

Midday measurements of leaf water potential and stomatal conductance are highly correlated with daily water use of Thompson Seedless grapevines

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Abstract A study was conducted to determine the relationship between midday measurements of vine water status and daily water use of grapevines measured with a weighing lysimeter. Water applications to the vines were terminated on August 24th for 9 days and again on September 14th for 22 days. Daily water use of the vines in the lysimeter (ET_{LYS}) was approximately 40 L vine⁻¹ (5.3 mm) prior to turning the pump off, and it decreased to 22.3 L vine⁻¹ by September 2nd. Pre-dawn leaf water potential (Ψ_{PD}) and midday Ψ_1 on August 24th were -0.075 and -0.76 MPa, respectively, with midday Ψ_1 decreasing to -1.28 MPa on September 2nd. Leaf g_s decreased from ~500 to ~200 mmol m⁻² s⁻¹ during the two dry-down periods. Midday measurements of g_s and Ψ_1 were significantly correlated with one another ($r = 0.96$) and both with ET_{LYS}/ET_o ($r = \sim 0.9$). The decreases in Ψ_1 , g_s , and ET_{LYS}/ET_o in this study were also a linear function of the decrease in volumetric soil water content. The results indicate that even

modest water stress can greatly reduce grapevine water use and that short-term measures of vine water status taken at midday are a reflection of daily grapevine water use.

Introduction

Irrigated agriculture needs to become more water use efficient due to increasing demands and when annual rainfall within a crop production area is below normal (Larus 2004; Morison et al. 2008). This is especially true in California where the competition among environmental, agricultural and urban demands for limited water supplies continues to increase. Grapevines grown at most locations in California are irrigated at least some time during the growing season due to the fact that the majority of rainfall will occur during the dormant portion of the growing season and that grapevine water use will exceed the amount of water held in the soil reservoir (Williams and Matthews 1990). Seasonal evapotranspiration (ET_c) of young to mature grapevines grown in the San Joaquin Valley can range from 200 to 800 mm, while estimated ET_c of mature wine grape vineyards at different locations in California may vary from 450 to 800 mm per growing season (Williams and Baeza 2007; Williams et al. 2003a, b; Williams and Ayars 2005a, b). Differences in ET_c among and within the different grape commodities are a function of trellis type and row spacing (Williams and Ayars 2005b).

Fereres and Soriano (2007) have suggested that the potential for water conservation in tree and vine crops may be greater than those of field crops since they are more highly coupled to the atmosphere. However, they also pointed out that the use of deficit irrigation in orchards and vineyards will require close monitoring of soil and/or plant water status so as to minimize risk. There are numerous

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tools one can use to monitor vine water status or assist in scheduling vineyard irrigations (Cifre et al. 2005; Jones 2004).

Currently, the most widely used technique to monitor vine water status in California's commercial vineyards is midday Ψ_1 and to a lesser extent midday Ψ_{stem} (L.E. Williams, personal observation). Recently, porometers are being used in the north coast wine production regions (Sonoma and Napa counties) of California by both consultants and growers to aid in irrigation management (R. H. Smith, personal communication). Soil water availability also is being monitored with neutron probes by a few crop consultants, while some grape growers may use tensiometers or electrical resistance type sensors. For the aforementioned techniques to be useful in an irrigation management program, the determination as to whether they are actually correlated with grapevine water use would be beneficial.

A weighing lysimeter was installed in 1986 (Williams et al. 2003a) and used to measure water use of two Thompson Seedless grapevines to develop seasonal crop coefficients for the San Joaquin Valley of California (Williams et al. 2003a, b; Williams and Ayars 2005a, b). During August of 2005, the lysimeter pump was turned off for 9 days, irrigation resumed for 11 days and then the pump turned off a second time for 21 days. During this time frame, midday Ψ_1 and g_s and soil volumetric water content were measured frequently to determine whether daily grapevine water use during these periods was correlated with these short-term measures of vine/soil water status. Measurements were taken at midday since grapevine stomatal conductance and Ψ_1 reach their maximum and minimum diurnal values, respectively, during this time frame (Grimes and Williams 1990; Williams and Baeza 2007). It was also felt that limiting these measurements to the two vines growing in the lysimeter would reduce potential plant to plant variation one may encounter in vineyards (van Leeuwen et al. 2006) and orchards (Naor et al. 2006) while accurately measuring water use of mature grapevines with a weighing lysimeter (Allen et al. 1998).

Materials and methods

A weighing lysimeter was installed at the University of California's Kearney Agricultural Center located in the San Joaquin Valley of California (36°48'N, lat, 119°30'W, long.) in 1986. Two *Vitis vinifera* L. (cv. Thompson Seedless clone 2A) grapevine cuttings were planted in the lysimeter and in the surrounding 1.4-ha (168 m × 82 m) vineyard on 9 April 1987. The soil was a Hanford fine sandy loam (coarse-loamy, mixed, non-acid, thermic Typic Xerorthent). The trellis of the vines used in the study

consisted of a 2.13-m wooden stake driven 0.45 m into the soil at each vine. A 0.6-m cross-arm was placed atop the stake and wires attached at either end of the cross-arms to support the vine's fruiting canes. Row direction was approximately east/west. A detailed description of the lysimeter and calculations used to measure grapevine evapotranspiration (ET_o) are given elsewhere (Williams et al. 2003a, b). Reference ET (ET_o) data were obtained from a California Irrigation Management Information System (CIMIS) weather station located 2 km from the vineyard site. Variables measured and calculations used to determine hourly and daily ET_o from CIMIS can be found in Synder and Pruitt (1992).

Prior to the initiation of the study, two layers of 30-gauge, clear PVC film (Goss Plastic Film Corp., Los Angeles, CA) were used to cover the soil surface of the lysimeter on August 22 (day of year [DOY] 234) and held in place with weights. The soil remained covered by the plastic throughout the study except on September 13th and 14th (DOYs 256 and 257). On those days, the plastic was rolled to the edges of the lysimeter, exposing the wetted soil surface. Water use of the grapevines in the lysimeter will be designated ET_{LYS} to denote the fact that the soil surface was covered with plastic, so as to minimize soil evaporation (Steinberg et al. 1990).

The irrigation pump to the lysimeter was turned off on August 24 (DOY 236) at 1700 h. The pump was turned back on September 2 (DOY 245) at 1800 h. The next day, the lysimeter pump was run for five hours to supply additional water (~ 120 L vine⁻¹) to the soil. Thereafter, the lysimeter pump was activated when the vines used the equivalent of 2 mm of water or 8 L vine⁻¹. The lysimeter pump was turned off again on September 14 (DOY 257) at 1700 h and remained such until October 4 (DOY 278). The pump was activated for 1.5 h the next day and then allowed to irrigate as stated above.

Water potential measurements were conducted as described by Williams and Araujo (2002). Specifically, pre-dawn Ψ (Ψ_{PD}) measurements began at ≈ 0430 h and were finished prior to sunrise using a pressure chamber (Model 1000, PMS Instrument Co., Corvallis, Ore.). Mid-day measurements of leaf water potential (Ψ_1) generally were taken between 1230 and 1330 h, Pacific Daylight Time (PDT). Leaf blades for Ψ_{PD} and Ψ_1 determinations were covered with a plastic bag, quickly sealed, and petioles then cut within 1–2 s. The time between leaf excision and chamber pressurization was generally <10–15 s. Leaves, chosen for Ψ_{PD} and Ψ_1 were fully expanded and mature. At midday, Ψ_1 was measured on leaves exposed to direct solar radiation located on the top or south sides of the canopy. Two to three leaves from each of the lysimeter vines were measured and used for data analyses. While the number of leaves removed from each vine in the lysimeter

to measure Ψ_1 would have been upwards of 60 per vine, the total number of leaves from primary shoots on a mature Thompson Seedless grapevine can be greater than 1,500 (Williams 1987) with a total leaf area in excess of 20 m² vine⁻¹ (Williams 1987; Williams et al. 2003b, 2010a). Therefore, the removal of these leaves would only have had a minimal effect, if any, on water use and/or water status of these vines.

The difference between measured Ψ_1 of the lysimeter vines on a particular day and a fully irrigated Ψ_1 baseline as a function of vapor pressure deficit (VPD) at the time of measurement was calculated. The equation used to determine the fully irrigated baseline, taken from Williams and Baeza (2007), was:

$$\text{Fully irrigated } \Psi_1 = -0.49 - 0.079 \times \text{VPD} \quad (1)$$

Stomatal conductance (g_s) was measured with a steady-state diffusion porometer (Model 1600, LiCor, Lincoln, NE) on leaves similar to those used for Ψ_1 measurements. Measurements were taken on four to five leaves per vine. Temperature and relative humidity at the location of the lysimeter were measured with two temperature/relative humidity probes (Model DM-84 Multimeter with a MultiMeterMate RH/T probe, using a Vaisala HUMIDCAP[®] RH sensor, A.W. Sperry Inst., Inc., Hauppauge, NY). The probes were positioned just beneath the canopy of the two vines on either side of the lysimeter (making sure they were in the shade).

Soil water content (SWC) within the lysimeter was monitored using the neutron back-scattering technique with a neutron moisture probe (Model 503 DR Hydroprobe moisture gauge: Boart Longyear, Martinez, California). Two access tubes were placed 0.5 m from each vine within the lysimeter (approximately 1.0 m between the two tubes beneath the drip line) and inserted to a depth of 1.5 m. Readings were taken at depths of 0.23, 0.46, 0.76, 1.07, and 1.37 m from the soil surface. Field capacity of this soil type was approximately 22.8 percent by volume (θ_v), while SWC at a soil moisture tension of -1.5 MPa was approximately 8.0 θ_v (Araujo et al. 1995).

A comparison of midday Ψ_1 and g_s between the two vines growing in the lysimeter and vines growing elsewhere in the vineyard were made in response to: (1) the termination of irrigation during the first dry-down period and (2) the continued irrigation of vines during both dry-down periods. The vineyard was divided into quadrants and irrigation terminated in 3, half-rows during the first dry-down period, beginning August 24 (DOY 236). The continuously irrigated vines were in the same half-row in which the lysimeter was located during both dry-down periods.

The irrigation pump for the rest of the vineyard, to include the row the lysimeter was located, was controlled

by the lysimeter's datalogger (Campbell Scientific 21X Micrologger, Logan, Utah). Whenever vines within the lysimeter used 2 mm of water, the vineyard pump was activated and an irrigation event took place with an equivalent amount of water; 8 L vine⁻¹. The activation of a solenoid valve at the head of the row provided the appropriate amount of applied water. An in-line water meter upstream from the solenoid valve measured actual applied water amounts. It should be pointed out that the amount of water applied to these vines, once the lysimeter pump was turned off, slowly decreased and was less than that normally applied to vines at full ET_c .

Data were analyzed via correlation analysis or regression analysis using linear, quadratic, cubic, or other terms. Values presented in the figures represent the means of measurements from the two lysimeter-grown vines for midday Ψ_1 and g_s versus ET_{LYS} on the day measurements were taken. Measurements of Ψ_1 and g_s taken on vines growing outside the lysimeter represent the means of 6 individual replicates for Ψ_1 and 9 for g_s (two and three measurements per row for the vines outside the lysimeter for Ψ_1 and g_s , respectively). Differences in Ψ_1 and g_s between days or measurements made on vines in the lysimeter, the irrigated vines or the non-irrigated vines located elsewhere in the vineyard were analyzed via analysis of variance and means separated using Tukey's test.

Results

Maximum daily water use by the lysimeter vines during 2005 was almost 50 L vine⁻¹ on July 24th ($ET_o = 6.85$ mm), while mean daily ET_{LYS} was approximately 40 L vine⁻¹ just prior to turning the lysimeter pump off (Fig. 1). Subsequently, ET_{LYS} decreased to 22.3 L vine⁻¹ nine days later, increased to 30 L vine⁻¹ upon re-watering, and it ultimately decreased to 10 L vine⁻¹ at the end of the study just before turning the pump back on. During this time frame, ET_o ranged from greater than 6 mm per day to less than 3 mm per day. The ET_{LYS}/ET_o ratio was greater than 0.85 on August 26th and decreased to 0.53 and 0.39 on the last dates of the first and second dry-down periods, respectively. The ET_{LYS}/ET_o ratio increased from 0.75 to 0.85 when the plastic was rolled back to the edges of the lysimeter on DOY 256 and 257 and then back to 0.75 when the soil was covered again.

The uppermost soil depth was saturated with water when the vines were being irrigated (Fig. 2). The two uppermost soil depths experienced the greatest variation in θ_v during the course of the study, while the lowest depth varied only slightly during the first dry-down period. During the second dry-down period, θ_v decreased at all depths. The mean θ_v decreased shortly after irrigation was terminated during

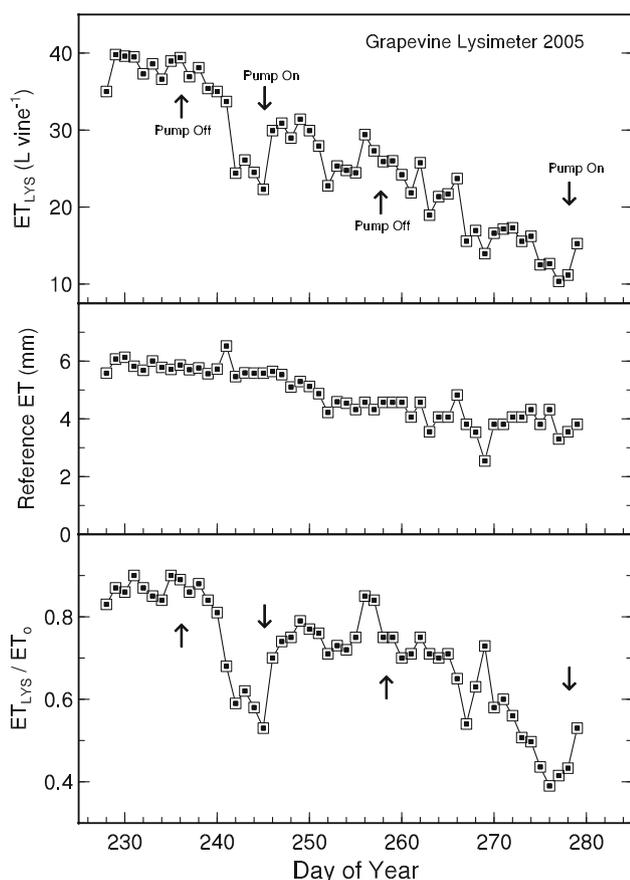


Fig. 1 Daily grapevine lysimeter water use (ET_{LYS}), reference ET (ET_o), and the ET_{LYS}/ET_o ratio measured from August 16 (DOY 228) to October 6 (DOY 279) in 2005. The arrows indicate the days in which the lysimeter pump was turned off or on during the study. The plastic covering the soil surface of the lysimeter was rolled back to the edges on the morning of September 15 (DOY 256) and back over the soil surface late afternoon on September 16 (DOY 257). The value of $L\ d^{-1}$ divided by 7.55 equals $mm\ d^{-1}$. Fruit from the vines was harvested September 30 (DOY 273)

both dry-down periods. The decrease in θ_v from August 24th to September 2nd and from September 15th to October 5th was equivalent to 222 and 302 $L\ vine^{-1}$ (assuming a rooting volume of 6 $m^3\ vine^{-1}$), respectively. The cumulative ET_{LYS} values during the same time frames were 294 and 374 $L\ vine^{-1}$, respectively.

Hourly ET_{LYS} of the vines having received no applied water for 9 days (September 2) increased to 90% of the daily maximum (which occurred at 1300 h) by 1100 h and started to decrease by 1400 h (Fig. 3). This differed from hourly ET_{LYS} data collected earlier (August 23–26) where the daily maximum occurred at 1400 h and ET_{LYS} at 1100 h was only 76% of the daily maximum. The diurnal time course of ET_{LYS} from September 11 to 15 (Fig. 4) mimicked that of the irrigated vines in August with the hourly maximum occurring at 1400 h. Toward the end of the second dry-down period, ET_{LYS} at 1100 h was 94% of the

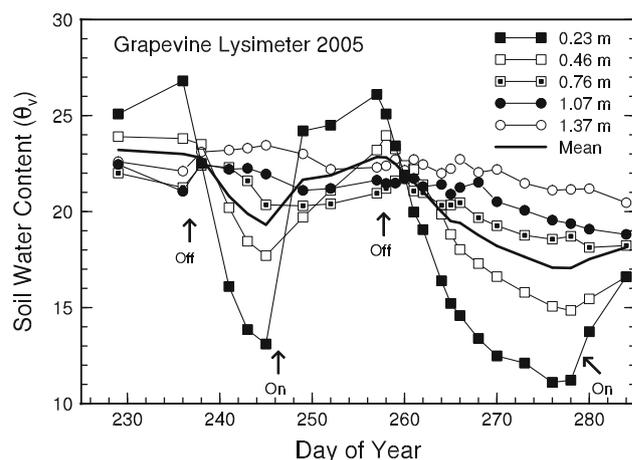


Fig. 2 Soil water content (θ_v) measured in the lysimeter at five depths from August 28 to October 11 in 2005. The mean θ_v of the five depths is also given. The arrows indicate the dates in which the lysimeter pump was turned off and on. The scale on the x axis is the same as that in Fig. 1

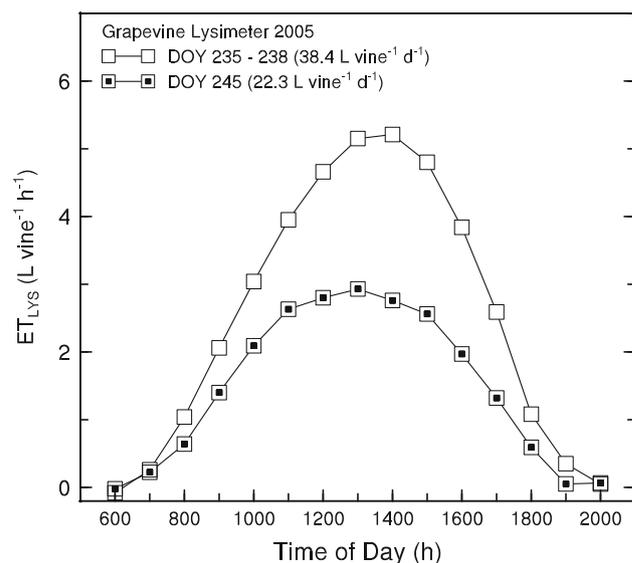


Fig. 3 The diurnal course of hourly ET_{LYS} measured from two days before to two days after the irrigation pump was turned off (August 23–26; DOYs 235–238) and the day before the pump was turned back on (September 2; DOY 245). The pump was turned off at 1700 h on August 24. Hourly data points for DOYs 235–238 and the daily ET_{LYS} values given in the figure are the means of those days. Daily ET_o for DOYs 235–238 and for DOY 245 was 5.76 and 5.58 mm, respectively. Maximum ambient temperature, solar radiation, and vapor pressure deficit for the two data sets were 36.0 and 35.5°C, 874 and 834 $W\ m^{-2}$, and 5.11 and 4.47 kPa, respectively. All days were cloud free

maximum, which occurred at 1200 h and had decreased to 76% of maximum by 1500 h. There was a significant ($P < 0.001$) linear relationship between daily ET_{LYS}/ET_o and midday (1200–1400 h) ET_{LYS}/ET_o during the course

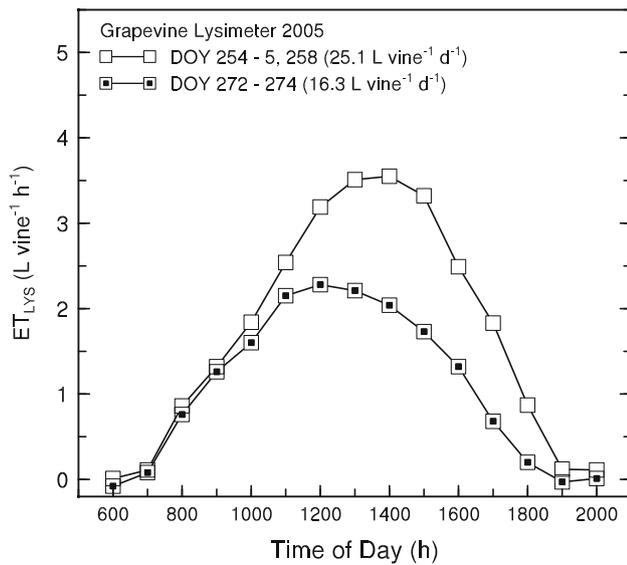


Fig. 4 The diurnal course of hourly ET_{LYS} measured two days before (September 11 and 12; DOY 254 and 255) and the day after the irrigation pump was turned off a second time (September 15; DOY 258) and from September 29 to October 1 (DOYs 272–274). The pump was turned off at 1700 h on September 14. Hourly data points and the daily ET_{LYS} values given in the figure are the means of those days. Mean daily ET_o for DOYs 254, 255 and 258 and for DOYs 272–274 was 4.48 and 4.15 mm, respectively. Mean daily maximum ambient temperature, solar radiation, and vapor pressure deficit for the two data sets were 29.1 and 32.5°C, 784 and 727 W m⁻², and 2.76 and 3.47 kPa, respectively. All days were cloud free

of the study (midday $ET_{LYS}/ET_o = -0.13 + 1.25 \times$ daily ET_{LYS}/ET_o , $r = 0.97$).

Pre-dawn leaf Ψ (Ψ_{PD}) and midday Ψ_1 on the day prior to turning the lysimeter's irrigation pump off were -0.075 and -0.75 MPa, respectively (Fig. 5). The value of midday Ψ_1 decreased to -1.28 MPa 9 days later and rapidly increased to values similar to those measured earlier once irrigation resumed. There was a significant ($P < 0.001$) decrease in midday Ψ_1 , from -0.76 to -0.94 MPa, for vines being irrigated outside the lysimeter during the first dry-down period (Ψ_{PD} was -0.09 MPa on the date midday Ψ_1 was -0.94 MPa). As pointed out in the Materials and Methods while these vines were being irrigated daily, it was with water amounts at less than full ET_c (water application amounts controlled by the lysimeter). For example, those vines had been irrigated five times per day on August 24th, while only three times per day on August 31st and September 2nd. The lowest values of Ψ_{PD} and Ψ_1 for the lysimeter vines during the second dry-down period were -0.29 and -1.25 MPa, respectively.

The variation in midday values of g_s for the lysimeter-grown vines during the study mimicked those of midday Ψ_1 (Fig. 5). Consequently, midday g_s and Ψ_1 were highly correlated with one another (Fig. 6). There was also a significant ($P < 0.001$) correlation between g_s and Ψ_1 for

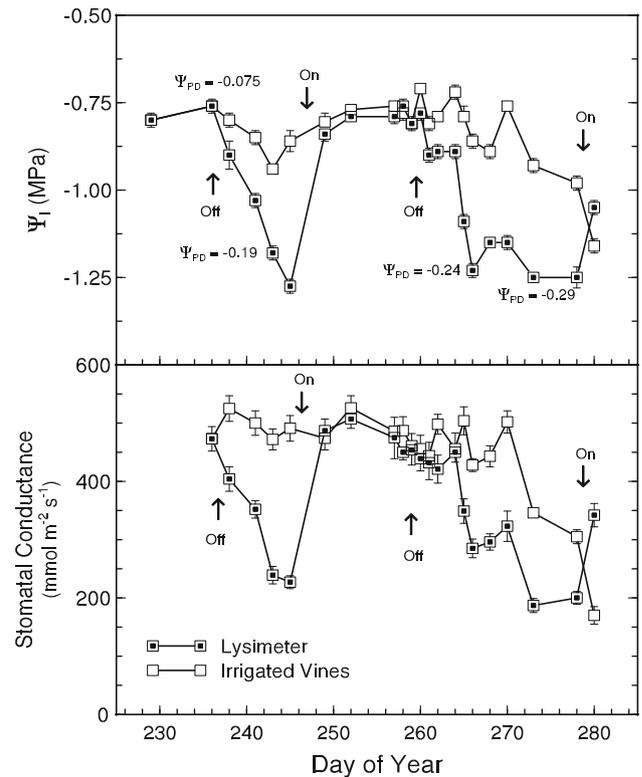


Fig. 5 Midday leaf water potential (Ψ_1) and stomatal conductance (g_s) measured during the course of the study. Data points are the means of individual measurements taken on leaves from the two vines growing in the lysimeter or irrigated vines growing outside the lysimeter. Bars represent one standard error and are shown when larger than the symbol. On the day in which the lysimeter pump was turned back on at the end of the study, water applications to the vines growing outside the lysimeter were terminated. The values of Ψ_{PD} (MPa) measured during the study are directly to the left, above or below corresponding Ψ_1 data points within the figure. The scale on the x axis is the same as that in Fig. 1. Other information is as given in Fig. 1

the irrigated vines grown outside the lysimeter ($g_s = 1037 + 406 \times \Psi_1$, $r = 0.85$). In addition, there was a significant ($P < 0.001$) correlation between g_s and Ψ_{PD} using the 8 Ψ_{PD} data points from the lysimeter vines and the irrigated vines ($g_s = 1199 + 530 \times \Psi_{PD}$, $r = 0.91$).

Midday Ψ_1 and g_s were significantly lower for the non-irrigated vines growing outside the lysimeter on DOYs 238–241 during the first dry-down period when compared to the two vines in the lysimeter on those dates (Table 1). Subsequently, there were no significant differences in Ψ_1 and g_s between those two sets of vines on DOYs 243 and 245. The vines within the vineyard did not receive additional water once irrigations resumed on September 3rd and this is reflected in significantly lower values of Ψ_1 and g_s on DOY 245 for these vines compared to the lysimeter vines.

There was a significant linear relationship between the ET_{LYS}/ET_o ratio and midday measurements of g_s (Fig. 7)

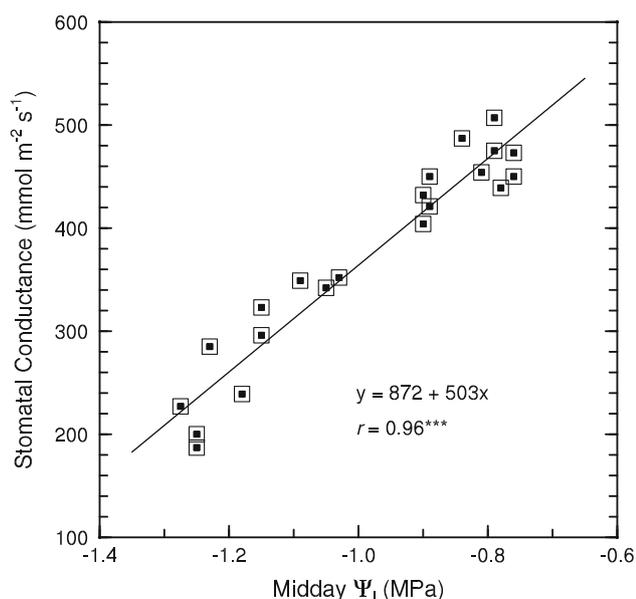


Fig. 6 The relationship between midday leaf water potential (Ψ_1) and stomatal conductance (g_s) measured on the two vines growing in the lysimeter during the course of the study. Data are those found in Fig. 5

and Ψ_1 (Fig. 8) with similar correlation coefficients for both. The correlation coefficients between midday measurements of g_s and Ψ_1 and daily grapevine water use (expressed as $L \text{ vine}^{-1}$) were only 0.54 and 0.58, respectively. The difference between measured Ψ_1 and the calculated Ψ_1 baseline for fully irrigated vines was also significantly correlated with the ET_{LYS}/ET_o ratio (Fig. 9), and the correlation coefficient was slightly greater than that for the midday Ψ_1 comparison with the ET_{LYS}/ET_o ratio (Fig. 8). The relationship between the ET_{LYS}/ET_o ratio and Ψ_{PD} (using the 4 Ψ_{PD} data points given in Fig. 5 for the lysimeter vines) was also significant ($ET_{LYS}/ET_o = 1.0 + 1.68 \times \Psi_{PD}$, $r = 0.96$, $P < 0.05$).

There was a slight difference in the coefficient of determination for a linear relationship between mean θ_v and the ET_{LYS}/ET_o ratio and a non-linear one (Fig. 10). Lastly, both midday measurements of Ψ_1 and g_s were significantly ($P < 0.001$) correlated with mean θ_v over the course of the study ($r = 0.87$ and 0.82 for the correlation between Ψ_1 and g_s and mean θ_v measured at all depths, respectively).

Discussion

The significant correlations between midday Ψ_1 and g_s and midday Ψ_1 (and g_s) and the ET_{LYS}/ET_o ratio found in this study were similar to those of Mata et al. (1999). They found that the decrease in daily peach (*Prunus persica* L.) tree transpiration (measured with a weighing lysimeter)

Table 1 Comparisons of midday leaf water potential (Ψ_1 —MPa) and stomatal conductance (g_s — $\text{mmol m}^{-2} \text{ s}^{-1}$) for the lysimeter-grown vines and vines growing in the surrounding vineyard receiving no water during the first dry-down period (1st ddp)

Day of year	Parameter measured	Lysimeter vines	Vineyard vines (1st ddp)	No applied water vines
236	Ψ_1	-0.83	-0.83	-1.32
	g_s	573	602	116
238	Ψ_1	-0.90 a	-1.04 b	—
	g_s	504 a	398 b	—
241	Ψ_1	-1.03 a	-1.12 b	-1.39
	g_s	— ^a	—	—
243 ^b	Ψ_1	-1.18	-1.20	—
	g_s	239	203	—
245	Ψ_1	-1.28	-1.29	—
	g_s	257	229	—
249	Ψ_1	-0.84 a	-0.95 b	—
	g_s	500 a	437 b	—
251	Ψ_1	-0.79	-0.77	-1.32
	g_s	507	521	159

Water applications were terminated on August 24 (DOY 236) at 1700 h. Values of Ψ_1 and g_s measured on vines within the vineyard surrounding the lysimeter that had received no applied water at any time during the 2005 growing season are shown for comparison

Values in the 'Parameter measured' rows of the 'Lysimeter vines' and 'Vineyard vines (1st ddp)' columns followed by a different letter are significantly different at the $P < 0.05$ level. Values in the rows of the same two columns not followed by a letter are not significantly different

^a Not measured

^b Pre-dawn leaf water potential for the lysimeter vines, vineyard vines (1st ddp), and vines receiving no applied water season long were -0.19, -0.19 and -0.41 MPa, respectively, on DOY 243

was linearly related to midday Ψ_{stem} during a dry-down period of 20 days (deficit irrigation followed by no-irrigation). The relationship between lysimeter grapevine Ψ_{stem} and ET_{LYS}/ET_o would probably have been similar to that of Mata et al. (1999) in this study if Ψ_{stem} had been measured as it and Ψ_1 are highly correlated with one another in grapevines (Salón et al. 2005; Stevens et al. 1995; Williams and Araujo 2002; Williams and Trout 2005). Mata et al. (1999) also found that tree water use and Ψ_{stem} were highly correlated with soil water content, similar to that found in this study for Ψ_1 and g_s and soil water content. Williams and Trout (2005) previously had found that midday Ψ_{stem} and Ψ_1 were highly correlated with soil water content when measured throughout the season in this same vineyard. Lastly, it has been demonstrated that the ET_c/ET_o ratio was linearly related to Ψ_{PD} of table grapes grown in Italy (Rana et al. 2004). A similar result was found in this study, albeit using only four values of Ψ_{PD} .

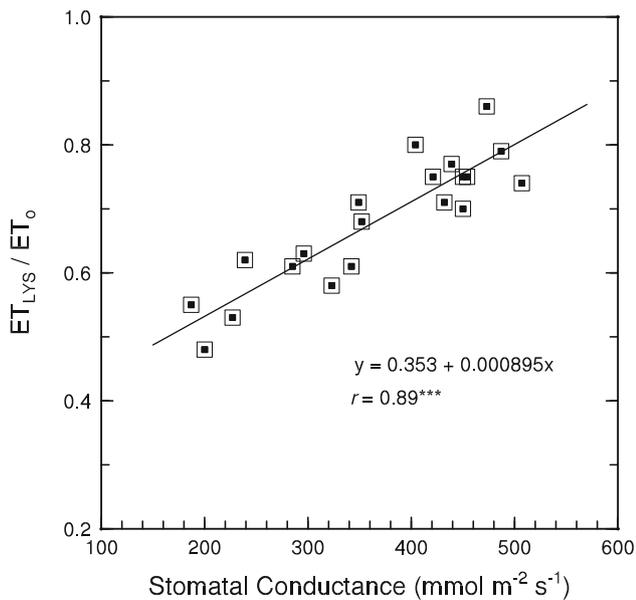


Fig. 7 The relationship between midday stomatal conductance (g_s) and the ET_{LYS}/ET_o ratio measured during the course of the study. The ET_{LYS}/ET_o data are those calculated on the day midday g_s was measured

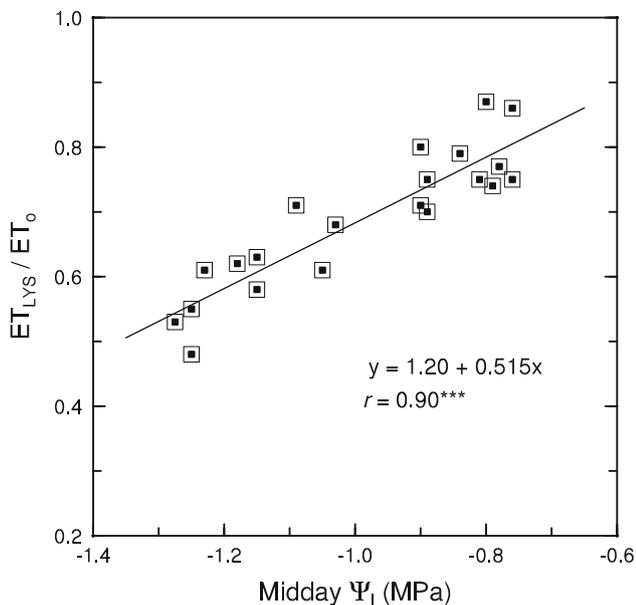


Fig. 8 The relationship between midday leaf water potential (Ψ_1) and the ET_{LYS}/ET_o ratio measured during the course of the study. The ET_{LYS}/ET_o data are those calculated on the day midday Ψ_1 was measured

There are a few studies in which short-term measures of plant water status and daily or hourly whole plant water use, measured with sap flow sensors, have been compared in grapevines. Sousa et al. (2006) found that sap flow of grapevines measured at 1400 h was significantly correlated ($r = 0.75$) with Ψ_1 measured at 1400 h but not with g_s

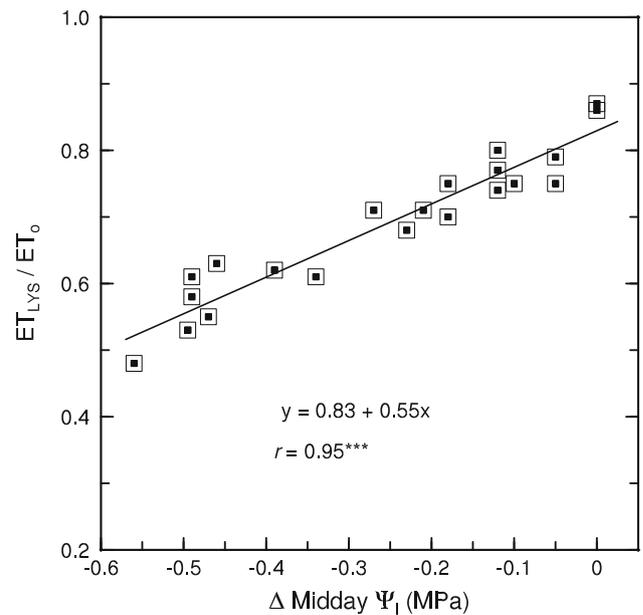


Fig. 9 The relationship between the difference in the calculated Ψ_1 of a fully irrigated grapevine as a function of vapor pressure deficit (VPD) at the time of measurement and the actual value of Ψ_1 measured on that day and the ET_{LYS}/ET_o ratio during the course of the study. See “Materials and methods” section for the derivation of the relationship between Ψ_1 of fully irrigated grapevines and VPD at the time of measurement

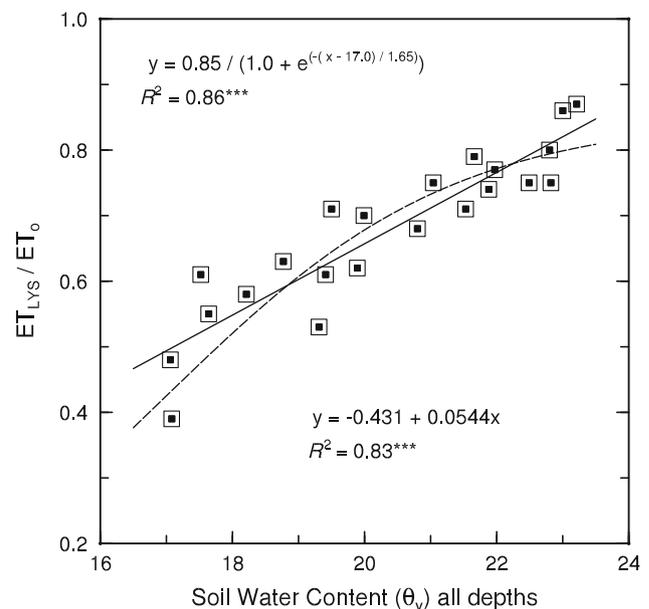


Fig. 10 The linear relationship and the best fit of a non-linear relationship between mean soil water content and the ET_{LYS}/ET_o ratio

measured at the same time. They also found that sap flow and Ψ_1 measured at 1400 h were significantly correlated with soil water content. In that study, mean Ψ_1 measured at 1400 h was -1.17 and -1.45 MPa for the fully irrigated and non-irrigated treatments, respectively. Patakas et al.

(2005) found that the ratio of the mean daily sap flow of their water stressed vines (SF_{T1}) divided by the mean daily sap flow of their fully irrigated vines (SF_{TI}) was highly correlated ($R^2 = 0.83$) with midday measurements of Ψ_{stem} ranging from -0.35 to -1.15 MPa. No such relationship was found when the ratio was compared to measures of Ψ_1 (midday Ψ_1 averaged -1.45 MPa for all treatments in that study). Escalona et al. (2002) found that sap flow and short-term measures of leaf g_s and transpiration of irrigated and non-irrigated, potted grapevines differed significantly, but Ψ_1 did not differ between the two treatments.

While the Sousa et al. (2006) study somewhat agrees with results presented in this paper (relationship between midday Ψ_1 and grapevine water use) those of Patakas et al. (2005) and Escalona et al. (2002) do not. One possible explanation for the differences between the two latter studies mentioned above and this study could be related to the method and/or technique in which Ψ_1 was measured. It has been demonstrated that the failure to enclose the leaf blade in a plastic bag just prior to cutting the petiole can dramatically affect the values of Ψ_1 one measures (Turner and Long 1980). For example, the senior author of this study found that midday Ψ_1 of fully irrigated vines used in this study on a high evaporative day was 0.6 MPa lower for leaves that were not bagged versus bagged leaves (-1.3 vs. -0.7 MPa, respectively). In addition, the difference in Ψ_1 values between bagged and non-bagged leaf blades is greater in rapidly transpiring leaves compared to those that are not (Turner and Long 1980; Williams and Araujo 2002). Leaf Ψ was measured in the Sousa et al. (2006) study by enclosing the leaf blade in a plastic bag prior to cutting the petiole (noted in their “Materials and methods” section). Patakas et al. (2005) only enclosed the leaves in plastic bags after severing the petiole (personal communication). The exact technique used to measure Ψ_1 in the Escalona et al.’s (2002) paper was not given but based upon the above discussion and the results from the measurements of Ψ_1 from their study, it can be assumed that they did not bag the leaf blade prior to cutting the petiole, probably resulting in erroneous values. In addition, since Ψ_1 and Ψ_{stem} are highly correlated with one another in grapevine (Salón et al. 2005; Stevens et al. 1995; Williams and Araujo 2002; Williams and Trout 2005), it is not surprising that Patakas et al. (2005) did not find Ψ_1 to be correlated with the SF_{T1}/SF_{TI} ratio since they did not measure Ψ_1 as outlined by Turner and Long (1980). Alternatively, measuring grapevine transpiration via the sap flow technique could have underestimated grapevine water use resulting in unreliable values (Shackel et al. 1992; Tarara and Ferguson 2001).

It has been suggested that Ψ_1 is not a sensitive water stress indicator for woody horticultural crops (Higgs and

Jones 1990; Jones 1990; 2004; Noar 1998) or that Ψ_{stem} is a better indicator of plant stress than Ψ_1 for deciduous tree crops (McCutchan and Shackel 1992; Shackel et al. 1997) or grapevines (Chone et al. 2001; Patakas et al. 2005). Others feel that Ψ_{PD} is a better indicator of grapevine water status (Cifre et al. 2002; Medrano et al. 2003; Schultz 2003). Jones (2004) pointed out that temporal fluctuations, such as passing clouds, make the interpretation of Ψ_1 measured during the day as an indicator of irrigation need unsatisfactory. We assume that the same would be true for the use of Ψ_{stem} . Jones (2004) also mentioned that such an indicator requires a reference or threshold value to be useful in irrigation scheduling. In the arid southern San Joaquin Valley of California, cloud cover is the exception during the summer months. During the course of this study (from August 16 until October 6), there was only one day in which clouds were present. Thus, the measurement of midday Ψ_1 and g_s occurred at non-limiting light levels. A fully irrigated baseline of Ψ_1 (and Ψ_{stem}) as a function VPD at the time of measurement has been developed for grapevines (Williams and Baeza 2007). This is similar to that developed for trees using Ψ_{stem} as a function of VPD (McCutchan and Shackel 1992; Shackel et al. 1997). It was shown here that the ET_{LYS}/ET_o ratio was more highly correlated with the difference in the calculated Ψ_1 of a fully irrigated grapevine as a function of VPD and the actual value of Ψ_1 measured on the vines in the lysimeter during the course of this study than with measurements of midday Ψ_1 .

Flexas and Medrano (2002) suggested that stomatal closure is one of the earliest responses of plants to drought and the dominant limitation to photosynthesis at mild to moderate drought. Jones (2004) also indicated that over short time-scales, stomata are sensitive indicators of water deficits. The linear decrease in g_s (and ET_c/ET_o ratio) with Ψ_1 reported in this study would indicate that measurements of midday Ψ_1 reflect the reductions in both individual leaf g_s and whole plant transpiration due to soil water deficits. The same could be said for midday Ψ_{stem} in the study by Mata et al. (1999). Shackel (2007) also found that there was a linear relationship ($R^2 = 0.88$) between g_s and Ψ_1 of Pinot noir grapevines. These results differ from conclusions by Lovisolo et al. (2010) who after a review of the literature stated that there is no clear relationship between g_s and Ψ_1 in grapevines and that g_s is better correlated with Ψ_{PD} . The correlations between Ψ_1 and g_s in this study and those found by Shackel (2007) are better than those between Ψ_{PD} and g_s reported by Lovisolo et al. (2010), Medrano et al. (2003) and de Souza et al. (2005).

Stomatal control of leaf transpiration can affect plant tissue water status in response to various environmental and soil factors (Jones 1998). Plant species may respond differently to these stresses and have been categorized as ‘isohydric’ in which stomatal control maintains midday Ψ_1

similarly across varying soil water deficits and ‘anisohydric’ in which less stomatal control allows for midday Ψ_1 to decrease in response to soil water deficits (Tardieu and Simonneau 1998). It is often assumed that grapevines (*Vitis spp.*) are isohydric (Medrano et al. 2003; Patakas et al. 2005) or near-isohydric (Cifre et al. 2005) due to the fact that midday Ψ_1 doesn’t differ between vines that are ‘well-watered’ or ‘irrigated’ and those experiencing soil water deficits. If this were the case, then midday Ψ_1 measurements could not be used in an irrigation management program. Others have found that some cultivars of *V. vinifera* should be categorized as isohydric while other cultivars anisohydric (Schultz 2003; Vandeleur et al. 2009). However, Soar et al. (2006) stated that grapevines may be categorized as generally anisohydric. Williams and Baeza (2007) concluded that Cabernet Sauvignon, Merlot and Thompson Seedless grapevines should be classified as anisohydric based upon significant differences in midday Ψ_1 of well-watered vines compared to vines receiving no applied water or were being deficit irrigated (leaf blades were covered with a plastic bag prior to severing the petiole and putting both in the pressure chamber in that study when Ψ_1 was measured). The data presented in this study would confirm that Thompson Seedless was an anisohydric cultivar. Midday Ψ_1 progressively decreased subsequent to the irrigation pump being turned off, and it was highly correlated with decreases in both single leaf g_s and the ET_{LYS}/ET_o ratio.

The diurnal patterns of water use for the lysimeter vines when being irrigated (Figs. 3 and 4) are typical to those one would expect for latent heat flux of a well-watered crop (Allen et al. 1998). These patterns coincide with diurnal solar radiation values similar to that shown in Williams et al. (2003b). Conversely, maximum hourly water use of the vines plateau earlier in the day during the first dry-down period and hourly water use began to decrease by 1200 h (PDT) at the end of the second dry-down period in this study. These diurnal patterns for both fully irrigated and stressed vines in this study are similar to those reported by Mata et al. (1999) on peach trees grown in a weighing lysimeter prior to and during a dry-down period, respectively. The diurnal patterns of water use during both the irrigated and non-irrigated periods of this study differ from diurnal patterns obtained in several studies where sap flow sensors were used to quantify grapevine transpiration (Lopes et al. 2004) even those for supposed, well-watered vines (Lu et al. 2003; Patakas et al. 2005; Yunusa et al. 2000). In many of those studies, sap flow is maximized between 0800 and 1000 h, remains constant thereafter, and then decreases rapidly later in the afternoon. It is also interesting to point out that grapevine transpiration in those studies differs only slightly from one day to the next even though evaporative demand changes significantly from one day to the next. The differences between the diurnal

patterns of grapevine water use found in this study and Williams et al. (2003b) and those reported elsewhere using sap flow sensors would indicate that the latter technique may not accurately measure whole vine transpiration (Tarara and Ferguson 2001; Shackel et al. 1992) and casts doubt on values of grapevine water use others have reported.

The differences in diurnal water use of vines irrigated at ET_c and that after the irrigation pump was turned off are similar to those reported by Williams and Ayars (2005a) for vines prior to and after the trunks were girdled (removal of the phloem from around the trunk), respectively. Girdling grapevines will reduce leaf g_s (Harrell and Williams 1987; Hofacker 1978; Kriedemann and Lenz 1972; Roper and Williams 1989), and it will remain lower until the girdle heals (Williams et al. 2000). Therefore, diurnal and daily water use of girdled vines will be lower than vines that are not girdled (Williams and Ayars 2005a). It is thought that girdling reduces g_s due to an accumulation of abscisic acid (ABA) in the leaves of grapevines (During 1978; Loveys and Kriedemann 1974; Williams et al. 2000). ABA has also been implicated in reducing g_s of grapevines in response to soil and atmospheric water deficits and the classification of grapevine cultivars as being either isohydric or anisohydric (Schultz 2003; Soar et al. 2004, 2006). Interestingly, Ψ_1 is greater for girdled grapevines compared to those that are not girdled due to a reduction in transpiration (Roper and Williams 1989; Williams and Ayars 2005a; Williams et al. 2000). Thus, a reduction in g_s due to girdling will keep Ψ_1 values higher than those of non-girdled vines, while a reduction in g_s due to soil water deficits in this study did not increase Ψ_1 . There is evidence that plant hydraulic conductance may also play a role in the response of plants to soil water deficits and their classification as isohydric or anisohydric (Franks et al. 2007; Lovisolo et al. 2010; Schultz 2003). This may account for the results presented in this study.

Schultz and Stoll (2010) consider a Ψ_{PD} value in the vicinity of -0.2 MPa as no stress for field-grown grapevines. Ojeda et al. (2001) have categorized the level of water deficit experienced by grapevines with a Ψ_{PD} value of -0.2 MPa or greater as ‘nil’, while the level of water deficit experienced by vines with Ψ_{PD} values between -0.2 and -0.4 MPa as ‘weak’. Studies that have examined water relations in grapevines often report Ψ_{PD} values for their ‘fully irrigated’ vines as being close to -0.2 MPa or lower (Chaves et al. 2007; Correia et al. 1995; de Souza et al. 2005). Data presented in this study indicated as Ψ_{PD} decreased from -0.07 to -0.19 during the first dry-down period, the ET_{LYS}/ET_o ratio decreased 40%. The ET_{LYS}/ET_o ratio from September 15 to October 3, second dry-down period, decreased from 0.75 to 0.39, a 48% reduction when Ψ_{PD} decreased to -0.29 MPa. A reduction in the ET_{LYS}/ET_o ratio of 40% at a Ψ_{PD} -0.19 MPa is

considerable, not nil, while a reduction in the ratio of 48% at a Ψ_{PD} of -0.29 certainly isn't a weak level of water deficit. In addition, grapevines with g_s values decreasing from $200 - 500 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ to $150 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ are assumed to undergo a mild water stress with g_s values between 50 and $150 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ considered a moderate stress (Lovisol et al. 2010). In this particular study, a reduction in g_s from $\sim 500 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ to just less than $200 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ decreased the ET_c/ET_o ratio greater than 40%. It would appear that the current values of g_s assumed by many to indicate no or minimal water stress in grapevine needs to be reexamined.

The majority of grapevines planted on a worldwide basis are located in semi-arid to arid regions, locations with little or no rainfall during late spring and summer and with minimal cloud-cover. The results presented in this study would indicate that the measurement of midday Ψ_1 is a sensitive indicator of vine water status and a reflection of daily water use of grapevines under the arid conditions of the San Joaquin Valley. Measurements of Ψ_1 have been successfully used to indicate the water status/irrigation needs of apple trees grown in an arid region (Peretz et al. 1984) or to schedule deficit irrigation in a semi-arid region of Spain (Girona et al. 2006). Grimes and Williams (1990) reported that yield was highly correlated with seasonal mean values of Ψ_1 , g_s and the crop water stress index (CWSI). They also found that Ψ_1 and CWSI were highly correlated with one another (unpublished data). Williams et al. (2010a, b) found that both vegetative and reproductive growth of Thompson Seedless grapevines grown in the San Joaquin Valley were linearly related to seasonal, mean values of midday Ψ_1 . Therefore measurements of midday Ψ_1 (or Ψ_{stem}), or their departure from a fully irrigated baseline Ψ_1 as a function of VPD, could be used in a vineyard irrigation management program or to validate new stress monitoring techniques under arid or semi-arid growing conditions.

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