LEAF WATER POTENTIALS OF SUNLIT AND/OR SHADED GRAPEVINE LEAVES ARE SENSITIVE ALTERNATIVES TO STEM WATER POTENTIAL

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Abstract

Aims: Leaf (Ψ_l) and stem (Ψ_{stem}) water potentials were measured on grapevines to determine the effects of shoot location on both methods to assess vine water status.

Methods and results: Cabernet-Sauvignon and Merlot used in this study were grown at two locations in California. Measurements were taken at midday in July (Merlot) and at two times of the day (morning and afternoon), on two dates in August (Cabernet-Sauvignon). Measurements of Ψ_l and Ψ_{stem}, stomatal conductance and transpiration were taken on shoots entirely exposed to direct solar radiation or on shoots totally in the shade at the times of measurement. There were significant differences ($P < 0.05$) between Ψ_l and/or Ψ_{stem} measured on shoots exposed to direct solar radiation and those in the shade. Both Ψ_l and Ψ_{stem} were significantly greater on the shoots exposed to direct sunlight compared to those in the shade. There was no significant difference between Ψ_l measured on shaded leaves and Ψ_{stem} determined on the fully exposed shoots.

Conclusions: Regardless of method used, water potentials were highly correlated with stomatal conductance measured on leaves in direct sunlight at the same time. All means of measuring grapevine water potential used in this study were highly correlated with one another.

Significance and impact of the study: The data indicate that any of the techniques used in this study would be a sensitive indicator of vine water status and that the Ψ of shaded leaves would be an alternative to the measurement of Ψ_{stem}.

Key words: water potential, Cabernet-Sauvignon, Merlot

Résumé

Objectifs : Le potentiel hydrique foliaire (Ψ_l) et le potentiel tige (Ψ_{stem}) ont été mesurés au niveau des vignes pour déterminer l'influence de la position des rameaux sur les deux mesures utilisées pour la détermination de l'état hydrique de la vigne.

Méthodes et résultats : Les cépages considérés dans cette étude sont le Cabernet-Sauvignon et le Merlot dans deux localités de Californie. Les mesures ont été réalisées à la mi-journée en juillet (Merlot) et deux fois pendant la journée (le matin et l'après-midi), à deux dates différentes en août (Cabernet-Sauvignon). Les mesures de Ψ_l et Ψ_{stem}, de la conductance stomatique et de la transpiration ont été faites au niveau des rameaux directement exposés au soleil ou des rameaux entièrement à l'ombre lors de la prise des mesures. Des différences significatives *($P < 0.05$)* ont été obtenues entre le Ψ_l et/ou le Ψ_{stem} mesurés sur les rameaux ensoleillés et ceux à l'ombre. Les deux potentiels (Ψ_l et Ψ_{stem}) ont été significativement plus importants pour les rameaux ensoleillés par rapport à ceux à l'ombre. Cependant, aucune différence significative n'a été notée entre le Ψ_l des feuilles à l'ombre et le Ψ_{stem} des rameaux ensoleillés.

Conclusions : Indépendamment de la méthode utilisée, les mesures simultanées des potentiels hydriques et de la conductance stomatique des feuilles exposées au soleil ont présenté une forte corrélation. Tous les moyens de mesure du potentiel hydrique de la vigne considérés dans cette étude ont été fortement corrélés entre eux.

Signification et impact de l'étude : Les données obtenues indiquent que toutes les techniques utilisées dans cette étude sont considérées comme des indicateurs sensitifs de l'état hydrique de la vigne et que le Ψ des feuilles à l'ombre pourrait être une alternative à la mesure du Ψ_{stem}.

Mots clés : potentiel hydrique, Cabernet-Sauvignon, Merlot

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INTRODUCTION

Methods to assess the water status of plants used in mechanistic and drought tolerant studies and for use in irrigation management have been reviewed (Jones, 2004; 2007). Pre-dawn leaf water potential (Ψ_{PD}) is often used in viticulture studies and critical values have been established for grapevines (Ojeda *et al.*, 2001). Pre-dawn Ψ has been shown to be correlated with stomatal conductance (g_s) and leaf net CO_2 assimilation rate (A) (Schultz and Stoll, 2010; Williams and Araujo, 2002). However, the main disadvantages for the use of Ψ_{PD} are the time of its measurement (Schultz and Stoll, 2010) and the fact that it may come into equilibrium with the wettest portion of the soil profile (Ameglio *et al.*, 1999) which would limit its use in drip irrigated vineyards (Williams and Trout, 2005). Santesteban *et al.* (2011) also concluded that similar Ψ_{PD} values among vineyards did not indicate similar levels of water stress.

Mid-morning, midday or mid-afternoon leaf (Ψ_l) and stem (Ψ_{stem}) water potentials are also used by scientists conducting research on grapevines and in commercial vineyards around the world as an irrigation management tool. Stomatal conductance and/or A have been shown to be highly correlated with midday Ψ_l (Williams, 2012; Williams and Araujo, 2002) and Ψ_{stem} (Patakas *et al.*, 2005). Midday Ψ_l has been shown to be highly correlated with daily water use of mature, field-grown grapevines (Williams *et al.*, 2012) while Choné *et al.* (2001) concluded that Ψ_{stem} or the difference between Ψ_l and Ψ_{stem} provided an indirect measurement of leaf transpiration. Both midday Ψ_l and Ψ_{stem} have been shown to better reflect differences in soil water content, soil matric potential and applied water amounts than Ψ_{PD} under drip irrigation (Williams and Trout, 2005). Lastly, non-water stressed values of Ψ_l and Ψ_{stem} have been established for potential use in vineyard irrigation management (Williams and Baeza, 2007; Williams and Trout, 2005).

Stem Ψ is determined by covering the leaf blade with a plastic bag and a reflective material for a certain amount of time allowing the leaf's Ψ to come into equilibrium with that of the stem's Ψ. The time allowed for this equilibrium to occur on grapevines ranges from placing the bags on the leaves the day before the measurements (Salón *et al.*, 2005), 2 h (Romero *et al.*, 2010) to 1.5 h (Santesteban *et al.*, 2011) before measurements and at least 10 minutes before measurements are taken (Shackel, 2007). A more typical time of 1 h has been used by many (Choné *et al.*, 2001; De la Hera *et al.*, 2007; Marsal et al, 2008; Olivo *et al.*, 2009; Patakas *et al.*, 2005; Williams and Araujo, 2002). Some feel that Ψ_{stem} has an advantage over Ψ_l since it is often assumed to better reflect the water status of the whole plant, is less affected by environmental factors and is able to detect differences among treatments to a greater extent than Ψ_l (Choné *et al.*, 2001; Patakas *et al.*, 2005; van Leeuwen *et al.*, 2006), but this view is not shared by all (Intrigliolo and Castel, 2006; Santesteban *et al.*, 2011). It has been demonstrated that Ψ_{stem} is affected by vapor pressure deficit (VPD) at the time of measurement in trees (McCutchan and Shackel, 1992; Shackel *et al.*, 1997) and grapevines (Olivo *et al.*, 2009; Williams and Baeza, 2007), similar to the response of Ψ_l to VPD in grapevines (Williams and Baeza, 2007). Olivo *et al.* (2009) also reported that the response of Ψ_{stem} to VPD varied across the growing season. Numerous papers have reported that Ψ_l and Ψ_{stem} are highly correlated with one another (Salón *et al.*, 2005; Stevens *et al.*, 1995; Williams, 2010; Williams and Araujo, 2002). Therefore it is surprising others have reported that changes in Ψ_{stem} are not mimicked by changes in Ψ_l (Choné *et al.*, 2001; Patakas *et al.*, 2005). Such would likely occur if the technique used in those studies to measure Ψ_l did not involve enclosing the leaf blade in a plastic bag just prior to severing the petiole. The failure to do so would result in erroneous values of Ψ_l (Turner and Long, 1980; Williams and Araujo, 2002; Williams *et al.*, 2012).

Shackel (2007) has demonstrated that Ψ_{stem} could differ by 0.2 MPa on the same grapevine due to random chance and/or measurement error. The first objective of this study was to determine if Ψ_{stem} varied significantly on an individual grapevine. To accomplish this, Ψ_{stem} was determined on shoots entirely exposed to direct solar radiation or completely in the shade on the same vine at the time of measurement. It was felt that shoot transpiration would differ considerably when these two were compared and possibly result in differing values of Ψ_{stem}. In addition, the choice of these two shoot types reflects differences among studies (referred to in the previous paragraph) in selecting which leaf will be bagged to measure Ψ_{stem}.

It has been demonstrated that the Ψ of shaded leaves on grapevines follows the same diurnal pattern as that of leaves exposed to direct sunlight and respond to differences in the amount of water applied similarly to that of Ψ_l (van Zyl, 1987). It has also been shown that the Ψ of shaded leaves on almond (*Prunus domestica* L.) trees is highly correlated with Ψ_{stem} (Goldhamer and Fereres, 2001) as is the Ψ of shaded leaves on pistachio (*Pistacia vera* L.) trees with the crop water stress index (Testi *et al.*, 2008). Therefore the second objective of this study was to compare Ψ_l of shaded leaves to that of Ψ_{stem} measured on the two shoot types (sunlit and shaded) on the same vine. This was to determine whether shaded leaf Ψ was correlated with other means of assessing water status of grapevines and if it were a viable alternative to measuring either Ψ_l or Ψ_{stem}.

MATERIALS AND METHODS

1. Vineyard sites

The first vineyard site was a *Vitis vinifera* L. cv. Merlot vineyard located near the city of Madera (lat. 36°55'N; long. 120°9'W) in the San Joaquin Valley of California. The vines were planted on their own roots with 2.13 and 3.66 m vine and row spacings, respectively. The vines were trained to a bilateral cordon. The trellis was a cordon wire at a height of 1.28 m and a foliage catch wire 0.3 m above that. The canopy that develops using this training/trellis system with no shoot positioning has typically been referred to as the 'California sprawl'. Vineyard rows were approximately east/west. Vines were drip-irrigated at 0.4, 0.8 or 1.2 of estimated evapotranspiration (ET_c) once irrigation commenced. The three irrigation treatments were achieved using different numbers of emitters or emitters with different discharge rates. Vineyard ET_c was estimated as the product of reference ET (ET_o) and seasonal crop coefficients (K_c) (Allen *et al.*, 1998). The seasonal K_cs used to schedule irrigations at this site were developed by measuring the shade cast on the ground beneath the canopy at solar noon and then using the relationship between the percentage of shade and the K_c given in Williams and Ayars (2005). The shaded area beneath the canopy was determined with a digital camera as outlined in Williams and Ayars (2005). Reference ET was obtained from the California Irrigation Management Information System (CIMIS) weather station (#145) located ~15 km from the vineyard. Variables measured and calculations used to determine daily ET_o from CIMIS can be found in Snyder and Pruitt (1992). Irrigation treatments each year in this vineyard did not commence until midday Ψ_l reached -1.0 MPa for vines in the 1.2 irrigation treatment. Vines were irrigated once weekly, beginning on Friday and ending by Sunday, with applied water amounts equal to that required for the week. Applied water amounts were measured with inline (in the drip line) water meters.

The second vineyard site, located near Paso Robles (lat. 35°41'N; long. 120°39'W), was planted to *V. vinifera* cv. Cabernet-Sauvignon grafted onto the rootstock 5C. Vine and row spacings in the vineyard were 1.83 and 3.05 m, respectively. The vines were trained to bilateral cordons and the trellis was a VSP (vertical shoot positioning). Row direction was approximately north/south. The first irrigation treatment consisted of vines irrigated at 1.12 of estimated ET_c. The second treatment consisted of irrigating vines once every two weeks with 90.7 L (16.2 mm) of water per vine and was designated as the DD (dry down) treatment. The seasonal crop coefficients used were those for a VSP trellis at a row width of 3.05 m (Williams, 2010). Reference ET was obtained from the PR1 weather station operated by the Paso Robles Wine Country Alliance (PRWCA), located ~3 km from the vineyard. Calculation of applied water amounts was similar to that described for the Merlot site. Vines were irrigated 1 to 3 times weekly, depending upon the required amounts.

2. Vine water status

Water potentials at both locations were measured as described by Williams and Araujo (2002). Specifically, leaf (Ψ_l) and stem (Ψ_{stem}) water potentials were measured with a pressure chamber (model 1000; PMS Instrument, Corvallis, OR) on fully expanded, mature leaves. Leaf blades for Ψ_l determinations were covered with a plastic bag, quickly sealed and petioles then cut within 1 to 2 sec. The time between leaf excision and chamber pressurization was generally less than 10 to 15 sec. Approximately 60 min before measurements, leaves for determination of Ψ_{stem} were enclosed in plastic bags covered with aluminum foil. The plastic bag and aluminum foil enclosing the leaf blades used for Ψ_{stem} measurements were also inserted into the chamber during pressurization. Stomatal conductance (g_s) and leaf transpiration (E) were measured with a steady-state diffusion porometer (model 1600; LI-COR, Lincoln, NE) on the leaves used for Ψ_l measurements.

Leaves selected for Ψ measurements were either from shoots entirely exposed to direct solar radiation (referred to as sunlit shoots) or shoots totally in the shade (referred to as shaded shoots) at the time of measurement. The leaves were generally located at node positions 7 or 8 from the base of the shoot. Leaves chosen for Ψ_l on the sunlit shoots were also exposed to direct sunlight. Leaves chosen for shaded Ψ_l were not exposed to any direct sunlight (such as sunflecks) prior to the time of measurement. Sunlit shoots were growing on the south side of the canopy while the shaded shoots were selected beneath shoots on the north side of the canopy in the Merlot vineyard. Measurements at this site were taken at midday (1300 – 1500 h Pacific daylight time [PDT]) on a single date. Measurements of Ψ and gas exchange were taken during the morning (0930 – 1030 h PDT) and afternoon (1530 – 1630 h PDT) on two different dates at the Paso Robles site. Sunlit and shaded shoots were selected from the east and west sides of the canopy, respectively, at this location during the morning measurement periods and just the opposite during the afternoon measurement periods. An additional sheet of aluminum foil was placed above the leaf chosen for Ψ_{stem} on the sunlit shoots at midday (Madera site) and during the afternoon (Paso Robles site) to further minimize heating effects. The sunlit and shaded shoots at both locations were growing on the same cordon close to one another but not necessarily on the same arm.

3. Temperature and relative humidity

Temperature and relative humidity were measured at both locations with two hand-held temperature/relative humidity probes (model DM-84 Multimeter with MultiMeterMateRH/T probe, A.W. Sperry Inst., Inc., Hauppauge, NY) and on occasions a Pocket Sling Psychrometer (Cole-Parmer, Vernon Hills, IL). The probes were positioned just beneath the canopy of vines trained to the VSP trellis (ensuring they were in the shade) and just below the fruiting zone of vines at the other vineyard site. The probes were placed at two different locations within two of the irrigation treatment plots. Measurements with the sling psychrometer were made between rows at a height of ~2 m. The probes were routinely calibrated in the laboratory and the outputs from the two were within 1°C and 2 % relative humidity. Photon flux density (PFD) was measured with a quantum sensor (model LI-190SA; LI-COR) or with the quantum sensor attached to the porometer when measuring shaded Ψ_l and g_s.

4. Data collection

Seven individual vines in each irrigation treatment at the Madera site were chosen for data collection. On each individual vine replicate a sunlit and shaded shoot were tagged and used for measurements. Ψ_l and Ψ_{stem} were determined on the same shoot of each shoot type (sunlit or shaded). At the Paso Robles site five and four individual vines within each irrigation treatment on the first and second data collection dates, respectively, were chosen and shoots tagged. The same vines were used for both the morning and afternoon measurements on the respective dates with other information as given for the Merlot study site. Data were analyzed via analysis of variance (ANOVA) using CoStat v. 6.400 (CoHort Software, Monterey, CA, USA). Means were separated using Duncan's Multiple range test. Linear correlations and regressions were also run on the data using CoStat.

Table 1. Comparisons among leaf (Ψ_l) and stem (Ψ_{stem}) water potentials measured on shoots that were fully exposed to direct solar radiation (sunlit) or those that were entirely in the shade of the canopy (shaded) of Merlot grapevines growing near Madera in the San Joaquin Valley of California. Irrigation treatments included vines receiving applied water amounts at various fractions (0.4, 0.8 and 1.2) of estimated ET_c. Stomatal conductance (g_s) and transpiration (E) values are also given for each treatment and shoot type.

Irrigation Treatment (Fraction of ET_c)	Sunlit Shoot		Shaded Shoot	
	(Ψ_l)	(Ψ_{stem})	(Ψ_l)	(Ψ_{stem})
			Ψ (MPa)	
1.2	-0.89 c	-0.59 b	-0.56 b	-0.46 a
0.8	-1.16 c	-0.92 b	-0.89 b	-0.80 a
0.4	-1.38 c	-1.18 b	-1.18 b	-1.06 a
			g_s (mmol m^{-2} s^{-1})	
1.2	658 ± 15	--	285 ± 20	--
0,8	483 ± 26	--	194 ± 14	--
0,4	237 ± 21	--	98 ± 5	--
			E (mmol m^{-2} s^{-1})	
1.2	29.9 ± 0.7	--	12.4 ± 0.9	--
0,8	20.6 ± 1.1	--	7.7 ± 0.6	--
0,4	10.2 ± 0.9	--	3.9 ± 0.3	--

Measurements were taken on 25 July, 2002, between 1300 and 1500 hours. Ambient temperature, vapor pressure deficit (VPD) and photon flux density (PFD) during the measurement period averaged 36.2°C 4.84 kPa and 1758 mmol photons m^{-2} s^{-1}, respectively. Mean PFD for leaves measured in the shade were 157, 157 and 137 mmol photons m^{-2} s^{-1} for the 0.4, 0.8 and 1.2 irrigation treatments, respectively. Values of Ψ within a row for a particular irrigation treatment followed by a different letter are significantly different at $P < 0.05$. Values of g_s and E represent the means ± SE. (n = 7)

RESULTS

Estimated ET_c the week prior to 25 July at the Madera site was 30.8 mm (240 L vine^{-1}). Applied water amounts the weekend prior to 25 July were 1.19, 0.79 and 0.42 of estimated ET_c for the 1.2, 0.8 and 0.4 irrigation treatments, respectively. Reference ET on 25 July was 6.6 mm at the Madera site.

This was the first year of the irrigation study in this Paso Robles vineyard and irrigation treatments were not imposed until 24 June. Estimated ET_c at the Paso Robles site for the week of 5 to 11 August was approximately 16.8 mm (~ 94 L vine^{-1}) while that for the week of 20 to 26 August was approximately 15.5 mm (~ 87 L vine^{-1}). Applied water amounts for the 1.12 treatment were 0.9 of estimated ET_c the week of 5 to 11 August while that for the week of 20 to 26 August was only 0.78 of estimated ET_c. As mentioned in the Materials and Methods section, the DD treatment was irrigated once every two weeks with ~ 90 L vine^{-1}, which would be equivalent to ~ 50 % of estimated ET_c over a two week period at this time of the season. Vines in this treatment were irrigated 13 days prior to 7 August with ~ 80 L vine^{-1} and then irrigated on 8 August with ~ 70 L vine^{-1}. Therefore, vines of the DD treatment had been irrigated 13 days prior to measurements taken on 21 August.

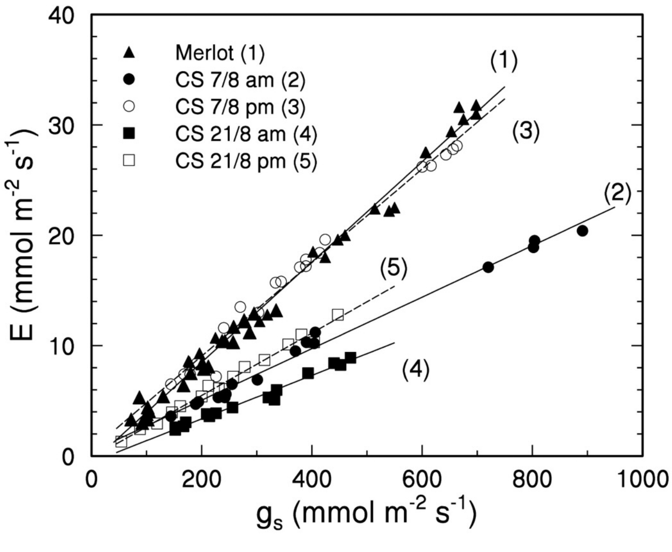

Figure 1. The relationship between leaf transpiration (E) and stomatal conductance (g_s) measured on Merlot and Cabernet-Sauvignon (CS) grapevines. Measurements on the Cabernet-Sauvignon vines took place on 7 and 21 August (7/8 and 21/8) either in the morning (am) or afternoon (pm). Data points include measurements taken on both sunlit and shaded leaves. Regressions for each data set are as follows: (1) y = -0.594 + 0.0454x, R^2 = 0.99; (2) y = 0.391 + 0.0233x, R^2 = 0.99; (3) y = 0.571 + 0.0424x, R^2 = 0.98; (4) y = -0.582 + 0.0197x, R^2 = 0.98; (5) y = -0.182 + 0.0283x, R^2 = 0.99.

There were significant differences between Ψ_l measured on leaves from the sunlit and shaded shoots of Merlot grapevines across the irrigation treatments (Table 1). There were also significant differences in Ψ_{stem} between the two shoot types. However, there was no significant difference between Ψ_{stem} of the sunlit shoot and Ψ_l of the shaded shoot. There were significant differences among irrigation treatments regardless of the method used to measure vine water status. All four methods of measuring vine water status were equally sensitive ($P < 0.001$ for all methods) in detecting those differences among treatments. Both g_s and E measured at midday decreased as applied water amounts decreased whether the measurements were taken on leaves in the sun or the shade.

Evaporative demand differed between dates and the two time-of-day measurement periods at Paso Robles. Ambient temperature and VPD the afternoon of 7 August was similar to those at the Madera site on 25 July. There were significant differences between Ψ_l measured on Cabernet-Sauvignon leaves of sunlit and shaded shoots regardless of irrigation treatment, time of day or date of measurement (Table 2). Similar results were obtained with the Ψ_{stem} data except on 21 August at 1000 h for the 1.12 irrigation treatment. There were no significant differences across treatments, dates or times between Ψ_{stem} of the sunlit shoot and Ψ_l of the leaves on the shaded shoots. There were significant differences in vine water status between the two irrigation treatments regardless of which technique was used across dates and time of day ($P < 0.001$ for all comparisons). Values of g_s and E of Cabernet-Sauvignon were affected by irrigation treatment, shoot type (sunlit vs. shaded) and time of day (Table 3). The response of leaf E to g_s at the Paso Robles site was affected by time of day and the date the measurements were taken (Figure 1). The slope of that relationship the afternoon of 7 August was similar to that of Merlot. The VPD at the time of measurement in the Cabernet-Sauvignon vineyard the afternoon of 7 August and in the Merlot vineyard were 4.65 and 4.84 kPa, respectively. The VPDs at the time of measurements at Paso Robles the morning of 7 August and both times on 21 August were less than 2.6 kPa.

Both g_s and E (measured on sunlit and shaded leaves) were linearly related to Ψ_l (measured on sunlit and shaded leaves, respectively) at the Madera site (Figure 2). Correlations between g_s (measured on sunlit leaves) and Ψ_{stem} measured on sun and shade shoots and Ψ_l measured on shaded leaves were similar to that of Ψ_l with *r* values being 0.95, 0.93 and 0.94, respectively ($P < 0.001$ for all correlations). Similar types of correlations with g_s data

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Table 2. Comparisons among leaf (Ψ_l) and stem (Ψ_{stem}) water potentials (MPa) measured on sunlit and shaded shoots of Cabernet-Sauvignon in a vineyard near Paso Robles, California. Irrigation treatments consisted of vines receiving applied water amounts at 1.12 of estimated ET_c (1.12) and vines that had not been irrigated for two weeks prior to measurement (DD). Ambient temperature and vapor pressure deficit (VPD) at the time of measurement are also given.[a]

Date (day/mo)	Time[b] of Day (h)	Temp. (°C)	VPD (kPa)	Irrigation treatment	Shoot Type: Sunlit (Ψ_l)	Sunlit (Ψ_{stem})	Shaded (Ψ_l)	Shaded (Ψ_{stem})
7/8	1000	25,2	2,19	1,12	-0.71 c	-0.52 b	-0.51 b	-0.46 a
				DD	-1.16 c	-0.93 b	-0.91 b	-0.83 a
	1600	34,1	4,65	1,12	-1.02 c	-0.83 b	-0.83 b	-0.68 a
				DD	-1.40 c	-1.21 b	-1.18 b	-1.08 a
21/8	1000	22,6	1,53	1,12	-0.56 c	-0.37 ab	-0.39 b	-0.35 a
				DD	-1.25 c	-0.93 b	-0.92 b	-0.78 a
	1600	28,4	2,64	1,12	-0.92 c	-0.68 b	-0.68 b	-0.53 a
				DD	-1.30 c	-1.05 b	-1.08 b	-0.91 a

[a] Values of Ψ within a row for a particular irrigation treatment are significantly different at $P < 0.05$. (n = 5 on 7 August and 4 on 21 August)
[b] The PFD on 7/8 and 21/8 at 1000 and 1600 hours were 1836 and 1825 and 1501 and 1541 μmol photons m^{-2} s^{-1}, respectively

Table 3. The effect of date, time of day, irrigation treatment and shoot type on leaf stomatal conductance (g_s) and transpiration (E) measured on Cabernet-Sauvignon grapevines. Other information is as given in Tables 1 and 2.

Date (day/mo)	Time of Day (h)	Irrigation treatment	Shoot Type: Sunlit (g_s) (mmol m^{-2} s^{-1})	Shaded (g_s)	Sunlit (E)	Shaded (E)
7/8[a]	1000	1,12	824 ± 70	254 ± 16	19.0 ± 0.7	5.8 ± 0.4
		DD	393 ± 8	196 ± 23	10.3 ± 0.4	4.9 ± 0.6
	1600	1,12	645 ± 14	360 ± 30	27.1 ± 0.5	14.4 ± 0.4
		DD	384 ± 27	182 ± 14	16.6 ± 0.2	7.4 ± 0.3
21/8[b]	1000	1,12	439 ± 15	190 ± 17	8.3 ± 0.3	3.3 ± 0.3
		DD	311 ± 16	171 ± 15	5.2 ± 0.3	2.8 ± 0.3
	1600	1,12	398 ± 19	248 ± 14	11.1 ± 0.6	6.9 ± 0.4
		DD	216 ± 40	112 ± 25	5.8 ± 1.2	3.1 ± 0.8

[a] The PFD measured at the leaf blade surface for leaves on shaded shoots at 1000 and 1600 hours were 239 and 215 μmol photons m^{-2} s^{-1}, respectively.
[b] The PFD measured at the leaf blade surface for leaves on shaded shoots at 1000 and 1600 hours were 175 and 186 μmol photons m^{-2} s^{-1}, respectively.

from the Paso Robles site were made but separating them as a function of time of day and date (Table 4). Stomatal conductance of sunlit leaves was significantly correlated with Ψ_l of sunlit leaves on both dates and times of day at Paso Robles (Table 4). Comparisons of g_s measured on sunlit leaves with Ψ_{stem} (sunlit shoot), Ψ_{stem} (shaded shoot) and Ψ_l (shaded leaves) were similar to that described for Ψ_l across dates and time of day. The relationships between all measures of vine water status and E of sunlit leaves were comparable to those shown for g_s; *r* and *P* values were similar.

There was a significant relationship between E (measured on sunlit leaves) and the difference between Ψ_l measured on sunlit leaves and Ψ_{stem} measured on shaded shoots ($r = 0.73$, $P < 0.001$) at the Madera site (data not given). There was also a significant relationship between E (measured on sunlit leaves) and the difference between Ψ_l measured on sunlit leaves and Ψ_{stem} measured on shaded shoots the morning of 7 August ($r = 0.90$, $P < 0.01$) and in the afternoon on 21 August ($r = 0.94$, $P < 0.01$) at the Paso Robles site. However, there were no significant relationships between E and the difference between Ψ_l and Ψ_{stem} the afternoon of 7 August or the morning of 21 August at Paso Robles (data not given).

Morning and afternoon values of all techniques to measure vine water status at the Paso Robles site on both dates were significantly ($P < 0.05$ on 7 August and < 0.001 on 21 August) correlated with one another. The r values were > 0.76 for all but the Ψ_{stem} (shaded shoots) comparison which was 0.65 on 7 August. The r values for all techniques to measure vine water status comparing afternoon with morning measurements on 21 August were in excess of 0.96 (this value being for the Ψ_{stem} of shaded shoots). Similar types of relationships were found between morning and afternoon measurements of g_s on sunlit leaves.

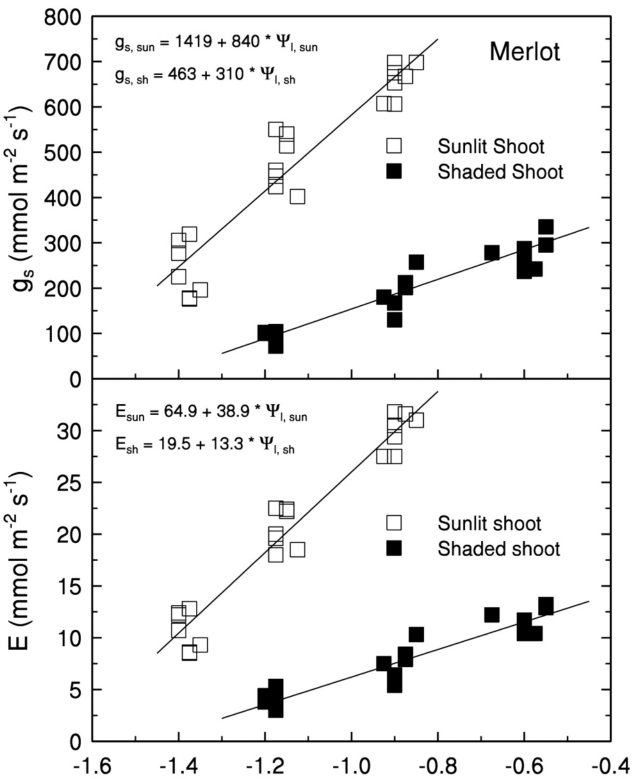

Figure 2. The relationships between stomatal conductance (g_s) and leaf transpiration (E) and leaf water potential (Ψ_l) measured on Merlot grapevines. Stomatal conductance, E and Ψ_l data were measured either on sunlit or shaded shoots. The r values for the sun and shade g_s linear correlations were 0.95 and 0.94, respectively. The r values for the sun and shade E linear correlations were 0.97 and 0.95, respectively.

Comparisons were made between all techniques to measure vine water status across locations, time of day and dates (Table 5). All techniques were significantly correlated with one another. There was almost a 1:1 relationship between values of shaded Ψ_l and Ψ_{stem} of sunlit shoots (Figure 3).

DISCUSSION

The data indicate that Ψ_{stem} can vary significantly on the same vine. The difference in Ψ_{stem} between the two shoot types of Merlot across irrigation treatments was fairly similar (~ 0.1 to 0.12 MPa). The differences in Ψ_{stem} between the two shoot types of Cabernet-Sauvignon ranged from none (the morning of 21 August for the 1.12 irrigation treatment) to 0.15 MPa. Shackel (2007) reported that any two values of Ψ_{stem} measured on the same grapevine differed by $\pm$ 0.1 MPa about 30 % of the time with differences of $\pm$ 0.15 MPa occurring 10 % of the time. The maximum difference between any two measurements reported by Shackel (2007) was $\pm$ 0.2 MPa. The maximum difference between any two Ψ_{stem} measurements on the same vine reported here was 0.3 MPa (1 out of 57 measurements) with a difference of 0.2 MPa the next highest value (2 out of 57 measurements). While the mean, maximum differences

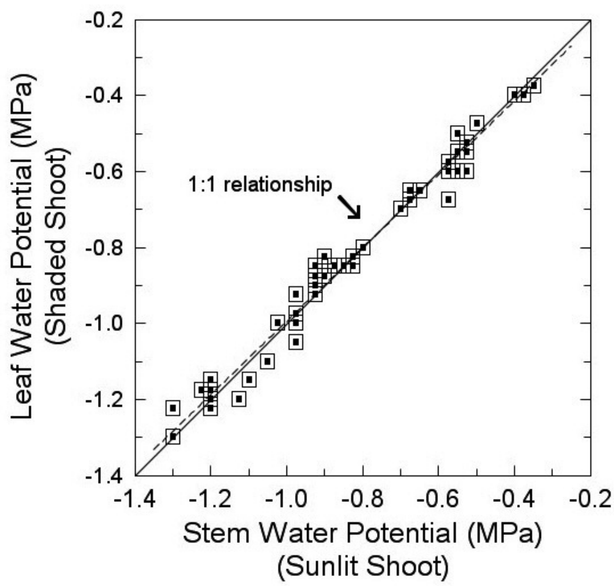

Figure 3. The relationship between leaf water potential measured on shaded leaves and stem water potential measured on a sunlit shoot. Values represent data collected in the Merlot vineyard and across time of day and between dates in the Cabernet-Sauvignon vineyard.
The dotted line represents the linear correlation between these two parameters (see Table 5).
The solid line represents a 1:1 relationship.

Table 4. The Pearson Product Moment Correlation Coefficient (r) for the relationship between stomatal conductance (g_s) measured on sunlit leaves and leaf (Ψ_l) and stem (Ψ_{stem}) water potentials of Cabernet-Sauvignon grapevines on two dates and two times of day in 2002. Other information is as given in Tables 2 and 3.

Date (day/mo)	Time (h)	Shoot Type	Water Potential Method	*r*	Significance[a]
7/8	1000	Sun	Ψ_l	0,97	***
			Ψ_{stem}	0,97	***
		Shade	Ψ_l	0,98	***
			Ψ_{stem}	0,97	***
	1600	Sun	Ψ_l	0,95	***
			Ψ_{stem}	0,97	***
		Shade	Ψ_l	0,98	***
			Ψ_{stem}	0,97	***
21/8	1000	Sun	Ψ_l	0,93	***
			Ψ_{stem}	0,93	***
		Shade	Ψ_l	0,93	***
			Ψ_{stem}	0,93	***
	1600	Sun	Ψ_l	0,87	**
			Ψ_{stem}	0,82	*
		Shade	Ψ_l	0,82	*
			Ψ_{stem}	0,86	**

a *, ** and *** represent significance at $P < 0.05$, < 0.01 and < 0.001, respectively.

reported in this study (0.15 MPa) between the two shoot types would appear to be minimal, measurements of vine water status in commercial vineyards are generally used to assign a 'critical value' after which an irrigation event would occur. The selection of a shoot located in the shade or the sun would provide differing values of Ψ_{stem} for the same vine.

The Ψ_{stem} of the sunlit shoot was always lower than that of the shaded shoot, never greater in this study. This was by design here as it was assumed transpiration of the sunlit shoot would be greater than that of the shaded shoot. The effect of an increase in E on Ψ_l due to increased frictional losses in the water pathway of plants can be described by rearranging the van den Honert (1948) equation (Jones, 1998):

$$\Psi_l = \Psi_{soil} - R_{sl} * E \quad (1)$$

where Ψ_{soil} is soil water potential and R_{sl} is the combined soil to leaf water flow resistance. The equation demonstrates that any change in E would affect Ψ_l. Transpiration of leaves on exposed shoots were 2 to almost 3 times greater than E of the shaded leaves on the same vine with Ψ_l more negative for the sunlit leaves compared to the shaded leaves as would be predicted by Equation 1. One could also conclude that differences in shoot E would affect Ψ_{stem} for shoots on the same vine and that Ψ_{stem} of the shaded shoot would be less negative than that of the exposed shoot as was shown in this study.

All techniques used to asses vine water status (Ψ_l, Ψ_{stem} and g_s on both sunlit and shaded shoots and leaves) in this study were highly correlated with one another. This would indicate that any of the techniques used would be a sensitive indicator of vine water status under the conditions of this study. The choice of which technique to use would be a function of the effect of the environment on the technique, reliability of the technique and its ease of use. It is often assumed that Ψ_l is more variable due to the effects of local environmental factors on E whereas Ψ_{stem} is less variable since the blades are covered and not transpiring (Choné *et al.*, 2001). However, Jones (1990) concluded that nearly all criticisms against the use of Ψ_l as a means to assess plant water status would be applicable to Ψ_{stem} to include that it is affected by environmental factors (Santesteban *et al.*, 2011). McCutchan and Shackel

Table 5. Linear correlations among the various determinations of vine water status measured in this study. Data were generated from Merlot and Cabernet-Sauvignon grapevines (see Tables 1 and 2 for specific details). All equations were significant at the P < 0.001 level. The term in the subscripts of the variables column following the comma, 'sun' and 'sh' represent shoot type, i.e. those that were exposed to direct sunlight or those that were entirely in the shade, respectively. The Pearson Product Moment Correlation Coefficient (r) is given in the rightmost column. n = 57

Variables	Equation	*r*
$\Psi_{l,sun}$ vs. $\Psi_{stem,sun}$	y = -0.285 + 0.943x	0.972
$\Psi_{l,sun}$ vs. $\Psi_{l,sh}$	y = -0.264 + 0.968x	0.975
$\Psi_{l,sun}$ vs. $\Psi_{stem,sh}$	y = -0.353 + 0.991x	0.956
$\Psi_{l,sh}$ vs. $\Psi_{stem,sun}$	y = -0.028 + 0.966x	0.989
$\Psi_{l,sh}$ vs. $\Psi_{stem,sh}$	y = -0.086 + 1.031x	0.987
$\Psi_{stem,sh}$ vs. $\Psi_{stem,sun}$	y = 0.044 + 0.923x	0.986

(1992) and Shackel *et al.* (1997) found that Ψ_{stem} of prune and deciduous nut and fruit trees, respectively, was responsive to VPD. Williams and Baeza (2007) found that Ψ_l and Ψ_{stem} of grapevines across cultivars and locations responded linearly to VPD, both decreased as VPD increased. Olivo *et al.* (2009) found that the response of a vine's Ψ_{stem} to VPD varied across the growing season but in general decreased as VPD increased. Both Ψ_l and Ψ_{stem} were also shown to be linearly reduced by increased ambient temperature (Williams and Baeza, 2007). Lastly, this study also demonstrated that the light environment of the shoot significantly affected Ψ_{stem}.

It is often assumed that Ψ_{stem} is able to detect differences in vine water status to a greater extent than that of Ψ_l and is more reliable (Choné *et al.*, 2001 ; Patakas *et al.*, 2005 ; van Leeuwen *et al.*, 2006). Values of Ψ_l and Ψ_{stem} in this study and those of Williams (2010), Williams and Araujo (2002) and Williams and Trout (2005) were significantly correlated with one another, as shown by others (Salón *et al.*, 2005 ; Stevens *et al.*, 1995). They were equally effective in detecting differences among irrigation treatments. Differences among studies concerning reliability and repeatability could be related to the method in which Ψ_l was measured. The technique used to measure Ψ_l in this study followed that described by Turner and Long (1980). The leaf blade was covered by a plastic bag just prior to severing the petiole and it remained on the blade through pressurization. This minimizes errors arising from rapid water loss subsequent to the blade being placed in the pressure chamber. Williams and Araujo (2002) and Williams *et al.* (2012) reported that differences in the Ψ of bagged leaves and those not bagged or only bagged after severing the petiole could result in differences of up to -0.6 MPa. Choné *et al.* (2001) did not bag leaves for the measurement of Ψ_l (X. Choné personal communication) while Patakas *et al.* (2005) only bagged the leaves after cutting the petiole (A. Patakas personal communication). The techniques used in those two studies would have resulted in erroneous values, thereby affecting the reliability of Ψ_l in detecting differences among treatments.

A disadvantage of using Ψ_{stem} to determine plant water status is the fact that the leaf blade needs to be covered in order to stop E and allow the Ψ of the leaf to come into equilibrium with that of the stem. The time used for this equilibrium in many grapevine studies is on average 1 h (Choné *et al.*, 2001 ; De la Hera *et al.*, 2007 ; Marsal *et al.*, 2008 ; Olivo *et al.*, 2009 ; Patakas *et al.*, 2005 ; Williams and Araujo, 2002). This would require one to bag leaves in the vineyard and then return 1 h later to take measurements. Shackel (2007) reported that grapevine leaves in his study were bagged a minimum of 10 min to determine Ψ_{stem} on leaves in the lower canopy (it is assumed that those leaves were either in the shade or at least partially shaded). Fulton *et al.* (2001) had previously determined that an equilibrium period of 10 min or longer appeared suitable to provide an accurate Ψ_{stem} measurement on three different tree species (*Prunus dulcis*, *P. domestica* and *Juglans regia*). The minimal amount of time used in the Shackel (2007) and Fulton *et al.* (2001) studies to determine Ψ_{stem} indicates that the Ψ_l of the leaves chosen were close to that of Ψ_{stem}. In this study, the difference between Ψ_l of shaded leaves and Ψ_{stem} of the shaded shoots ranged from 0.04 to 0.15 MPa, not a large difference. Therefore, the selection of leaves in the shade may lessen the time required for equilibration and shorten the interval between bagging the leaves and measuring Ψ_{stem}. Unfortunately, the time required for the sunlit leaves' Ψs to come into equilibrium with the stems' Ψs were not determined in this study. It is also unknown whether a study such as that conducted by Fulton *et al.* (2001) has been conducted on grapevines.

Goldhamer and Fereres (2001) found that the Ψ of shaded almond leaves were highly correlated ($R^2 = 0.94$) with Ψ_{stem} measured on the same trees. This only occurred once precautions were taken (shaded leaves were covered with a damp cloth prior to leaf excision) to minimize water loss during the measurement of shaded Ψ_l. In the Goldhamer and Fereres study, shaded Ψ_l was generally lower than that of Ψ_{stem}, similar to that found in this study for shaded Ψ_l compared to shaded shoot Ψ_{stem}. The high correlation between shaded Ψ_l and all other measures to assess vine water status in this study and the data of Goldhamer and Fereres (2001) and Testi *et al.* (2008) would indicate that shaded Ψ_l would be a viable alternative to the measurement of Ψ_{stem}. In addition, the almost 1:1 relationship between shaded Ψ_l and Ψ_{stem} of sunlit shoots would provide values of Ψ similar to Ψ_{stem} on a grapevine. Therefore the use of shaded Ψ_l to assess vine water status would not require an equilibrium period (bagging a leaf for a certain period of time to determine Ψ_{stem}), thus saving time. The same could be said for the measurement of the Ψ of sunlit leaves. However, as with the measurement of Ψ_l precautions should be made to minimize water loss from the time the petiole is severed until the blade is placed in the pressure chamber to determine shaded Ψ_l.

Choné *et al.* (2001) reported that E was significantly correlated with Ψ_{stem} or the difference between Ψ_l and Ψ_{stem}, but not with Ψ_l. This differs from that found in this study where all measures of vine water status were significantly correlated with E. It was found here that the difference between Ψ_l of sunlit leaves and Ψ_{stem} of the shaded shoots (similar to the comparison in Choné *et al.*, 2001) was significantly correlated with E but the correlation coefficient (0.73) was much less than those for the comparisons of E (of sunlit leaves) and Ψ_l (of both sunlit and shaded leaves) and Ψ_{stem} (of both sunlit and shaded shoots). If the difference between Ψ_l and Ψ_{stem} were truly predictive of E then one would have found a significant correlation between shaded Ψ_l and shaded Ψ_{stem} and shaded leaf E. None were found in this study (data not given). Differences regarding the relationship of E and Ψ_l between this and the Choné *et al.* (2001) study is probably due to the method in which Ψ_l was measured in the two studies. Such differences have been noted earlier in the Discussion.

All measures of vine water status in this study were highly correlated with g_s. Shackel (2007) reported that g_s of Pinot noir was also highly correlated with both Ψ_l and Ψ_{stem} ($R^2 = 0.88$ and 0.85, respectively) as did Williams *et al.* (2012) for Ψ_l. The results from this study, those of Shackel (2007) and Williams *et al.* (2012) and that of De Bei *et al.* (2011), who stated that a good correlation exists between Ψ_l and g_s for many grapevine cultivars, are counter to the conclusions of Lovisolo *et al.* (2010), who reported that there is no apparent relationship between midday measurements of grapevine g_s and Ψ_l.

The regulation of g_s in plants it thought to be controlled by hydraulic and/or non-hydraulic factors (Jones, 1998; Tardieu and Simonneau, 1998). The relationship between g_s and Ψ_l or shaded leaf g_s and shaded leaf Ψ_l in this and other studies on grapevines indicates possible hydraulic control of g_s with the direct mechanistic link being Ψ_l. However, Jones (1998) argued that the true driving variables for control of g_s are VPD and Ψ_{soil}. It has been demonstrated that grapevine Ψ_l and Ψ_{stem} are highly correlated with Ψ_{soil} (Williams and Trout, 2005). Therefore, the good relationship between g_s and all measures of vine water status in this study could be the result of the latter measurements being highly dependent upon Ψ_{soil}. In addition, g_s of vines in the 1.12 irrigation treatment at the Paso Robles site significantly decreased from morning to afternoon on 7 August, when VPD increased from 2.19 to 4.65 kPa, respectively, and corresponded to increases in E at a particular VPD (Figure 1). This is similar to the results of Cuevas *et al.* (2006), who found decreases in g_s between morning and afternoon measurements on Tempranillo grapevines planted to north/south rows. These results would indicate that VPD was also a driving variable of g_s. However, no such differences were found between g_s measurements in morning and afternoon for the DD treatment on 7 August or for the 1.12 treatment on 21 August. The small differences in VPD between morning and afternoon on 21 August may explain the lack of differences in g_s (sunlit leaves) of the 1.12 treatment vines whereas soil water availability for the DD treatment on 7 August would predominate with Ψ_{soil} controlling g_s.

Conversely, Ψ_l may be the dependent variable with g_s, via changes in E, the independent variable (Jones, 1998). The dependence of Ψ_l on E is also illustrated in this study. When leaf E increased from 12.4 (for the shaded leaves) to 29.9 mmol m^{-2} s^{-1} (for the sunlit leaves) of Merlot grapevines irrigated at 1.2 of estimated ET_c (Table 1), Ψ_l decreased from -0.56 to -0.89 MPa, respectively, (a change of 0.33 MPa) as one would predict from Equation 1. As leaf E increased, comparing leaves in the shade to those in the sun, by 12.9 (for the 0.8 treatment) and 6.3 mmol m^{-2} s^{-1} (for the 0.4 irrigation treatment), Ψ_l decreased by 0.27 and 0.2 MPa, respectively. Again the decreases in Ψ_l and their magnitude for these two treatments would be predicted from Equation 1. These results indicate that variations (to include diurnal changes) in Ψ_l and/or Ψ_{stem} on a single vine or vines within, for example an irrigation treatment, are the result of changes in g_s or E due to environmental factors (VPD and light). However, absolute values of Ψ_l (Ψ_{stem}) and g_s are a function of the amount of water in the soil profile (or Ψ_{soil}) once the soil is below field capacity (Williams *et al.*, 2012). Thus, the influence of the environment on regulating Ψ_l via its effect on g_s and E diminishes as the soil dries and this has been demonstrated by Williams and Baeza (2007).

While all techniques used to measure vine water potential in this paper were sensitive indicators of vine water status and highly correlated with one another their relationships with vine growth and productivity were not assessed. However, the relationships between midday Ψ_l and daily whole vine E or various aspects of vine growth have been determined. It has been demonstrated that midday measurements of Ψ_l and g_s are highly correlated with the daily ET_c / ET_o ratio (Williams *et al.*, 2012) and that seasonal mean values of Ψ_l are highly correlated with vegetative and reproductive growth of Thompson Seedless (Grimes and Williams, 1990 ; Williams *et al.*, 2010a ; 2010b) and Cabernet-Sauvignon grapevines (Williams, 2010). Based upon the results presented herein the other techniques used in this study to determine vine water status would more than likely also be correlated with those growth parameters and effectively used in an irrigation management program.

CONCLUSIONS

The values of Ψ_l (ranging from -1.4 to -0.39 MPa) or Ψ_{stem} (ranging from -1.21 to -0.35 MPa) measured in this study provided a wide range of values in which conclusions could be drawn. All methods to assess vine water status, whether measuring Ψ_l or Ψ_{stem} on sunlit or shaded shoots (leaves) at mid-morning, midday or mid-afternoon, across cultivars and dates, were highly correlated with one another. They also reflected differences in the amount of water applied to vines in the various irrigation treatments. In addition, Ψ_l, Ψ_{stem} and g_s measurements taken mid-morning at Paso Robles were highly correlated with those measurements taken during the afternoon. The above would indicate that any means to assess vine water status with the techniques utilized in this study would be an integrative indicator of whole vine water status under the conditions of this study. An important advantage of measuring Ψ on either sunlit or shaded leaves would be the increased numbers of samples one could take since it would not be necessary to bag the leaves from minutes to hours for equilibration as done with Ψ_{stem}. This would be most helpful where the measurement of vine water status is used as a tool in an irrigation management program. However, one would have to ensure that the measurement of Ψ_l included precautions to minimize water loss from the time the petiole was severed until pressurization within the chamber.

There are other factors which should be considered as a source of variation if any of the above techniques are used in basic research or as a tool in an irrigation management program. The author in this study measured all variables, normalizing the data across locations, days and times. One may intuitively assume that Ψ_{stem} would provide a more reliable data set by minimizing operator error. However, Goldhamer and Fereres (2001) found that Ψ_{stem} values obtained by three different operators using the same trees varied significantly from one another throughout the day. Another source of significant variation in the use of plant based measures of vine water status would be vine to vine variability, even when Ψ_{stem} was utilized (van Leeuwen *et al.*, 2006). Such may have been minimized in this study as all treatments were irrigated on a regular basis and the vines' water status not entirely dependent upon soil water availability.

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