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Interactive effects of warming and water deficit on Shiraz vine transpiration in the Barossa Valley, Australia

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Abstract

Anticipating vineyard irrigation requirements in future climates is of strategic importance to maintain sustainability and wine regional identity. In the context of worldwide warming and climate-driven shifts in amount and seasonality of rainfall, we investigate the interactive effects of warming and water deficit on Shiraz vine transpiration under the conditions of the Barossa Valley, Australia. Transpiration of Shiraz vines was measured with thermal dissipation sap flow probes in a factorial experiment combining two thermal (*heated* with open-top chambers and *control* at ambient temperature) and two water regimes (*wet* and *dry*). Increased vapour pressure deficit (VPD) and canopy size in heated vines led to higher transpiration rates in irrigated vines during the first season. However, faster depletion of soil water by highly transpiring vines, followed by insufficient soil water replenishment by rain and irrigation, resulted in a negative feedback on vine transpiration the following season when *heated* vines were more water stressed than *controls*. The effect of warming was thus reversed the second season, with higher transpiration under ambient temperature. Therefore, dry soil, we suggest, could over-ride the effect of warming on the other variables driving transpiration (VPD, canopy size, and possibly stomatal conductance). Water scheduling will need to incorporate increased water demand under elevated temperature to maintain grapevine production in the long term.

Key words: climate change, sap flow, vapour pressure deficit, canopy size, stomatal conductance, water availability

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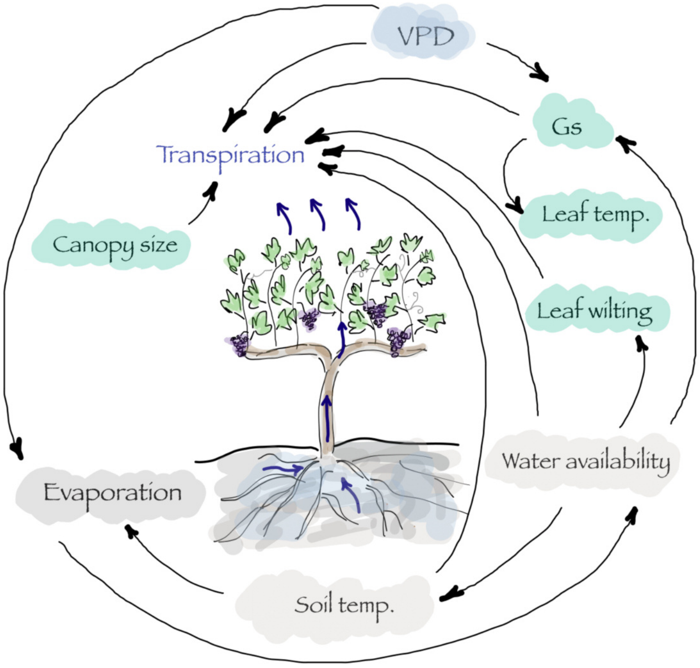
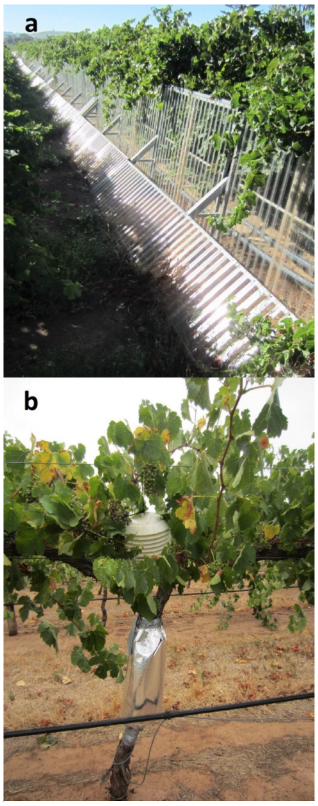


Figure 1. Temperature-associated factors driving vine transpiration.
Changes in transpiration by warming depend on atmospheric (blue), crop (green) and soil factors (grey).

Introduction

Multiple factors converge into a scenario of global water scarcity that may constrain crop production or shift current systems toward more water-conservative and profitable crops (Fereres *et al.*, 2011). Grapevine is grown under a broad range of water regimes from rainfed to fully irrigated, and water supply affects both yield and berry composition, which in turn drive profitability (Sadras and Schultz, 2012). In the Barossa Valley of Australia, the target region of this study, quality grapes are grown relying mainly on soil moisture stored during the rainy winter and complementary irrigation during the growing season. The combination of restricted water for irrigation and predictions of winter-rainfall decline (Cai and Cowan, 2012) are concerning. Anticipating irrigation requirements in future climates is therefore strategic to maintain wine regional identity (Bonada *et al.*, 2015; Fraga *et al.*, 2018) and the sustainability of the wine industry (Costa *et al.*, 2016; Fereres *et al.*, 2011).

Against the backdrop of climate change, irrigation strategies will need to incorporate changes in plant water requirements in response to the three-fold interaction between warming, water availability and ambient CO_2 concentration; here our focus is restricted to the water-temperature interaction. Information on water-related traits of vines in response to warming is fragmented. Changes in transpiration rate with warming depend on atmospheric, soil and crop factors (Figure 1). Elevated temperature and associated increase in vapour pressure deficit (VPD) would increase evaporative demand and actual transpiration, if plant water uptake is not restricted by soil, plant or other factors (e.g. root pathogens). Crop traits that modulate transpiration and are responsive for temperature include stomatal conductance (Gs), leaf folding and canopy size (Fereres *et al.*, 2014; Jarvis and McNaughton, 1986; Matthews *et al.*, 1988). Under elevated temperature in field conditions, well-watered Shiraz increased stomatal conductance and gas exchange rate per unit leaf area (Sadras *et al.*, 2012b; Soar *et al.*, 2009). The increased transpiration per unit leaf area could be cancelled, however, if warming reduces leaf area or intercepted radiation per unit leaf area in response to wilting (Matthews *et al.*, 1988). The thermal effects on canopy size remain unclear. Way and Oren (2010) reviewed the growth response to temperature of trees at the level of functional groups and biomes, concluding that elevated temperature enhanced growth in deciduous species more than in evergreen trees and in temperate and boreal species more than in



Supplementary Figure 1. a) Overview of open-top heating system in a Shiraz vineyard. Note the canopy growing freely over the chambers exposed to natural sunlight and wind. b) Installed and insulated sap flow sensors. Air temperature and humidity sensors located at mid-canopy level.

their tropical counterparts. Whereas some factors (increased evaporative demand and stomatal conductance) could enhance transpiration under elevated temperature, faster depletion of soil water may feedback negatively on transpiration if soil water content is not maintained by rain or irrigation.

Insights on the dynamics of transpiration could be provided by measuring the sap flow (Granier, 1985; Green, 2008), especially in deficit irrigation studies where the aim is to quantify reduction of net transpiration related to plant water stress (Ballester *et al.*, 2013). This paper reports measurements of sap flow in Shiraz vines in experiments which combined two thermal (*heated* with open-top chambers and *control* at ambient temperature) and two water regimes (*wet* and *dry*) in the field over two consecutive seasons (2010/11 and 2011/12).

Materials and methods

Experimental settings, including plant and site description, experimental design, vineyard management, and approaches to manipulate and characterise thermal and water regimes have been fully described in previous papers (Bonada *et al.*, 2013; Sadras and Moran, 2012; Sadras *et al.*, 2012b). Here we summarise key aspects of the experiment, and provide full detail of techniques used to measure transpiration flux, complementary measurements and data analysis central to this paper.

1. Field experiment

Own-rooted Shiraz vines were planted in 2004 at a spacing of 2.25 x 3.0 m on north-south oriented rows in an experimental vineyard in the Barossa Valley, SA (34^{o}S, 139^{o}E). Vines were spur pruned to 40-50 buds per vine and trained freely to a single-wire trellis. A 2^2 factorial experiment combining two thermal regimes, *control* and *heated*, and two water regimes, *wet* and *dry*, was established. Treatments were laid out in a split-plot design with three replicates, with thermal regime assigned to main plot and water regime assigned to subplots. Each replicate included nine vines where the seven central plants were used for research purposed, while the remaining two were considered as buffer. To avoid interference between treatments, perimeter rows were left as guards of the experimental row (7 m) and replicates were separated by a buffer zone of six vines (□ 13.5 m).

2. Thermal regimes

Control vines at ambient temperature were compared with *heated* vines using open-top chambers. Full construction details, limitations and performance of the open-top chambers during the seasons 2010/11 and 2011/12 have been fully addressed in Sadras *et al.* (2012a). Briefly, these automated chambers combine passive heating during clear sky day's hours and active heating, with pressured hot water, during cloudy or night's hours (Supplementary Figure <1). Automated open-close panels allow for dissipation of heat when temperature exceeds the target and heat irradiates through hot water circulating through polyethylene pipes at soil level when passive heating is insufficient. In each treatment, air temperature and humidity were measured continuously and recorded at 15-min intervals using shielded sensors that were located in the centre of each replicate at mid-canopy level (TinyTag Ultra2 loggers, Hastings Dataloggers, Port Macquarie, New South Wales, Australia).

In opposition to closed systems, the open-top heating system used in this experiment reduces the secondary effects typical of enclosure related to the lack of wind and altered radiation and VPD regimes. Potential for confounded effects and artefacts between these heating methods have been recently reviewed (Bonada and Sadras, 2015). Likewise, potential important secondary effects of the heating chambers, i.e. thermal gradient between extreme positions and rainfall pattern distribution, have been fully address previously (Sadras *et al.*, 2012a).

3. Water regimes

In this winter-rainfall region, vines grow with stored soil water during spring, and local practice includes restricted (□ 100 mm ha^{-1} $season^{-1}$) complementary irrigation applied during summer (Gladstones, 2004). In the trial irrigation was applied through a single lateral per row with pressure-compensated button drippers of 2.2 L h^{-1} spaced at 0.75 m, at approximately 8 h per irrigation event. The *wet* treatment was irrigated weekly and the *dry* only when basal primary leaves showed defoliation symptoms or yellowing.

4. Transpiration flux and complementary measurements

Vine sap flow was continuously monitored using probes TDP-30 mm (Plant Sensors, Nakara, NT, Australia) on the central vine of each treatment replicate. A pair of probes was radially inserted in the south side of the stem at half way between ground and vine cordon (□ 50 cm). Owing to the fundaments of the thermal dissipation method, which measures the dissipation of heat by the cooling effect of sap, the upper probe with the heating element was positioned approximately 10 cm above the reference probe. To minimise any unrealistic heating effect by direct sunlight and soil irradiation, probes were insulated with a layer of bubble-wrap and aluminium foil. Sampling frequency was every 30 minutes using a CR 1000 data logger (Campbell Scientific Inc., Utah, USA). The system was fully powered by solar energy. Sap flow measurements were performed using the Granier heat dissipation technique as outlined in Braun and Schmid (1999). Volumetric sap flux was integrated over the sapwood area at the heated probe insertion point (Braun and Schmid, 1999; Lu *et al.*, 2004).

Reference evapotranspiration (ET_o) was calculated with the Penman-Monteith equation (Allen *et al.*, 1998) using the meteorological data recorded by an automated station located at the plot site. VPD was calculated as a function of temperature and relative humidity (Jones, 1992). Basal crop coefficient (K_{cb}) was reckoned as the ratio between vine transpiration estimated by sap flow measurements and ET_o (Allen *et al.*, 2005).

Pre-dawn water potential (Y_{PD}) was determined as previously reported in Sadras and Moran (2013b). Integral water stress (S_Y) was calculated as described in Myers (1988) from the summation of Y_{PD} on every day during each season, and used as an indicator of soil water availability (Williams and Araujo, 2002). Water stress integral is calculated using negative notation but expresses as absolute values, therefore larger S_Y relates to larger accumulated water stress (Myers, 1988). Gs was measured on clear days between 12:00 and 15:00 on three tagged, fully expanded and well-lit leaves per replicate using a steady-state leaf porometer (Decagon SC1, Pullman, WA, USA). Canopy temperature was measured with an infrared camera FLIR B360 (FLIR Systems, Portland USA) as described by Fuentes *et al.* (2012). Infrared image analysis was performed using the FLIR QuickReport® software (FLIR Systems, Portland, USA). Biomass accumulation was taken as the summation of yield and pruning weight (Sadras and Moran, 2013a).

5. Data analysis

Plant transpiration is influenced by multiple factors outlined in Figure 1. To account for this complexity, data were analysed using three complementary approaches.

First, vine traits were analysed by the two-way analysis of variance (ANOVA) to test for the effect of water, temperature and the interaction between temperature and water using StatView version 5.0 (SAS Institute Inc., Cary, NC, USA). Fisher's LSD multiple range test was used to compare differences among significant means within treatments with a 1 or 5% level for rejection of the null hypothesis.

Second, we calculated an "environmental mean" of the daily sap flow across the four treatments. This method has been widely used in both annual

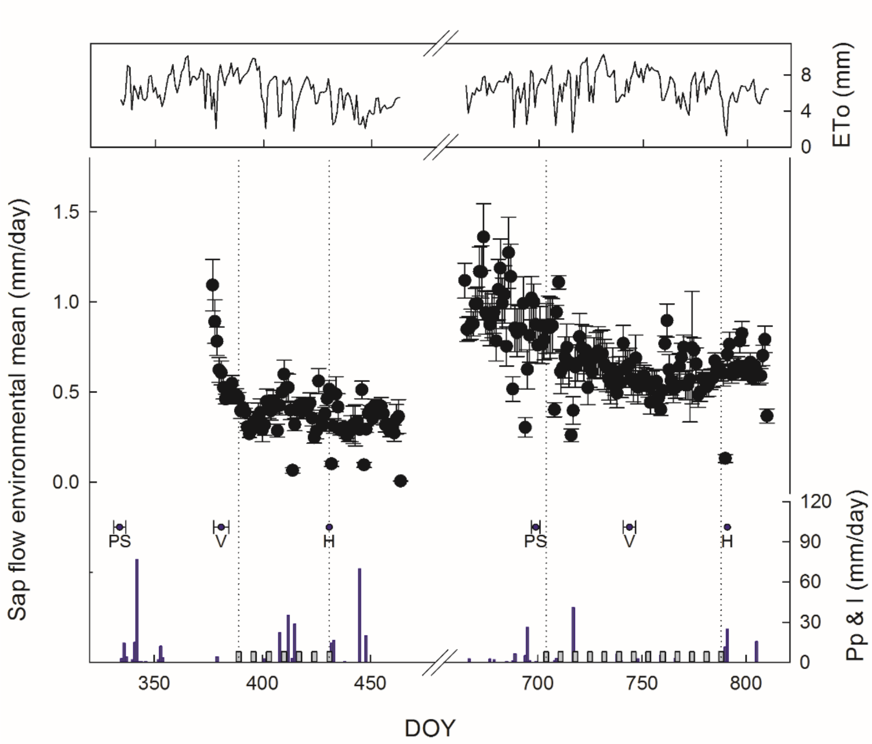


Figure 2. Seasonal patterns of sap flow environmental mean (●) of own-rooted Shiraz vines in the Barossa Valley, South Australia. We used a continuous time scale where day of year (DOY) starts on 01/01/2010. Values are averages of four treatments including two temperature and two water regimes, and bars correspond to one standard error. Reference evapotranspiration (ET_0, solid line), rainfall (blue bars) and irrigation events (grey bars) are also shown. Vertical dotted lines indicate beginning and end of irrigation. Blue circles indicate key phenological stages (mean ± SD): pea size (PS), veraison (V) and harvest (H).

and perennial crops for developmental, growth and water-related traits (Sadras *et al.*, 2009; Trentacoste *et al.*, 2011). The null hypothesis is that there is no difference among treatments, so the scatter plots of sap flow for each treatment against the environmental mean should align with the y = x line. Significant deviations around the y = x line by the two-way analysis of variance (ANOVA) would thus indicate treatment effects. The slopes of the regression between sap flow of each treatment and the environmental mean is taken as the effect of treatment on the plasticity of the trait (Sadras and Richards, 2014).

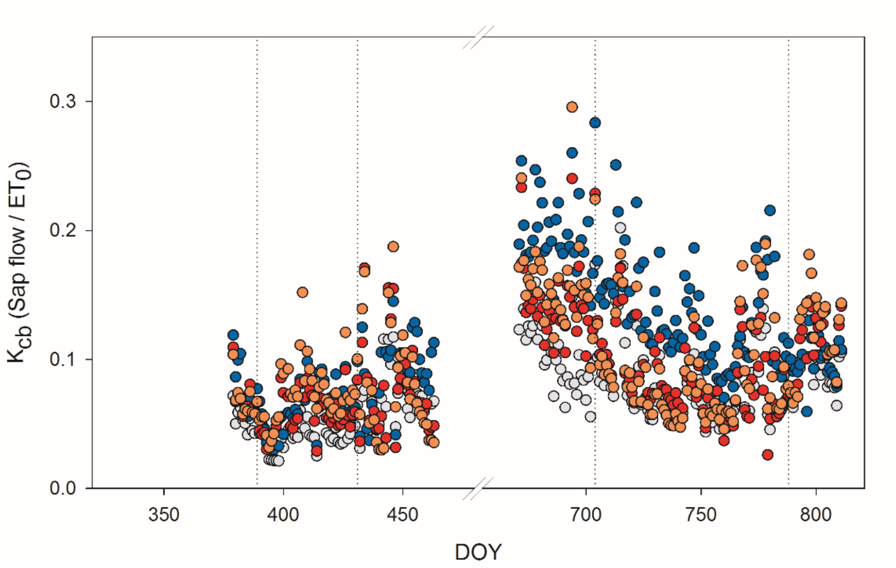
Third, we investigated the relation between atmospheric (VPD), soil (water availability) and crop factors (Gs, leaf temperature and canopy size) affecting transpiration (Figure 1) with a multivariate approach using principal component analysis (PCA) with XLSTAT 2016 software (Addinsoft SARL, Paris, France).

Results

1. Growing conditions

During the growing season (September to March) total rainfall and reference evapotranspiration (ET_0) were 505 and 1161 mm in 2010/11 and 257 and 1344 mm in 2011/12, respectively (Figure 2). From September 2010 to March 2012, including the dormancy period, mean daily temperature measured at canopy level in the *heated* treatments was 1.3 °C higher than that in *controls* (Sadras and Moran, 2013b). In *control* treatments, VPD reached up to 5.81 kPa during season 2010/11 and up to 4.26 kPa in season 2011/12. In *heated* treatments, VPD peaked at 6.16 kPa in season 2010/11 and at 4.62 kPa in season 2011/12.

During the irrigation period, the *wet* treatment was watered at 7.8 mm week^{-1} from 21st January to 7th March in 2010/11 (total: 55 mm) following a wet spring (292 mm from September to



Supplementary Figure 2. Seasonal patterns of daily basal crop coefficient (K_{cb}) calculated as the ratio between sap flow of own-rooted Shiraz vines and reference evapotranspiration (ET_o) in Nuriootpa, SA. We used a continuous time scale where day of year (DOY) starts on 01/01/2010. Values are averages of three replicates per treatment. The factorial combination of temperature and water defined four treatments: (blue) control-wet; (grey) control-dry; (orange) heated-wet; and (red) heated-dry. Vertical dotted lines indicate beginning and end of irrigation.

December), and from 2nd December to 27th February in 2011/12 (total: 102 mm), following a drier spring (180 mm from September to December) (Figure 2). In contrast, *dry* vines were irrigated with the same rates but only twice in each season; 21st January and 18th February in 2011, and 24th January and 17th February in 2012, hence receiving a total 16 mm in each season (Figure 2).

2. Seasonal patterns of sap flow, K_{cb}, Y_{PD}, Gs and canopy temperature

Sap flow environmental mean (i.e. averaged across treatments) followed a similar pattern in both seasons (Figure 2). In 2010/11, sap flow decreased from 1.1 to 0.5 mm day^{-1} between days 377 and 381 and was maintained at □ 0.4 mm day^{-1} from day 382 to 462. In 2011/12, sap flow ranged from around 1.1 to 0.6 mm day^{-1} between days 665 and 744 and stabilized around 0.6 mm day^{-1} from day 745 onwards. Seasonal pattern of K_{cb} followed the expectable trend for vines under soil water constrictions, showing slightly higher values for both *wet* treatments, *heated* and *control* (Supplementary Figure 2).

Pre-dawn leaf water potential is shown in Figure 3a, and captures the difference between *wet* and *dry* treatments in most of the irrigation period. Differences started to develop around veraison and lasted for approximately three weeks in the wet conditions of 2010/11 and until harvest in the drier summer of 2011/12. While shorter in span, water stress in 2010/11 was more pronounced than in 2011/12 for both water regimes. *Dry* vines, both *control* and *heated*, reached potentials up to -1.02 and -0.85 MPa in the first season and up to -0.68 and -0.72 MPa in the second season, respectively. The S_Y during the irrigation period showed a large difference between water regimes, and the lack of difference between thermal regimes except for the more stressed condition of *heated* and *wet* vines in the second season (Figure 4).

Leaf Gs tracked the progress of Y_{PD} during the irrigation period (Figure 3b). In the first season, when Y_{PD} was between -0.5 and -1 MPa at the beginning of the irrigation period, Gs was lower than 200 mmol m^{-2} s^{-1}. When Y_{PD} ranged between □ -0.2 and -0.3 MPa at the end of the irrigation period, Gs reached between □ 200 and 300 mmol m^{-2} s^{-1}. There was a tendency during this period when *wet* treatments (both *control* and *heated*) had higher Gs. However, the analysis of the variance detected only one out of five dates where irrigation increased Gs regardless of the temperature treatment. Differences in Gs were more evident during the

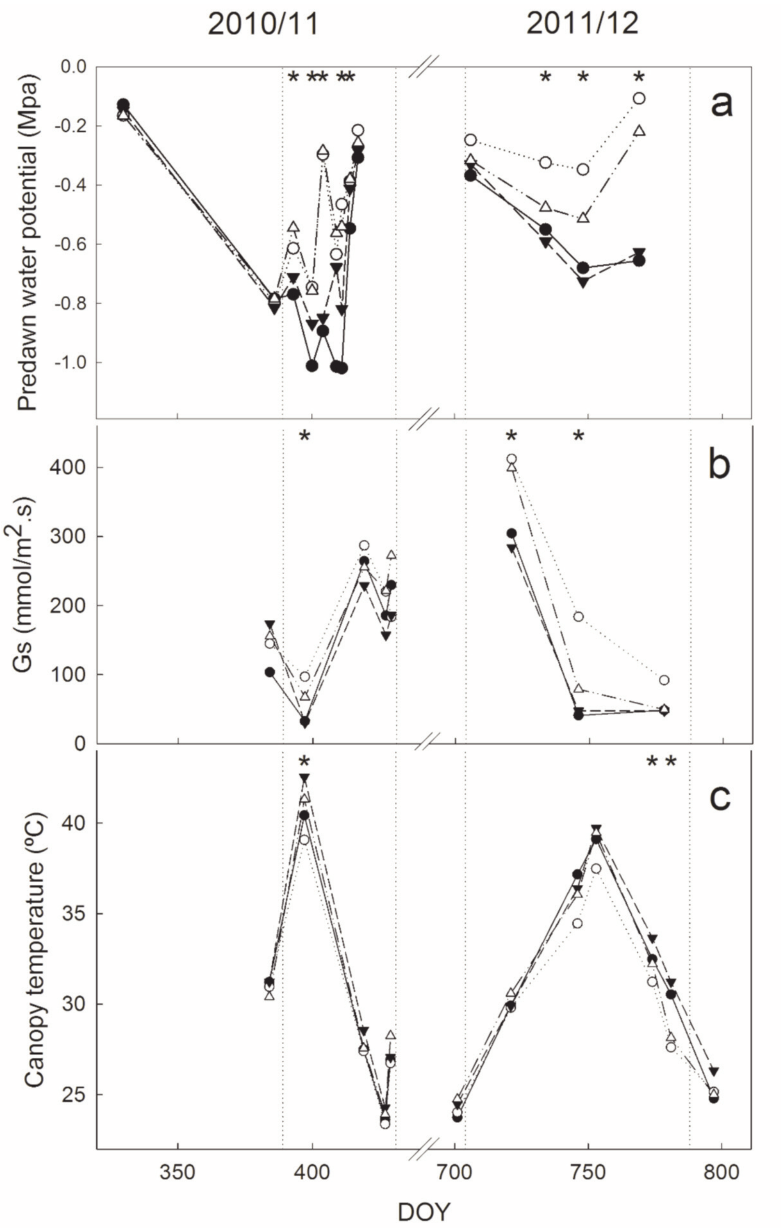


Figure 3. Seasonal patterns of: a) pre-dawn water potential, b) Gs, stomatal conductance and c) canopy temperature from Shiraz vines grown under two temperatures, control (circles) and heated (triangles), and two water regimes, wet (empty) and dry (full). Vertical dotted lines indicate beginning and end of irrigation in seasons 2010/11 and 2011/12. Asterisks show F values significant at p < 0.05 for single and combined water and temperature effects.

second season where *wet* treatments, *control* and *heated*, showed significantly higher Gs in two out of three dates assessed. In this season, at the beginning of the irrigation period, Y_{PD} between -0.3 and -0.4 MPa corresponded to Gs between □ 300 and 400 mmol m^{-2} s^{-1}. As the stress increased during the progress of the season Gs decreased.

Canopy temperature ranged between □ 25 to 45 ^{o}C on both seasons and was tied to the progress of Gs and Y_{PD} (Figure 3c). High canopy temperature normally corresponded to low Gs and low Y_{PD}. A quantitative analysis of associations among variables is presented in the section “*Relationship between soil, plant and atmospheric factors driving sap flow*”.

3. Effects of temperature, irrigation and their interaction on sap flow

Sap flow responded to the high order interaction between temperature, water regime and season (p < 0.001). To disentangle this complex

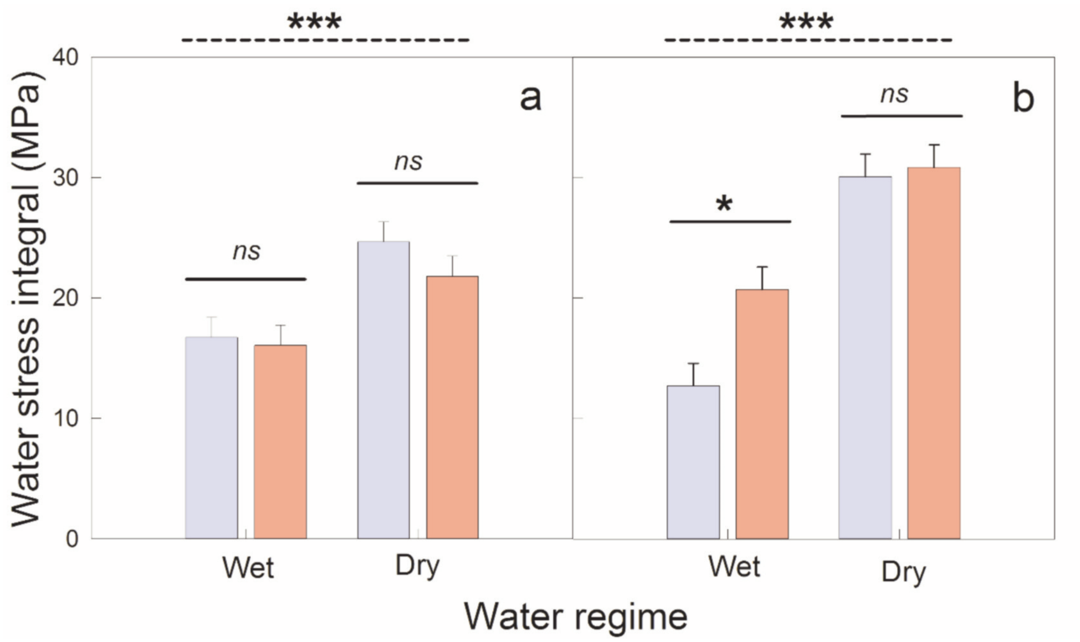


Figure 4. The cumulative integral of pre-dawn leaf water potential over the irrigated period of Shiraz vines growing under two water regime, dry and wet, and two temperatures, control (blue) and heated (red) in 2010/11 (a) and 2011/12 (b). Error bars are one standard error of the mean. *, *, and ns indicate significant differences for Fisher's LSD test at $p < 0.05$, $p < 0.001$ and not significant, respectively.**

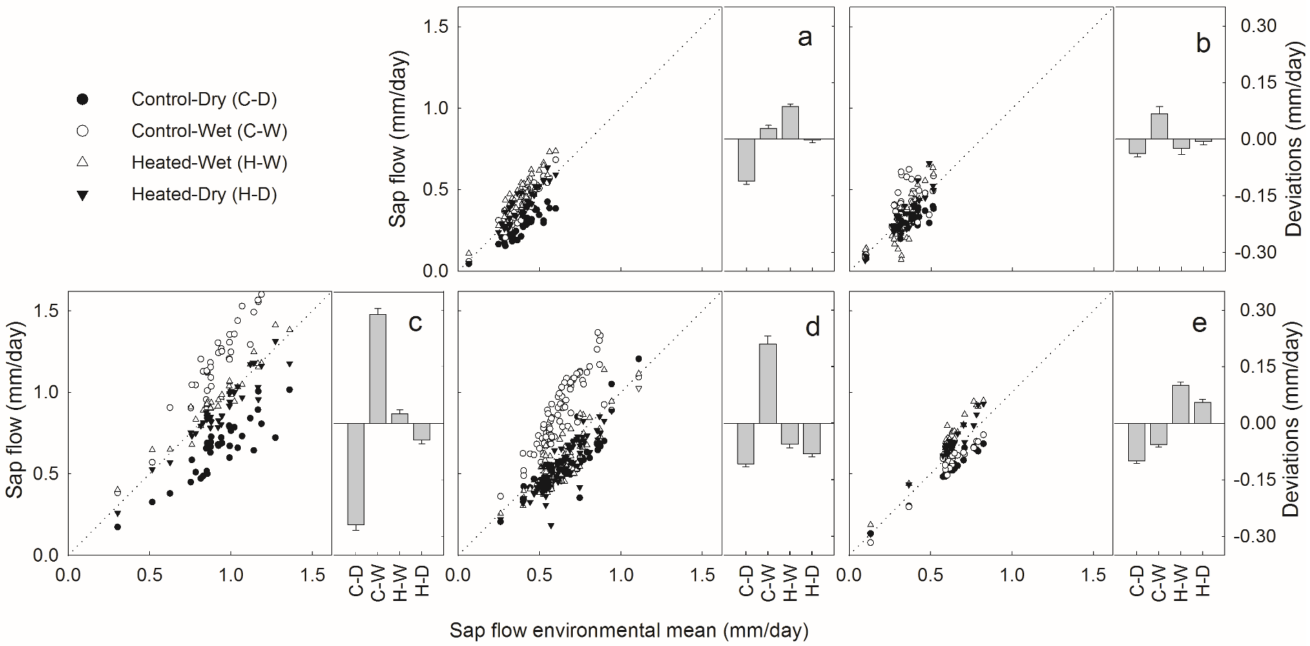


Figure 5. Scatter plots relating daily sap flow for each treatment and sap flow environmental mean in 2010/11 (a and b) and 2011/12 (c, d and e); the dotted line is y=x. Analyses were performed based on the beginning and end of irrigation, defining three periods: pre-irrigation (c), irrigation (a and d) and post-irrigation (b and e). Bar plots show deviations for each treatment (mean and standard error) around the y = x line. The period pre-irrigation in 2010/11, including the period of installation and stabilization of the sap flow sensors, was not included in the analysis.

Supplementary Table 1. Yield, vegetative growth and biomass accumulation of Shiraz vines in a factorial 2 x 2 temperature and water experiment in two consecutive seasons in the Barossa Valley, SA. Values are means ± one standard error. p value indicates effect of temperature, water and interaction. Biomass accumulation is the summation of yield and winter pruning. Data previously published by Sadras and Moran (2013a).

Season	Temperature (T)	Water regime (W)	Yield (Kg/vine)			Prunning (Kg/vine)			Biomass (Kg/vine)		
2010/2011	*Control*	*Dry*	6.61	±	0.481	3.31	±	0.201	9.92	±	0.678
	Heated		5.95	±	0.362	4.59	±	0.477	10.54	±	0.375
	Control	*Wet*	9.03	±	0.489	4.06	±	0.321	13.09	±	0.785
	Heated		7.41	±	0.438	5.06	±	0.434	12.48	±	0.869
	Source of variation (*p* value)										
	T			**0.034**			**0.016**			0.996	
	W			**0.002**			0.140			**0.007**	
	T × **W**			0.314			0.713			0.402	
2011/12	*Control*	*Dry*	3.44	±	0.508	2.80	±	0.205	6.25	±	0.661
	Heated		8.30	±	0.471	3.20	±	0.097	11.50	±	0.510
	Control	*wet*	5.22	±	0.591	3.48	±	0.251	8.69	±	0.834
	Heated		10.31	±	0.971	3.68	±	0.267	13.99	±	1.183
	Source of variation (*p* value)										
	T			**< 0.001**			0.204			**< 0.001**	
	W			**0.022**			**0.028**			**0.018**	
	T × **W**			0.862			0.658			0.981	

response, the progression of sap flow was analysed for each season, and for three periods bounded by the beginning and end of irrigation events (Figure 2).

Figure 5 compares the sap flow of each treatment with the environmental mean; treatment effects are reflected in significant deviations around the y = x line for both seasons in the three irrigation periods ($p < 0.001$). In 2010/11, *dry* treatments, both *control* and *heated*, had lower sap flow than their irrigated counterparts, except for the *heated-wet* treatment in the period post-irrigation, which had lower sap flow than the *heated-dry* treatment (insets Figures 5a and b). Temperature effect on sap flow, however, varied between periods and between water regimes. Consistently, warming increased the sap flow in *dry* vines, but only increased sap flow in *wet* vines during the irrigation period. In the period post-irrigation, *control-wet* vines had higher sap flow, whereas the sap flow in *heated-wet* vines was reduced to the level of *dry* treatments.

In the hotter and drier season 2011/12, *dry* treatments maintained a relatively lower sap flow. However, the sap flow of *heated-wet* vines was reduced along the season to a rate similar to that in *dry* treatments during the irrigated period. This drop in sap flow indicates constraints for water uptake from the soil, which was partially captured by the cumulative integral of pre-dawn leaf water potential (Figure 4b) and by the drop in Gs of *heated-wet* vines (Figure 3b). In the period post-irrigation, coincidently with rainfall events (Figure 2) and the equalization of stem water potential between treatments (Bonada *et al.*, 2013), *heating* increased sap flow (Figure 5e).

4. Relation between sap flow and vine growth

Vine yield and pruning weight were reported previously (Sadras and Moran, 2013a); Supplementary Table 1 summarises these data for convenience and further analysis of sap flow in relation to growth. The relation between plasticity of sap flow (defined by the slope of the regression between current sap flow and sap flow environmental mean) and pruning weight was bi-linear with a threshold about 3.5 kg vine^{-1} (Figure 6). Below this threshold, plasticity of sap flow increased in parallel with vine size ($r^2 = 0.81$, $p = 0.014$), whereas sap flow stabilizes as vine size increases above 3.5 kg vine^{-1} (slope not different from zero). During the second year all the treatments were below the threshold, revealing smaller canopies and a higher difference between treatments in sap flow rates. Plasticity of sap flow showed a quadratic relationship with yield ($r^2 = 0.81$, $p = 0.007$) and total plant biomass (pruning weight + yield; $r^2 = 0.83$, $p = 0.005$).

5. Relationship between soil, plant and atmospheric factors driving sap flow

We used three analytical approaches involving different levels of data aggregation. Analysis of

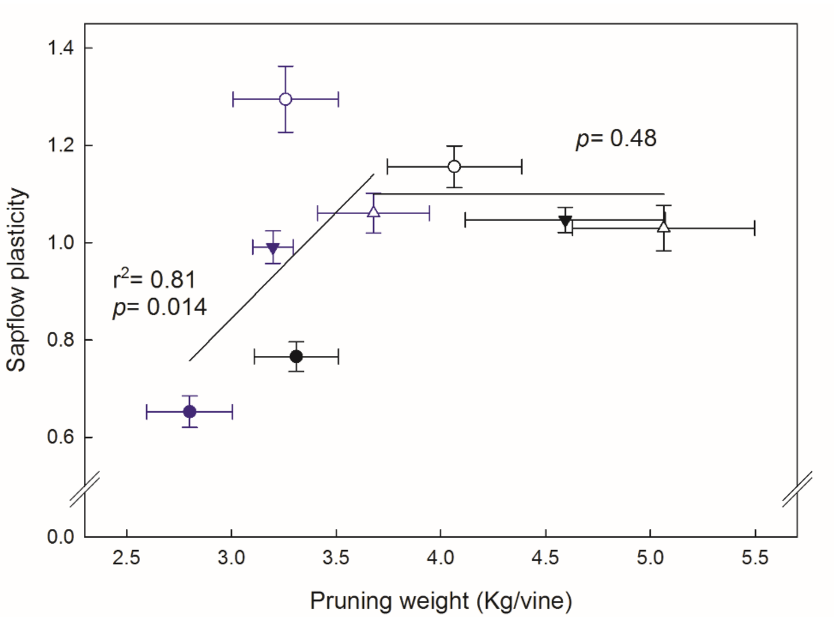


Figure 6. Relationship between sap flow plasticity (unitless) and pruning weight for Shiraz vines grown under two temperatures, control (circles) and heated (triangles), and two water regimes, dry (full) and wet (empty) in 2010/11 (black) and 2011/12 (blue). Lines represent the slopes of the linear regression for each region of this relationship. In the first section intercept was forced through zero, assuming no transpiration in the absence of canopy. Error bars are one standard error.

variance is at the lower end of aggregation, and differences between treatments are not always consistent (e.g. Figure 3). In the analysis of sap flow plasticity, data are more aggregated and effects of treatments on sap flow are more evident (Figure 5). The final step in our analysis seeks to establish associations between sap flow and its drivers in a highly-aggregated multivariate approach (Figure 7).

Principal component analyses were performed on the matrix of atmospheric, soil and crop factors affecting vine transpiration. Analyses were done separately by seasons and including the three replicates per treatment (Figure 7). Factors with eigenvalues greater than one were originally retained, accounting for □ 81% and □ 85% of the observed variation in season 2010/11 and 2011/12, respectively.

In the first season, PC1 explained □ 53% of the variation and was a function of the water treatment; the remaining 28% was explained by PC2, which was related to the temperature treatment (Figure 7a). There was a clear separation of treatments; *dry* treatments grouped on the negative region of PC1 and were strongly correlated ($r \geq 0.93$) with leaf water potential. The PCA component loadings on the positive side associated ($r \geq 0.81$) *wet* treatments with biomass, water applied, yield and sap flow. *Heated* treatments located on the positive portion of PC2 and were highly correlated ($r = 0.95$) to VPD and, to a lesser extent ($r \geq 0.7$), to pruning weight and canopy temperature. Unheated *control* treatments were in the negative portion of PC2. In the first season sap flow was positively correlated ($p < 0.05$, $0.65 \leq r \leq 0.8$) with pruning weight, total biomass, water supplied and VPD, but negatively associated with leaf water potential ($p < 0.05$, $r = 0.78$).

In the second season, PCs 1 and 2 explained □ 49 and 36% of the variation and were function of water and temperature treatments, respectively (Figure 7b). The distribution of the treatments was similar to that in the first season (Figure 7a). *Dry* treatments, grouped on the negative region of PC1, were correlated ($r \geq 0.84$) with canopy temperature and leaf water potential. *Wet* treatments loaded on the positive region of PC1 correlated ($r \geq 0.80$) with water applied, pruning weight and sap flow. *Heated* treatments loaded on the positive region of PC2 and correlated ($r \geq 0.85$) with VPD, biomass and yield. Sap flow in this season was positively associated with water supplied ($p < 0.05$, $r = 0.67$) and negatively

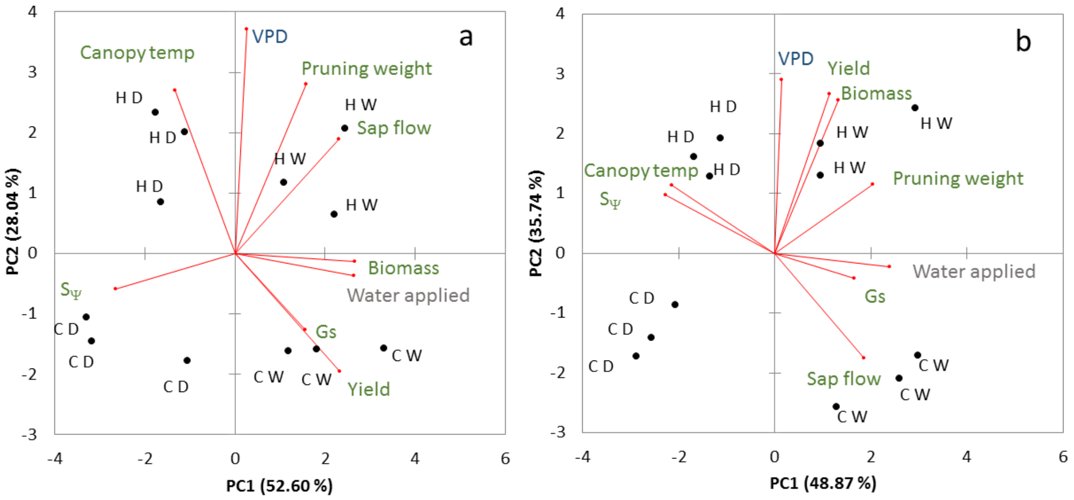


Figure 7. Principal component analysis of soil (gray), vine (green) and atmosphere (blue) traits, including replicates (black dots), measured during the (a) 2010/11 and (b) 2011/12 vintages in a 2^2 temperature x irrigation trial at the Barossa Valley, South Australia. The factorial combination of treatments is identified by temperature (C, control; H, heated) and water regime (D, dry; W, wet). Water applied, mm of water from supplementary irrigation; S_{Ψ}, water stress integral, as the cumulative integral of pre-dawn leaf water potential; Sap flow, residual of sap flow from the environmental mean; Biomass, total biomass from the summation of yield and winter pruning; Gs, leaf stomatal conductance; Canopy temperature, from infrared thermography; VPD, cumulative integral of vapour pressure deficit.

associated ($p < 0.05$, $0.75 \leq r \leq 0.85$) with leaf water potential and canopy temperature.

Discussion

Higher VPD associated with rising temperature could increase vine transpiration rate provided water supply is maintained and canopy size and conductance remain constant or increase. However, our understanding of the combined effects of high temperature and water supply on these traits is fragmented. An insight of the factors controlling vine transpiration is thus critical to anticipate how the industry would respond to a warmer and drier climate. We therefore approached this question empirically, measuring sap flow in an experiment where we manipulated temperature and irrigation in the field during two consecutive years.

Figure 1 summarises changes in transpiration that may be expected in warmer environments. Higher VPD, larger canopy size and higher Gs in heated vines would lead to higher transpiration. This was verified in the first season, where *wet* vines had higher sap flow in the *heated* treatment compared to unheated *controls* (Figure 5a). Data supported the roles of VPD and canopy size, measured with the surrogate pruning weight, as dominant drivers of vine-scale water use (Figure 7a). With the sole exception of *control-wet* vines, which maintained high transpiration rates on both seasons regardless of the canopy size, bigger canopies in *heated* vines corresponded with higher transpiration rates in the first season (Figure 6). In contrast to previous studies (Sadras *et al.*, 2012b; Soar *et al.*, 2006), no evidence of increased Gs in *heated* vines was found for the first season (Figures 3b, 7a). This may be associated to several causes (Sadras *et al.*, 2012b). Ambiguity in Gs data estimated using leaf porometry is widely reported (Pearcy *et al.*, 2000; Rochette *et al.*, 1991) and explains in part why up-scaled conductance from leaf to canopy do not correspond with down-scaled values obtained from modelling or direct methods with lysimeters or sap flow (Verhoef, 1997). Irrespective of the causes, higher transpiration in heated vines should lead to faster depletion of soil water, and this could lead eventually to the reversal of the heating effect. This could explain the reductions on sap flow on the *heated* treatments during the post-irrigation period of 2010/11 (Figure 5b) and during the core of the season 2011/12 (Figure 5d). Indeed, water stress integral in the second season was higher in the *heated* treatment than in the *control*

(Figure 4b), and transpiration was correspondingly higher in *controls* (Figures 5c and d). These results highlight not only how water stress reduces vine transpiration ratio as compared to potential (López-Urrea *et al.*, 2012) (Supplementary Figure 2), but also the complex relation of warming and water deficit on vine transpiration. Therefore, dry soil, we suggest, could over-ride the effect of warming on the other variables driving transpiration (VPD, canopy size, and possibly Gs). Nevertheless, longer experiments are needed that confirm this conclusion. Despite some vine traits may adapt to warming in the short term (Sadras *et al.* 2012b), interactive effects between warming and water deficit with other factors not explored in this study, e.g. atmospheric CO_2 concentration or the UV-B radiation (Martinez-Luscher *et al.*, 2015), may reveal new responses in the long term.

According to Way and Oren (2010), warming may reduce grapevine canopy size in hot environments and enhance growth in cool environments. Pair-wise comparisons of vines under elevated temperature and controls (ambient) in the Barossa Valley, SA, showed that the thermal response of pruning weight, an approximate measure of canopy size, ranged from -23 to 41% depending on seasonal conditions (Sadras and Moran, 2013b). Our data support the relation between canopy size and seasonal conditions but also demonstrate that warming may only increase grapevine biomass if irrigation compensates increments in transpiration rates (Figure 7a). Indeed, contrary to what happened in 2010/11, where available water was sufficient to not cause a sap flow difference in response to the extra demand of highly transpiring vines under warmer conditions, the insufficient soil water availability in 2011/12 could not buffer reductions in vine transpiration and canopy growth. As expected, transpiration rates were sensible to variation in vine size (Figures 7a and b).

The short term reduction in yield and vegetative growth observed under warm and dry conditions in this study might be accompanied by a long term depletion of carbohydrates reserves (Sadras and Moran, 2013a) and an increased partitioning of resources to leaves at the expense of roots (Smith and Holzapfel, 2009) if these conditions persist. Reduced water allocation in winter time or early spring may worsen this scenario if winter rain does not refill the soil profile. In the current study, the early differences in pre-dawn water potential between *control-wet* and *heated-wet* treatments at the beginning of the second season (Figure 3a) related to low transpiration rates (Figure 4c), which also support the seasonal carry over effect of insufficient irrigation. Scheduling irrigation against warming will therefore need to incorporate increased water demand to maintain functional and productive canopies.

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