dawn water potential in WW plants, meanwhile, remained close to 0 MPa. The difference in water potential along the soil-plant-atmosphere continuum (SPAC) is critical for water movement and must be considered when using water potential as a measure of plant water status (Tyree & Ewers, 1991). Water potential and water flux (*e.g.*, transpiration or stomatal conductance) are inversely related, with high stomatal conductance leading to more negative water potentials, and stomatal closure raising water potential (Klepper, 1968). In this experiment, the stomata of WS vines gradually closed when irrigation was reduced and, by the time temperature increased, stomatal conductance had reached a minimum of approximately 30 mmol m^{-2} s^{-1} (Figure 4), which was not recovered until rewatering (which took place approximately two weeks after the last irrigation). Stomatal closure proved to be a very effective tool for conserving water, as WS plants reduced the daily loss of transpirational water to less than 10 % of the values measured in well-watered plants. However, drastically lowering stomatal conductance also has negative consequences: leaf gas exchange is considered a trade-off, as CO_2 assimilation unavoidably comes at the cost of water loss (Düring, 2015; Chaves *et al.*, 2016). This was also found in this experiment, where the measured assimilation followed a similar pattern to stomatal conductance. This close similarity between net assimilation and stomatal conductance dynamics has also been found in other studies (Tombesi *et al.*, 2015). Understanding stomatal behaviour during heatwaves is crucial to understanding how to optimise water use efficiency in fruit crops and to optimise irrigation management (Zanotelli *et al.*, 2022). In a study carried out by Marchin *et al.* (2022), 20 species of evergreen trees and shrubs were subjected to similar abiotic stress conditions to this study, revealing a paradox effect of drought-stressed plants opening the stomata under heatwave conditions to allow for some transpirational cooling at the risk of hydraulic failure. Such a phenomenon was not encountered in this study. In fact, the lack of transpirational cooling in WS treatments caused the leaf surface temperatures to reach as high as 48.8 °C. In studies on Sémillon, drastic reductions in the photosynthetic rate were found at leaf temperatures of 45 °C (Greer & Weedon, 2012), a temperature that was surpassed in this experiment. These extreme temperatures likely caused not only stomatal-related reductions in photosynthesis but also thermal damage to Photosystem II, including a decrease in the activity of Rubisco activase and protein denaturation (Zhang *et al.*, 2018; Venios *et al.*, 2020). The impact on photosynthesis becomes evident when looking at the Fv/Fm readings of the present study (Figure 7). While Fv/Fm remained stable at the onset of water stress, it declined rapidly as soon as there was the combined stress of drought and high temperatures. The high standard error found especially in the WS control vines during the heatwave can be attributed to the partial loss of photosynthetic pigments due to the intense drought stress, with Fv/Fm values reaching as low as 0.5. These results are in agreement with other studies, in which a drop in Fv/Fm was only recorded when drought stress reached a severe level of intensity (Zulini *et al.*, 2005) or was combined with a heatwave (Shtai *et al.*, 2024). Notably, the plants in this study showed impressive Fv/Fm recovery, with the Fv/Fm values of WS plants not being significantly different – despite being slightly lower – to those of WW vines on the first day after rewatering. Similar results have been found for a *Vitis* hybrid: on the third day of recovery from heat stress, Fv/Fm values recovered to more than 80 % of the control plants (Kadir *et al.*, 2007).

2. Leaf removal

Apical leaf removal that reduced 40 % of the leaf area was carried out with the aim of reducing water loss and therefore mitigating the effects of drought and heat stress on young grapevines. Leaf removal had no significant effect on soil

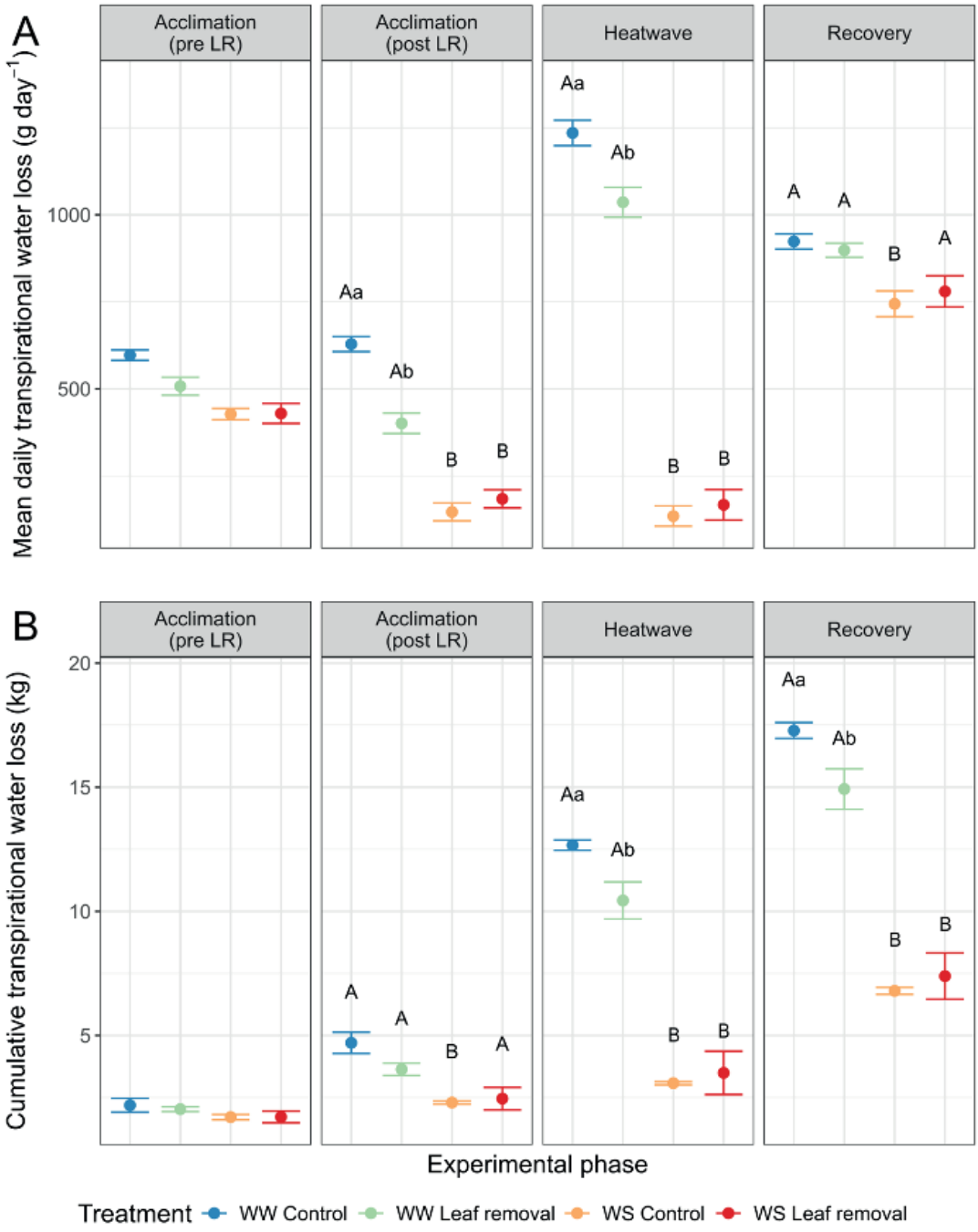


FIGURE 8. Cumulative (B) and mean daily transpiration (A) with standard error over the main experimental phases. The acclimation period is split into pre- and post-leaf removal (LR). Cumulative transpiration was calculated throughout the entire experiment, with values presented in the graph corresponding to the final day of each experimental phase (*i.e.*, days 4, 8, 15, and 20, respectively). Mean daily transpiration represents a mean of five days each. Uppercase letters indicate a significant effect of water status in each leaf removal treatment (leaf removal or control), lowercase letters indicate a significant effect of leaf removal within each water status (WW or WS).

and pre-dawn water potential (Figure 3). The observed difference in soil water potential between the two water stress treatments needs to be interpreted with caution, as the employed sensors are subject to lower accuracy when brought towards the upper limit of measurement range. The explanation that the observed faster decrease in soil water potential in non-defoliated WS plants was due to the larger leaf area is neither backed by stomatal conductance nor daily transpiration (Figure S2). On DoE 5-7, where a separation in soil potential values between WS leaf removal and WS control vines, stomatal conductance in both WS treatments was already below 50 % of values measured in WW treatments, indicating an advanced degree of stomatal closure. Further, and most importantly, mean daily transpiration revealed no significant differences between the two WS treatments during that period, meaning that the observed differences in soil water potential were not clearly linked to differences in daily water loss.

Well-watered, leaf removal plants showed higher stomatal conductance and assimilation than WW control vines. During the heatwave, stomatal conductance was approximately 20 % and net assimilation almost 24 % higher in WW leaf removal than in the WW control (Figures 4 and 6), showing a clear trend even though they were statistically significantly different only on day 12 of the experiment. This compensation mechanism has been observed before in grapevine, confirming that a reduction in leaf area results in increased gas exchange of the remaining leaves (Palliotti *et al.*, 2011). Further, an increase in photosynthesis and stomatal conductance after leaf removal has also been observed for several other species, such as wheat, eucalyptus, mustard, acacia and alnus (Ahmadi & Joudi, 2007; Alcorn *et al.*, 2008; Khan & Lone, 2005; Medhurst *et al.*, 2006; Ruess *et al.*, 2006). However, probably due to stomatal closure, no differences were found for leaf removal treatments in the stomatal conductance and net assimilation rates of water-stressed vines. These findings suggest that the mechanism responsible for the compensation in the reduced overall canopy assimilation potential is overridden by drought-induced stomatal closure mechanisms, which are either hormonal or hydraulic (Gambetta *et al.*, 2020; Tombesi *et al.*, 2015). The recovery of stomatal conductance and net assimilation found in this study is in line with existing literature (Flexas *et al.*, 1999; Hernández-Montes *et al.*, 2019). Even though by the end of the recovery period (five days after rewatering) both WS treatments were back on a par with WW values, stomatal conductance in WS leaf removal vines showed a swifter recovery, with similar values to WW plants on day 3 of the recovery period. A possible explanation for this swifter recovery is that, following rewatering, stomata regained functionality, allowing the same compensation mechanism observed in WW vines to be visible in (previously) WS plants. A second explanation could be that WS leaf removal vines were less stressed, since recovery speed is correlated with stress intensity (Flexas & Medrano, 2002). These findings are supported by the Fv/Fm values found in the present study. During the heatwave, Fv/Fm values in WS leaf removal vines were significantly higher than WS stressed control vines (Figure 7). In WW vines on the other hand, no differences in Fv/Fm between leaf removal and non-defoliated control were observed. Leaf temperature was also not significantly influenced by leaf removal in both WW and WS treatments. This can be explained by a reduction in self-shading as well as a higher light interception of leaves that were partially shaded before leaf removal, thus offsetting the hypothesised effect of increased transpirational cooling in leaf removal treatments (Valladares & Pearcy, 1997).

Mean daily transpirational water losses in WW plants were significantly lower in the leaf removal treatment, amounting to approximately 15 % lower total water loss during the course of the experiment (Figure 8). The reduced water loss in WW leaf removal vines is likely due to the decreased leaf area, as well as higher water use efficiency (Palliotti *et al.*, 2011; Poni *et al.*, 2013). However, it is important to underline that the effectiveness of this measure is limited by water availability and other agronomic factors influencing stomatal conductance, including variety, rootstock and soil type (Hugalde & Vila, 2014; Tombesi *et al.*, 2014; Tramontini *et al.*, 2013; Tramontini *et al.*, 2014). In this study, SO4 was used as the rootstock, as it is the most commonly used rootstock in the growing region of the present study. However, it is known to be less drought-tolerant compared to alternatives like 1103 Paulsen or 110 Richter, commonly employed in Mediterranean vineyards (Serra *et al.*, 2014). If these more drought-adapted rootstocks had been used, they might have enhanced water-use efficiency under stress conditions and could have potentially led to different results, especially when considering WS vines. Another key consideration for implementing apical leaf removal on young vines in the field is its practicality. In a Guyot trellis system, manual leaf removal represents a workload of about 30 hours per hectare, whereas mechanisation reduces this time to 2-4 hours per hectare (Müller & Walg, 2013). Given the scarcity and increased cost of manual labour, apical leaf removal before a heatwave would make sense for vine growers who are already equipped with the necessary machinery, given that canopy management only differs to regular leaf removal in terms of the working height of the machine (Gatti *et al.*, 2019). It is also important to consider the long-term consequences of a drastic reduction in leaf area. For instance, leaf removal alters carbohydrate partitioning and reduces starch reserves, resulting in lower infloresence numbers and lower yield in the following season (Holzapfel *et al.*, 2006; Vaillant-Gaveau *et al.*, 2014). Taken together, these results suggest that apical leaf removal could be a short-term measure to reduce water use in the context of a heatwave, if there is enough water to keep the vines irrigated above a water potential threshold that results in stomatal closure.

CONCLUSION

In this study, young Sauvignon blanc vines were subjected to progressive severe drought stress in combination with a heatwave, during which apical leaf removal was tested as a mitigation strategy, based on the hypothesis that reducing the leaf area decreases transpirational water losses and improves water status. Under drought stress, there were no differences in leaf physiological parameters between the vines whose leaves were removed and the control ones (no leaf removal), probably due to stomatal closure. However, under non-drought conditions, apical leaf removal reduced daily transpirational water losses on average by 15 %. The relevance of this work lies in the necessity of finding ways to mitigate the effects of extreme weather events, especially in contexts where irrigation water may be limited. Studying these mitigation strategies in young vines is particularly important, as early-stage vineyards are highly susceptible to multiple summer stresses due to their still-developing root system. Nonetheless, the findings of this study were obtained under controlled conditions, and field validation is necessary to assess the practical effectiveness of apical leaf removal in commercial vineyard settings.

Factors such as rootstock and scion choice, soil type and phenological growth stage at the moment of defoliation may influence outcomes in ways not captured here. Furthermore, viewing leaf removal not only as a mitigation strategy but also as a means of manipulating the source-sink balance raises interesting questions for further research; for example, how this source-limitation might affect lignification and carbohydrate storage in the vine, or how the increased radiation following defoliation might alter the microclimate and, consequently, impact grape quality and ripening dynamics. Further work should therefore also target practical aspects of the defoliation treatment, including the intensity of leaf removal and the variation in timing, as well as integration with irrigation management, to increase the potential of applying this technique in vineyard settings.

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