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Effects of applied water amounts at various fractions of evapotranspiration (ET_c) on leaf gas exchange of Thompson Seedless grapevines

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Abstract

Aims: To determine the effects of applied water amounts at various fractions (0.2, 0.6, 1.0 and 1.4) of grapevine evapotranspiration on leaf gas exchange of Thompson Seedless grapevines.

Methods and Results: Midday stomatal conductance (g_s) decreased linearly as leaf water potential (Ψ_l) and soil water content decreased. Leaf net CO_2 assimilation rate only decreased once midday Ψ_l values were less than −1.0 MPa and when ~50% of the soil water content at field capacity had been depleted. The mean seasonal midday A/g_s ratio (intrinsic water use efficiency) was greatest for the 0.2 irrigation treatment and decreased as applied water amounts increased. Diurnal A and g_s for vines irrigated at the 0.6 level or greater reached a maximum prior to midday remained constant thereafter before decreasing late in the afternoon, while those for vines that received less water decreased subsequent to the first measurement of the day.

Conclusions: A and g_s responded differently to vine and soil water statuses under the conditions of this study. There was no midday depression in either A or g_s for vines irrigated at full evapotranspiration.

Significance of the Study: The values of Ψ_l, A and g_s reported here would serve as criteria to indicate that vines were well watered.

Keywords: *grapevine, photosynthesis, stomatal conductance, water potential*

Introduction

Evapotranspiration (ET_c) of Thompson Seedless grapevines was determined with a weighing lysimeter from the time the vineyard was planted in 1987 through the 1993 growing season (Williams et al. 2003a,b). While the lysimeter provided important information regarding grapevine water use and the development of crop coefficients for use in irrigation scheduling, there was only one lysimeter. To expand the usefulness of the data collected from the lysimeter, irrigation treatments were imposed in the surrounding vineyard. These treatments ranged from no applied water to applied water amounts that ranged from 0.2 to 1.4, the amount of water the grapevines in the lysimeter used in 0.2 increments. The effects of these treatments on soil and vine (midday leaf water potential (Ψ_l)) water status, and vegetative and reproductive growth were recently published (Williams et al. 2010a,b). The results from these papers indicated that berry weight, pruning weights and yield were highly correlated with mean values of midday Ψ_l measured throughout the growing season. The data provided applied water amounts, referenced to grapevine ET_c, needed to maximize productivity of Thompson Seedless grapevines and optimize water use efficiency (WUE). Importantly, it also demonstrated that over-irrigation of Thompson Seedless grapevines reduced yield (Williams et al. 2010b).

Soil water deficits will reduce vegetative and reproductive growth of grapevines (Matthews and Anderson 1989, Grimes and Williams 1990, Williams and Matthews 1990, McCarthy et al. 2000, Marsal et al. 2008, Williams 2010). However, irrigation techniques, and applied water and precipitation amounts and their timing during the growing season may mitigate the negative effects of soil water deficits on productivity (Matthews and Anderson 1989, McCarthy et al. 2000, Williams et al. 2010a,b). Soil water deficits will also reduce net CO_2 assimilation rate (A), which has shown to limit productivity of grapevines (Medrano et al. 2003).

This study was conducted to measure leaf gas exchange of Thompson Seedless grapevines as a function of applied water amounts at various fractions of ET_c, determined with a weighing lysimeter (Williams et al. 2003b), across three growing seasons. The data presented here were collected simultaneously with the soil and vine water status data published previously (Williams et al. 2010a,b). Applied water amounts specifically used for data collection were 20 and 60% of ET_c (the 0.2 and 0.6 treatments), 100% of ET_c (the 1.0 treatment) and 40% greater than ET_c (the 1.4 treatment). A nonirrigated treatment was also used during the latter two growing seasons. The relationships among midday A and g_s and Ψ_l and A, g_s and Ψ_l and soil water content (SWC) were also determined.

Materials and methods

The vineyard used in this study was planted on 9 April 1987 with cuttings of *Vitis vinifera* L (cv. 'Thompson Seedless' clone 2A) at the University of California Kearney Agricultural Center located in the San Joaquin Valley of California (36°48′N, lat, 119°30′W, long.). Vine and row spacings were 2.15 and 3.51 m, respectively (7.55 m^2 per vine). Row direction was ~6° north of the east/west axis. The vineyard was approximately 1.4 ha (168 m × 82 m). The soil was a Hanford fine sandy loam

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(coarse-loamy, mixed, nonacid, thermic Typic Xerorthent). The trellis system used in the study to collect gas exchange data consisted of a 0.6 m cross arm placed atop the stake and wires attached at either end of the cross-arm to support the vine's fruiting canes. The vines were cane-pruned during the dormant portion of the growing season with each cane approximately 12–15 nodes in length. The number of canes per vine left after pruning was 6, 8 and 8 in 1991, 1992 and 1993, respectively. The canes were then wrapped around the fruiting cane wires on the trellis. Cultural practices to control diseases and insect pests were performed by field station personnel, as described previously (Daane and Williams 2003, Williams et al. 2003b).

The vineyard also contained a weighing lysimeter in which two grapevines were planted; at the same time, the rest of the vineyard was planted. The trellis system for the two, lysimeter vines consisted of a 0.6 m cross arm, similar to that described above. The operation of the lysimeter and other technical details can be found in Williams et al. (2003a,b). Vines within the lysimeter and the surrounding vineyard were irrigated with 4 L/h in-line drip emitters, spaced every 0.30 m in the vine row. The drip tubing was attached to a wire suspended 0.4 m above the soil surface. The lysimeter was weighed hourly to determine ET of the two vines, and when the decrease in weight exceeded an equivalent of 16 L (8 L/vine) threshold value, the lysimeter was irrigated. The number of irrigations per day throughout each growing season ranged from 0 to 7.

The irrigation pump for the rest of the vineyard was controlled by the lysimeter's data logger (21X Micrologger, Campbell Scientific, Inc., Logan, Utah, USA). Whenever the lysimeter was irrigated, the vineyard pump was activated, and an irrigation event took place. The irrigation treatments were applied water amounts at various fractions (0.2, 0.4, 0.6, 0.8, 1.0, 1.2 and 1.4) of lysimeter water use. A nonirrigated treatment was also included. Irrigation treatments within each of the eight blocks of the experiment were set up in a line-source design, going from the lowest to highest amounts, the direction within each block randomly assigned. Two rows separated each block with the border row irrigated at the respective irrigation amount given the irrigation treatment amount assigned to the data row of the respective block. Each irrigation treatment plot consisted of 18 vines down a single row. Within each plot, three trellises were installed using six vine trellis subplots. The activation of solenoid valves at the head of each row for various times was used to provide the differing fractions of applied water. In-line water meters upstream from the solenoid valves in each row measured actual applied water amounts. The water meters were initially calibrated in 1989 and again in before the 1992 growing season. At both times, all meters were within 3% of the calibration values.

SWC in the 0.2, 0.6, 1.0 and 1.4 irrigation treatments was monitored using the neutron back-scattering technique with a neutron moisture probe (Model 503 DR Hydroprobe Moisture Gauge, Campbell Pacific Nuclear, Martinez, CA, USA). Nine access tubes were placed in one quarter of an individual vine's rooting volume and inserted to a depth of 3 m. Three access tubes were placed down the vine row (directly below the drip line), one close to the trunk, one midway between vines within the row and the third midway between the two previously mentioned tubes. Another three tubes were placed midway between rows, perpendicular to each of the three tubes placed within the row. The last three tubes were placed midway between the former two sets of tubes. Readings were taken at a depth of 0.23 and 0.45 m beneath the soil surface and then in increments of 0.3 m down to a depth of 2.90 m. Each access tube site was replicated three times, in three of the eight replicated blocks, for each irrigation treatment mentioned previously. The neutron probe was calibrated according to Araujo et al. (1995) and SWC values expressed as per cent by volume (θ_v). The SWC content at field capacity of this soil type was approximately 22.0% by volume, while SWC at a soil moisture tension of −1.5 MPa was approximately 8.0% by volume. Therefore, total available water to a depth of 2.9 m for this soil at field capacity was equivalent to 406 mm.

No fertilisers had been applied prior to or during the course of this study. Nitrate concentrations were measured in the water used to irrigate the vineyard on 22 and 24 separate occasions in 1991 and 1992, respectively. Mean NO_3 concentrations of the water were 2.16 and 3.46 ppm in 1991 and 1992, respectively. These concentrations of NO_3 and the amount of water applied to the 1.0 irrigation treatment between the first irrigation and harvest were equivalent to 2.8 and 3.3 g N per vine in 1991 and 1992, respectively (equivalent to 3.7 and 4.4 kg N/ha each year).

Grapevine water potential was measured according to the procedures of Williams and Araujo (2002). Predawn Ψ (Ψ_{PD}) measurements began at ≈0330 h and were finished prior to sunrise using a pressure chamber (Model 1000, PMS Instrument Co., Corvallis, OR, USA). Midday measurements of Ψ_l generally were taken between 1230 and 1330 h Pacific Daylight Time (PDT). Leaf blades for Ψ_{PD} and Ψ_l 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 to 15 s. Leaves, chosen for Ψ_{PD} and Ψ_l, were fully expanded and mature. For midday and diurnal Ψ_l measurements, leaves exposed to direct solar radiation at the time of measurement were used. A single leaf from a minimum of six individual vine replicates were measured and used for data analysis. Measurements of Ψ_l and Ψ_{PD} were made in three (same blocks that SWC was measured) of the eight irrigation blocks.

Measurements of leaf net CO_2 assimilation rate (A) and stomatal conductance (g_s) were taken at the same time midday, or diurnal Ψ_l measurements were taken as described by Williams et al. (2000). Both measures of gas exchange were made with a portable infrared gas analyser (LCA2, Analytical Development Co., Hoddeson, UK) using the broad leaf chamber. Leaves chosen for gas exchange were similar to those used for Ψ_l in the same blocks, as mentioned earlier. Environmental and reference ET (ET_o) data were obtained from a California Irrigation Management Information System weather station located 2 km from the vineyard site.

Data were analysed via regression analysis using linear, quadratic and cubic terms. Regressions with the best fit are presented. The relationships among midday water status measurements (Ψ_l) and gas exchange (A and g_s) were analysed using the means of an individual irrigation treatment. Data were analysed using analysis of variance for specific days the data were collected or for the diurnal data as a function of irrigation treatments and means separated using Duncan's multiple range test.

Results

There were significant differences in midday A among treatments prior to the application of water in 1991 (Figure 1). Midday A of vines in the 0.2 irrigation treatment was significantly lower than those of the other three irrigation treatments for the remainder of the 1991 growing season. Midday A of vines from the 0.2 and 0.6 irrigation treatments from the first week in June onwards were considerably lower than vines being irrigated at ET_c or greater. Values of midday A for the nonirrigated vines were extremely low on the few dates they were measured in 1992, while they were significantly lower than any of the irrigated vines on most dates in 1993. Leaf net CO_2 assimilation rate of vines irrigated at

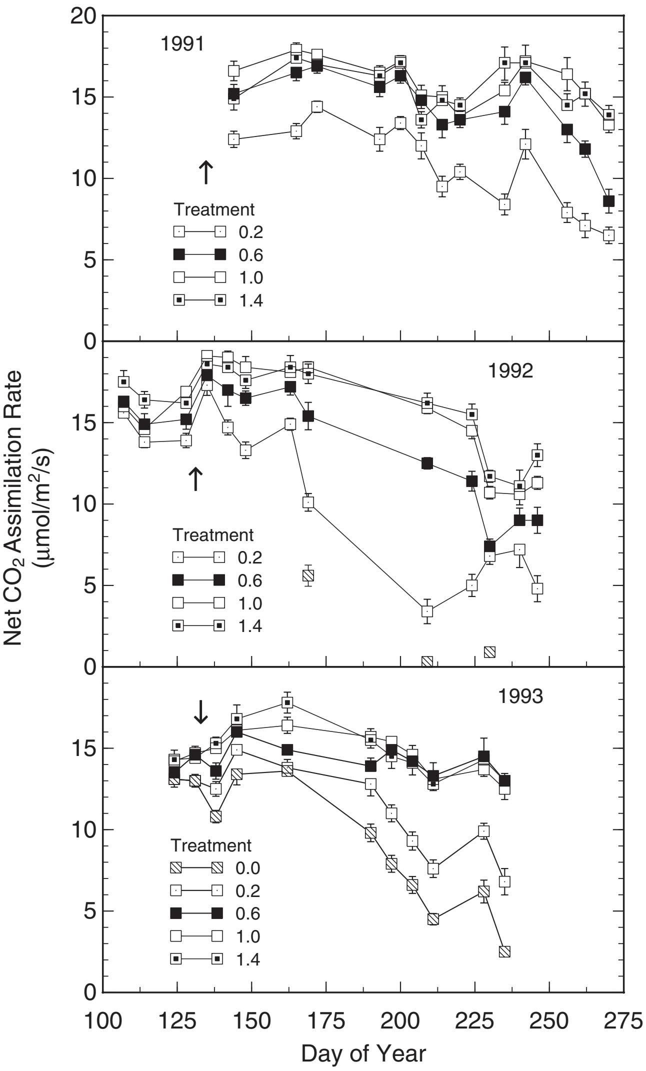

Figure 1. Leaf net CO_2 assimilation rates measured at midday on Thompson Seedless grapevines across three growing seasons. The treatments were applied water amounts at various fractions of evapotranspiration measured with a weighing lysimeter. Each value is the mean of a minimum of six individual leaf replicates (at least two leaves were measured in three of the experimental blocks). The bars denote one standard error and are shown when larger than the symbol. Measurements on the nonirrigated vines were not routinely taken until the 1993 growing season.

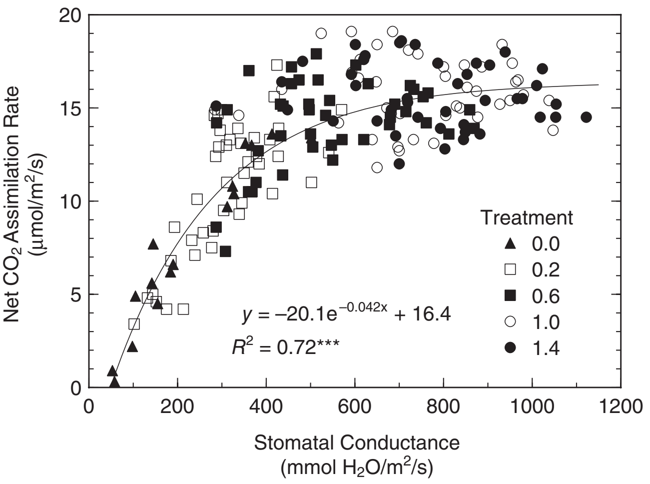

Figure 2. Net CO_2 assimilation rate as a function of stomatal conductance, both measured at midday, of Thompson Seedless grapevines across irrigation treatments and years. *** indicates significance at $P < 0.001$. Other information is as given in Figure 1 ($n = 162$).

Table 1. Intrinsic water use efficiency (A/g_s) measured on Thompson Seedless grapevines as a function of applied water amounts across each growing season.

Irrigation treatment	Year (μmol CO_2/mol H_2O)		
	1991	1992	1993
0.0	—	32.2	31.7 a
0.2	33.6 a	39.5 a	29.8 a
0.6	23.9 b	35.0 b	23.1 b
1.0	19.8 c	27.6 c	19.8 c
1.4	19.0 c	26.1 c	19.9 c

No data were collected for the no applied water treatment (—) in 1991. The no applied water treatment in 1992 consisted of only three measurements later in the growing season and therefore not included in the statistics for that year. $n = 13$, 13 and 11 in 1991, 1992 and 1993, respectively.

the 0.6 treatment amounts were lower than vines irrigated with more water in 1992 after the first week in June. During the latter portion of the 1993 growing season A of the vines irrigated at 0.6 of ET_c were similar to those being irrigated with more water. Values of midday A of vines irrigated at the 1.0 and 1.4 amounts generally were not significantly different from one another across seasons. Midday A increased in a curvilinear manner as g_s increased up to a value of approximately 400 mmol $H_2O/m^2/s$ (Figure 2). This type of relationship also occurred when values of A and g_s were obtained from diurnal measurements (unpublished data). Maximum values of g_s were in excess of 800 mmol $H_2O/m^2/s$ on numerous occasions for vines irrigated at the 1.0 and 1.4 levels. The intrinsic WUE ($WUE_i = A/g_s$) was greatest for the 0.2 treatment in 1991 and 1992, followed by the 0.6 treatment each year (Table 1). The WUE_is for the 0 and 0.2 irrigation treatments in 1993 were similar. There were no significant differences in WUE_i between the 1.0 and 1.4 irrigation treatments among years.

Midday Ψ_l was a curvilinear function of SWC (Figure 3). A linear relationship between the two resulted in a coefficient of determination close to that of the second order polynomial shown in the Figure 3 ($\Psi_l = -1.74 + 0.065 \times SWC$, $R^2 = 0.83$***).

Both A and g_s measured at midday were significantly correlated with midday Ψ_l (Figure 4) and SWC (Figure 5). g_s decreased linearly as both Ψ_l and SWC decreased. Leaf net CO_2 assimilation rate remained constant as Ψ_l decreased from −0.5 to −1.0 MPa, but it decreased almost linearly as midday Ψ_l became more negative. Leaf net CO_2 assimilation rate remained constant as the SWC decreased from field capacity to a SWC of ~13 θ_v. Once the θ_v decreased to a lower value, A decreased almost linearly.

Leaf Ψ decreased throughout the day for all irrigation treatments reaching a minimum value around solar noon, or shortly thereafter and subsequently increasing across dates (Figures 6,7). There were significant differences in Ψ_{PD} on 16 August 1993 among the irrigation treatments except between the 1.0 and 1.4 irrigation treatments (values given in legend to Figure 7). Leaf net CO_2 assimilation rate and g_s for the 1.0 and 1.4 irrigation treatments increased from the first measurement of the day reaching a maximum around midday and decreasing thereafter on both dates. Values of A and g_s for the 0 and 0.2 irrigation treatments generally decreased throughout the day subsequent

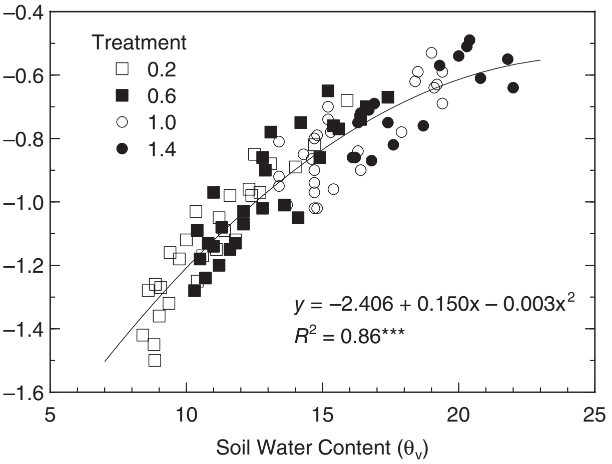

Figure 3. The relationship between midday leaf water potential measured on Thompson Seedless grapevines and soil water content (SWC). Leaf water potential values used here were those measured on vines on the same day or 1 day before or after SWC was measured. *** indicates significance at $P < 0.001$. Other information is as given in Figures 1 and 2 ($n = 120$).

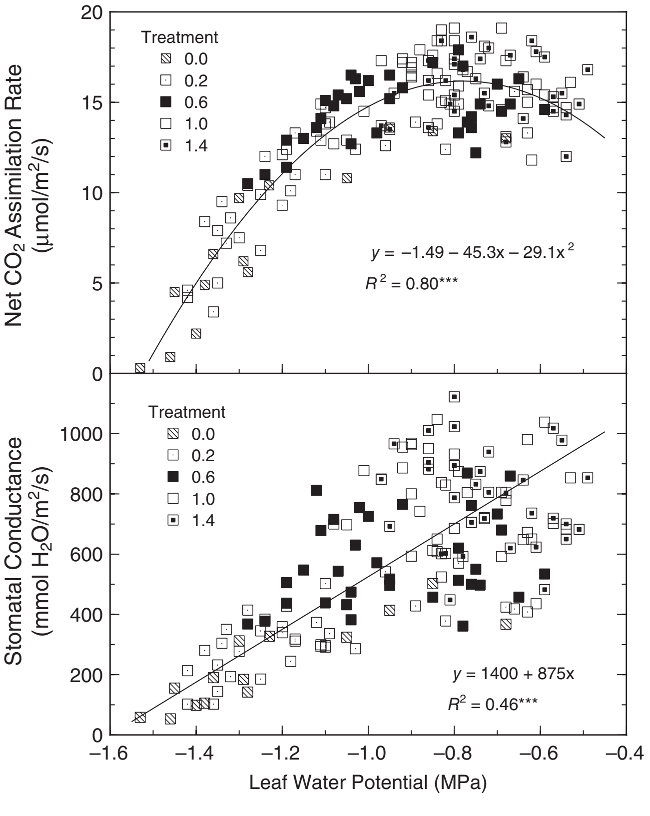

Figure 4. The relationships between net CO_2 assimilation rate and stomatal conductance, and leaf water potential measured at midday across the 3-year study. The values of leaf water potential in this figure were taken on the same vines as those used for the gas exchange measurements but not necessarily using the same leaves. The linear regression between stomatal conductance and leaf water potential was forced through the *y*-axis zero intercept ($n = 152$). *** indicates significance at $P < 0.001$.

to the first measurement time. Leaf net CO_2 assimilation rate and g_s of vines in the 0.6 irrigation treatment were very close to those of the 1.0 irrigation treatment on both dates even though Ψ_l was significantly different from the 1.0 irrigation treatment. Values of A and g_s for the nonirrigated and 0.2 irrigation treatments were generally lower on 16 August compared with 16 June.

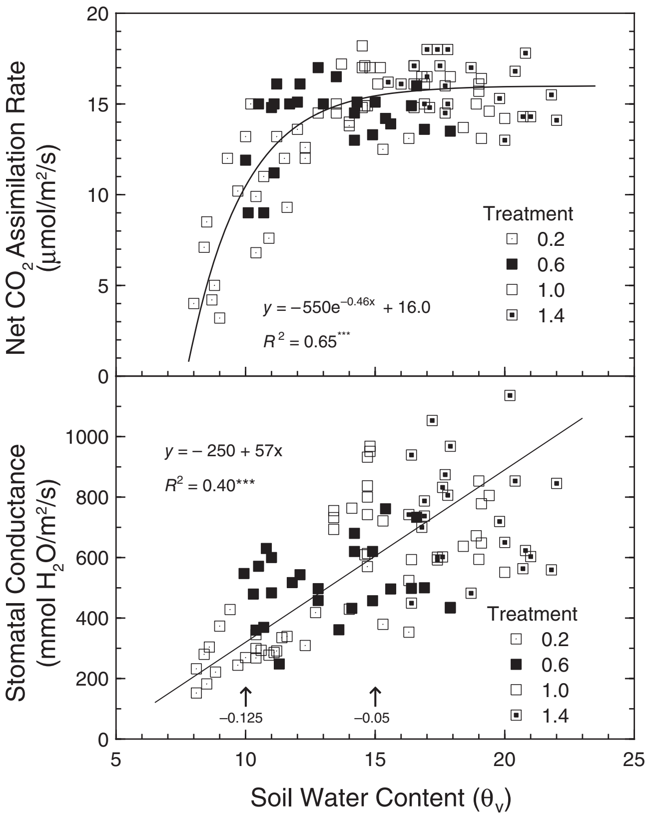

Figure 5. The relationships between net CO_2 assimilation rate and stomatal conductance measured at midday and soil water content in the Thompson Seedless vineyard. The values of gas exchange were used only if their measurements took place within three days of the soil water content being measured. The approximate soil matric potential (MPa) at a soil water content of 10 and 15 θ_v is given in the figure. Note that soil water content was not measured for vines in the no applied water treatment ($n = 100$). *** indicates significance at $P < 0.001$.

Discussion

Midday and diurnal measurements of A followed a curvilinear function of g_s in this study, similar to other studies on grapevines (Moutinho-Pereira et al. 2004, Cifre et al. 2005, de Souza et al. 2005, Soar et al. 2009, Flexas et al. 2010). Midday A was generally highest at g_s values greater than 400 mmol $H_2O/m^2/s$. With only a few exceptions, midday g_s values of vines in the 1.0 and 1.4 irrigation treatments were greater than 400 mmol $H_2O/m^2/s$, while those of vines that were not irrigated or irrigated at the 0.2 level were less than this value. The greatest values of g_s measured in this study on Thompson Seedless are some of the highest g_s values reported for grapevine with a few measurements even exceeding 1000 mmol $H_2O/m^2/s$. Values of grapevine g_s exceeding 800 mmol $H_2O/m^2/s$ have been reported by Cifre et al. (2005), Moutinho-Pereira et al. (2004) and Soar et al. (2009). The high values of g_s reported in this study are due to several factors. The vines in the 1.0 and 1.4 treatments were irrigated with water amounts at or greater than ET_c determined with a weighing lysimeter, with irrigation events occurring numerous times daily. Therefore, it can be assumed the vines in those treatments were not water stressed. Primary and lateral shoots continued to grow throughout the season with water applications at or greater than ET_c

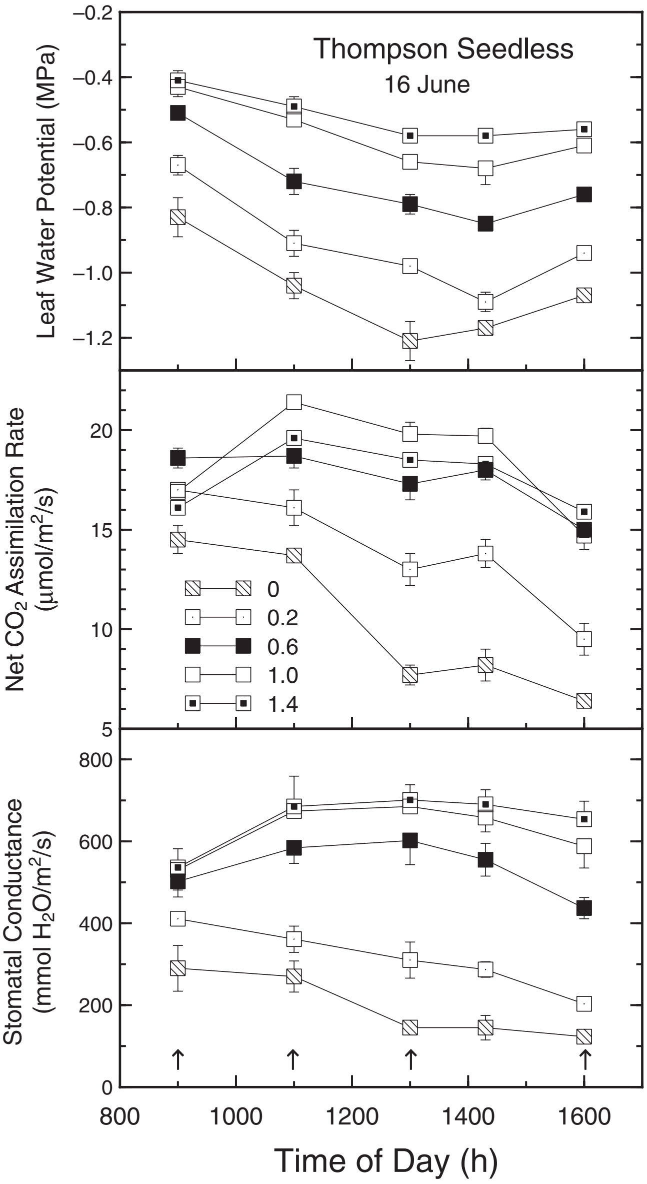

Figure 6. The diurnal time course of leaf water potential, net CO_2 assimilation rate and stomatal conductance of Thompson Seedless grapevines measured on 16 June 1992. The treatments were applied water amounts at various fractions of vine evapotranspiration measured with a weighing lysimeter. The arrows at the bottom of the figure represent an irrigation event automatically scheduled when the two vines in the lysimeter used 16 L of water. Applied water to the other irrigation treatments were their respective fractional amount. Each value is the mean of at least six individual leaf replicates, and the bars represent one standard error and are visible when larger than the symbol.

(Williams et al. 2010a). Leaves used for gas exchange measurements in this study were selected from the periphery of the canopy, and more than likely, the leaves chosen were recently expanded, mature leaves throughout the majority of the growing season. Lastly, it has been demonstrated that Shiraz grapevines will significantly increase g_s in response to increased ambient temperatures at a common vapour pressure deficit (Soar et al. 2009). In this study, maximum mean values of g_s measured during April, May, June and July of 1992 were 460, 640, 840 and 908 mmol $H_2O/m^2/s$, respectively. Therefore, maximum values of g_s increased as monthly mean high temperature increased during the growing season (data not given).

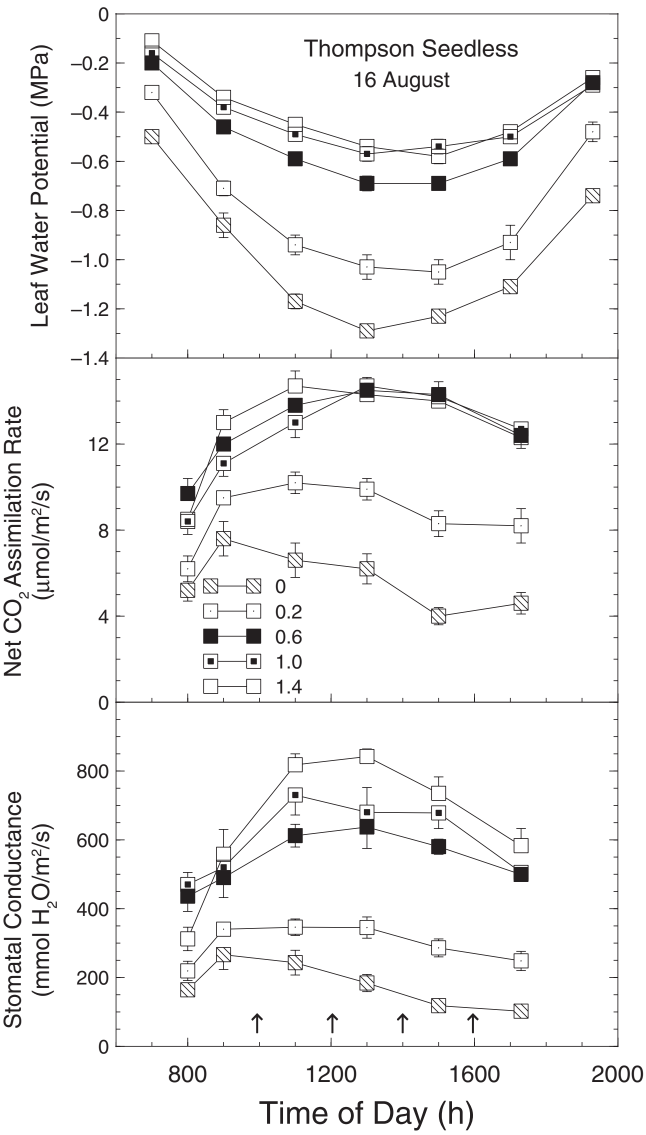

Figure 7. The diurnal time course of leaf water potential, net CO_2 assimilation rate and stomatal conductance of Thompson Seedless grapevines measured on 16 August 1993. Predawn Ψ_l for the 0, 0.2, 0.6, 1.0 and 1.4 irrigation treatments measured on this date were −0.50, −0.32, −0.18, −0.07 and −0.08 MPa, respectively. Other information is as given in Figure 6.

It has been proposed that g_s could be used to define the degree of water stress in grapevines (Cifre et al. 2005, Lovisolo et al. 2010). A mild water stress was defined as that when g_s decreases from greater than 500–150 mmol $H_2O/m^2/s$, a moderate stress when g_s decreases from 150–50 mmol $H_2O/m^2/s$ and a severe stress at a g_s less than 50 mmol $H_2O/m^2/s$. Midday g_s measured on vines irrigated at 0.2 of ET_c in this study were below 150 mmol $H_2O/m^2/s$ on a few occasions, while g_s of vines receiving no applied water were less than 100 mmol $H_2O/m^2/s$ only late in the afternoon (see Figures 5,6). Based upon the above classification of water stress, vines irrigated at 0.2 of ET_c were only moderately stressed. However, vegetative (Williams et al. 2010a) and reproductive (Williams et al. 2010b) growth of vines in this treatment (0.2 of ET_c) were greatly reduced compared with the highest pruning weights and yield obtained in those studies, respectively, indicating that those vines were not just exposed to a ‘mild to moderate’ stress. In addition, it was found that the ET_c/ET_o ratio decreased linearly as midday values of g_s decreased from 500 to 200 mmol/m^2/s (Williams et al. 2011). Results from this and the aforementioned studies would indicate that g_s values others have used to classify the severity of water stress in grapevines require re-evaluation.

The response of A to changes in g_s and their ratio (A/g_s or WUE_i) are potential physiological targets for improving water productivity (WP_b, as defined by Fereres and Soriano (2007) and Steduto et al. (2007)) of grapevines (Flexas et al. 2010). In this study, g_s decreased from greater than 1000 to 400 mmol H_2O/m^2/s without any significant reduction in A just by applying less water. This alone would have doubled WUE_i. The seasonal midday WUE_i was greatest for the 0.2 irrigation treatment across years, followed by the 0.6 treatment with no significant differences between the 1.0 and 1.4 irrigation treatments, similar to results of others examining the effects of irrigation treatments on this value (Flexas et al. 2010). The seasonal, midday WUE_i values calculated for the 1.0 and 1.4 irrigation treatments are the lowest so far reported for grapevines in the literature (Flexas et al. 2010). This low value is more than likely due to the high values of g_s measured on vines in those two treatments and that the WUE_i of grapevines grown in hot climates may normally be lower. The WP_b of these same Thompson Seedless grapevines significantly decreased as grapevine ET_c increased across the four irrigation treatments used in this study (Williams et al. 2010b). There were even significant differences between the 1.0 and 1.4 treatments because in part of lower yields of the vines being over-irrigated compared with the 1.0 treatment. Fresh yield per unit applied water decreased as seasonal applied water amounts increased (from the 0.2 to 1.4 irrigation treatments), but yield per unit ET_c was maximized at the 0.6 irrigation treatment each year of their study (Williams et al. 2010b). Flexas et al. (2010) suggested that an increase in WUE at the leaf level may not necessarily translate into increased WP_b at the whole plant level. This point is illustrated comparing the WUE_i reported herein and the data of Williams et al. (2010b). It would also indicate that prudent irrigation management would be as effective as any other means of increasing WUE at both the leaf and whole plant level while optimizing yields.

Midday Ψ_l was a curvilinear function of mean SWC (determined on $^1/_4$ of a vine's soil volume to a depth of almost 3 m) in this study, although a linear function would have fitted the data equally as well. This is similar to that reported by Williams et al. (2011) comparing midday Ψ_l with mean SWC of the vines growing in a weighing lysimeter after irrigation was terminated. However, in that study, access tubes were only placed beneath the drip line in the lysimeter. Williams and Araujo (2002) found that Ψ_{PD}, and midday Ψ_l and Ψ_{stem} were linearly related with SWC when those measurements were taken late in the growing season (R^2 values were 0.69, 0.68 and 0.63, respectively). Others have found that the fraction of transpirable soil water (FTSW) (the dependent variable) is a curvilinear function of Ψ_{PD} (independent variable) with coefficient of determinations between the two ranging from 0.68 to 0.82 (Lebon et al. 2003, Pellegrino et al. 2004).

The irrigation treatments imposed in this study had significant effects on midday A on individual dates, and A decreased as the season progressed for vines that were deficit irrigated. These results mimic the effects of the irrigation treatments on midday values of Ψ_l across growing seasons and among treatments (Williams et al. 2010a). Midday A was a curvilinear function of midday Ψ_l with 80% of the variation in A explained by changes in Ψ_l. Patakas et al. (2005) also found a curvilinear relationship between daily A_{max} (A_{max} was not necessarily measured at midday) and midday Ψ_{stem} with values of Ψ_{stem} explaining 84% of the variation in A_{max}. The coefficient of determination between midday Ψ_l as a measure of vine water status and A presented here is greater than that reported by others using Ψ_{PD} as a measure of vine water status (Williams and Araujo 2002, Medrano et al. 2003, Cifre et al. 2005, de Souza et al. 2005, Lovisolo et al. 2010).

Leaf net CO_2 assimilation rate began to decrease at a midday Ψ_l value of −1.0 MPa in this study. Patakas et al. (2005) reported that A decreased linearly once midday Ψ_{stem} values were less than −0.6 MPa. Using the relationship between Ψ_l and Ψ_{stem} in Williams and Araujo (2002), a Ψ_{stem} of −0.6 MPa would be equivalent to a Ψ_l of ~ −0.95 MPa. Naor et al. (1994) reported that A decreased linearly from a Ψ_l value of approximately −1.0 MPa (the highest Ψ_l value measured in the study) to less than −2.0 MPa. Kriedemann and Smart (1971) reported that A of Sultana vines did not decline until a Ψ_l value of −1.3 MPa was reached. It should be pointed out that there was no unique relationship between diurnal values of A and Ψ_l in this study similar to what others have found (Correia et al. 1995). The lack of a relationship between A and Ψ_l on a diurnal basis probably is due to the fact that the leaf blades used to measure A early in the morning or late in the afternoon are not exposed to saturating (photon flux density) PFD. It has been reported that A of nonwater stressed, field-grown grapevines does not saturate until a PFD value of 1500 μmol/m^2/s is reached (Downton et al. 1987, Mullins et al. 1992). In this study, PFD was always greater than 1500 μmol/m^2/s when both A and Ψ_l measurements were taken at midday.

The relationship between midday g_s and Ψ_l was best described as a linear function. While the regression was significant, it only explained 46% of the variation in g_s, but this is similar to the variation reported by others (given above) using Ψ_{PD} as the independent variable. The linear relationship between g_s and Ψ_l reported here agrees with Shackel (2007) and Williams et al. (2011), both of whom reported midday measurements of grapevine g_s and Ψ_l were highly correlated with one another. The greater correlation ($r = 0.96$) between g_s and Ψ_l reported by Williams et al. (2011) compared with the data presented in this paper was due to the fact that measurements were only taken on the two vines grown in the weighing lysimeter during a 'dry down' over a 6-week period, whereas measurements here were taken throughout the growing season and across irrigation treatments and years. The data obtained in this study and in the above cited references is opposite 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.

Liu et al. (1978) reported that partial stomatal closure for droughted, pot-grown vines only occurred at a Ψ_l value of −1.3 MPa, which differs from this study and that of Williams et al. (2011) where g_s is reduced across all values of Ψ_l. van Zyl (1987) reported that stomata remained open until a threshold Ψ_l of −1.6 MPa was reached. This is comparable with the data presented in this study where g_s is approximately nil at a Ψ_l value of −1.6 MPa (Figure 4) but differs from Williams and Araujo (2002) where the zero intercept for the relationship between g_s and Ψ_l was ~ −1.9 MPa. It would appear that the midday value of Ψ_l at which stomata are essentially closed may naturally vary.

The relationship between midday A and SWC was curvilinear. There was no decline in A until the SWC had reached a θ_v value of 13.0% at which time there was almost a linear reduction in A with further reductions in SWC. Approximately 50% of the available SWC at field capacity had been depleted at this θ_v value. It was demonstrated that leaf gas exchange (A and g_s) of *Nerium oleander* L. started to decreased once 50% of the extractable soil water had been depleted (Gollan et al. 1985), while that of *Helianthus annuus* L. did not start to decrease until two thirds of the extractable soil water had been depleted (Turner et al. 1985). Both of these studies were conducted on potted plants. Pellegrino et al. (2006) reported that A_{max} (A_{max} was not necessarily measured at midday) of grapevine started to decrease at an FTSW between 0.5 and 0.4 (corresponding to a depletion of 50 and 60%, respectively). Therefore, the response of midday A to SWC found here is similar to that reported by others on different plant species and grapevine.

The response of midday g_s with SWC in this study was best described as a linear function (Figure 3). This is similar to the response of g_s to the decrease in SWC reported by Williams et al. (2011) for vines growing in the weighing lysimeter, although the coefficient of determination between the two variables was less here compared with the referenced study. Cuevas et al. (2006) found that the relationship between g_s and SWC was dependent upon year, time during the growing season and time of day the measurements were taken. In general, they found the relationship to be linear to slightly curvilinear. Olivo et al. (2009) found that Ψ_{stem} decreased linearly as soil water was depleted. Using the data only from the 1991 and 1992 growing seasons in this study, the relationship between midday Ψ_l and SWC was linear ($\Psi_l = -1.71 + 0.057\theta_v$; $R^2 = 0.73^{***}$, $n = 80$). However, when SWC data from the 1993 growing season, which received more rainfall than the previous 2 years resulting in greater values of soil moisture (Williams et al. 2010a), is pooled with values of SWC from the 1991 and 1992 growing seasons, the relationship was curvilinear. Maximum values of midday Ψ_l levelled off at a θ_v of 20% similar to that reported by Williams and Trout (2005) using data from selected dates in this vineyard.

The two diurnal time courses of Ψ_l, A and g_s reported in this study were from late spring (Figure 6) and mid-August (Figure 7) but from two different growing seasons. Leaf Ψ underwent a diurnal fluctuation, with daily minimum values reached between 1300 and just subsequent to 1400 h PDT for all of the treatments on both dates. The time of the daily minimum Ψ_l in this study occurred earlier in the day for the irrigated treatments than what others have reported (van Zyl 1987, Naor and Wample 1994, Greenspan et al. 1996, Medrano et al. 2003, Schultz 2003). The time of the daily minimum Ψ_l for the nonirrigated treatment in this study actually occurred later in the day than for nonirrigated Syrah and Grenache vines (minimum reached as early as 0800 h) in the paper by Schultz (2003). The timing of the daily minimum Ψ_l may be a function of row direction, time of year, environmental conditions, severity of water stress and applied water amounts, and their timing of application prior to the day measurements took place (unpublished data). The daily minimum values of Ψ_l for vines irrigated with applied water amounts at ET_c were greater than −0.7 MPa (Figures 6,7), while midday Ψ_l of the 1.0 irrigation treatment throughout the growing season (data shown in Figures 3,4) and in Williams et al. (2010a) were generally greater than −1.0 MPa. These values are greater than those reported by others for vines that were grown at a wetter site compared with a drier site (Winkel and Rambal 1993) designated the irrigated control (Greenspan et al. 1996, Schultz 2003), continuously irrigated treatment (Naor and Wample 1994) or treatments irrigated at 100% of estimated ET_c (van Zyl 1987, Patakas et al. 2005). The diurnal minimum Ψ_l values of vines irrigated at ET_c here are similar to those reported by Grimes and Williams (1990) for Thompson Seedless, Medrano et al. (2003) for Tempranillo and Williams and Baeza (2007) for Merlot and Cabernet Sauvignon. It would appear that applied water amounts in the previously referenced studies with lower values of Ψ_l were not actually irrigated at 100% of measured ET_c, as was done in this study, or were perhaps waterlogged (Naor and Wample 1994). Alternatively, the method one uses to measure Ψ_l can significantly affect the value of Ψ_l one measures and if not done properly would result in lower values of Ψ_l (Turner and Long 1980, Williams and Araujo 2002, Williams et al. 2011).

The minimum Ψ_l values reported here for the 0.2 irrigation treatment and the nonirrigated treatment (Figures 6,7) are greater than what others have reported for their deficit irrigated treatment or their nonirrigated vines (Winkel and Rambal 1993, Greenspan et al. 1996, Schultz 2003). The lowest midday Ψ_l values for the 0.2 and nonirrigated treatments were less than −1.5 MPa (Williams et al. 2010a). The higher Ψ_l for these two treatments may be due in part to the fact that the leaf area of vines in these treatments in this study were much less than those of the other irrigated treatments because of both smaller shoot length and leaf abscission as water stress developed. This would have minimized their water use resulting in greater absolute values of Ψ_l. Leaf area of the vines in the 0.2 irrigation treatment were only 33% or less in those of vines irrigated at ET_c from mid-season onwards (Williams et al. 2010a). Lastly, it should be pointed out that the vines in this study were not only irrigated daily but multiple times each day. Vines were irrigated four times during the day on both 16 June and 16 August, which may have affected absolute values of Ψ_l across all irrigation treatments and their diurnal pattern.

It has been reported that A of grapevine will gradually decrease from a maximum value reached mid-morning (~2–3 h before solar noon) throughout the remainder of the day, even for well-watered vines (Correia et al. 1990, 1995). Examination of the diurnal leaf gas exchange data for the irrigated controls in Schultz (2003), the continuously irrigated treatment in Naor and Wample (1994), and whole vine net CO_2 exchange and transpiration rates of well-watered Lambrusco (Poni et al. 2009) would appear to confirm this observation. This is probably the reason that some researchers will measure A and g_s mid-morning to determine the effects of their irrigation treatments on leaf gas exchange (Romero et al. 2010) because one would obtain the highest values on a diurnal basis at this time. However, A of the 0.6, 1.0 and 1.4 irrigation treatments increased from the first measurement time on 16 June to the next, levelled off for the next 4 h before it decreased at 1600 h, while it increased from 0800 to 1100 h for the same irrigation treatments on 16 August and was only slightly lower at 1700 h than at midday in this study. Therefore, A did not decrease after reaching its mid-morning maximum value for the vines irrigated at ET_c in this study until late into the afternoon, possibly in response to nonsaturating PFD values.

Leaf net CO_2 assimilation rate and g_s for the 0.2 irrigation treatment (on 16 June) and the nonirrigated vines (on both dates) in this study generally decreased throughout the day, while A and g_s remained fairly constant for the 0.2 treatment on 16 August. These diurnal patterns resemble those patterns for the ‘well-watered’ or ‘irrigated’ grapevine treatments in earlier studies (Correia et al. 1990, 1995, Naor and Wample 1994, Schultz 2003, Poni et al. 2009). They also resemble diurnal patterns of leaf gas exchange for the fully irrigated vines in de Souza et al. (2005) and Chaves et al. (2007), and for grapevines with a sufficient water supply (unstressed vines) in Jacobs et al. (1996). Therefore, the diurnal patterns of leaf gas exchange presented in this paper and that of Medrano et al. (2003) for fully irrigated, deficit irrigated and nonirrigated vines would indicate that the term ‘well-watered’ or ‘irrigated’ in other studies does not necessarily mean that the vines are not water stressed. The water status of ‘well-watered’ or ‘irrigated’ treatments in many of the earlier referenced papers is determined by measurements of Ψ_{PD} that are not as well correlated as those of midday Ψ_l and Ψ_{stem} with SWC under drip irrigation (Williams and Trout 2005). In addition, a Ψ_{PD} of ~0.2 MPa assumed by many to indicate little or no stress in field-grown grapevines (Ojeda et al. 2001, Schultz and Stoll 2010) reduced the ET_c/ET_o ratio of Thompson Seedless grapevines by greater than 40% compared with the same vines not stressed for water ($\Psi_{PD} > -0.1$ MPa) (Williams et al. 2011). Therefore, the term 'well-watered' or 'fully-irrigated' should be used only under conditions in which applied water amounts are equivalent to measured grapevine ET_c, such as used in this study, or best estimates of ET_c, such as those given in Williams and Baeza (2007) and Williams (2010).

The diurnal pattern of Ψ_l and g_s across the irrigation treatments presented in this paper on two separate dates is similar to the diurnal pattern of *H. annuus* given in Tardieu and Simonneau (1998) as an example of an anisohydric plant species. The classification of a plant species as anisohydric or isohydric is related to the plant's stomatal control of transpiration. An anisohydric species' stomata will allow transpiration to increase as the day proceeds with Ψ_l becoming more negative for all treatments with those being deficit irrigated or not irrigated having significantly more negative values of Ψ_l than the well-watered treatment. Stomatal control of an isohydric plant species (or variety) will result in diurnal values of Ψ_l being similar among plants receiving differing amounts of applied water (Tardieu and Simonneau 1998). Schultz (2003) and Vandeleur et al. (2009) reported that varieties of *V. vinifera* could be classified as either anisohydric or 'near-isohydric' (Syrah and Chardonnay are the anisohydric varieties, respectively, and Grenache is the isohydric variety in both studies). Based on the diurnal patterns of Ψ_l and g_s presented in Figures 6 and 7, Thompson Seedless would be classified as anisohydric. It is often assumed that grapevines (*V. vinifera*) are isohydric (Medrano et al. 2003, Cifre et al. 2005, Patakas et al. 2005), although the diurnal Tempranillo and Manto Negro data of Medrano et al. (2003) would argue against such. Soar et al. (2006) concluded that grapevines in general are anisohydric as did Williams and Baeza (2007) for Thompson Seedless, Cabernet Sauvignon and Merlot. In most studies on grapevine, the classification of varieties as being either anisohydric or isohydric is dependent upon a 'well-watered' or 'irrigated' treatment included in the study, the use of Ψ_{PD} as a measure of vine water status to indicate differences in water status among treatments and whether there are significant differences in midday Ψ_l between or among the treatments. As pointed out previously and data provided in this study for the 0.2 irrigated treatment, an 'irrigated' treatment does not necessarily mean that the vines are not water stressed, Ψ_{PD} of drip-irrigated vines may equilibrate with only the wettest portion of the soil profile thereby not providing a reliable indicator of vine water status, and if one does not bag the leaf blade prior to cutting the petiole, midday values of Ψ_l of the 'well-watered' treatment would be lower than they would have been if the procedure had been done as outlined by Turner and Long (1980).

Conclusion

The irrigation treatments at various fractions of grapevine ET_c imposed in this study significantly affected leaf gas exchange throughout the growing season. Values of midday A were curvilinearly related to midday Ψ_l and SWC, whereas g_s was a linear function of both. The differing responses of A and g_s to measures of vine and soil water status would maximize A while minimizing water loss via the stomata. However, while the treatments imposed herein significantly affected WUE_i, they were not directly correlated with previously published values of WP_b or fresh yield per unit applied water or ET_c of these vines. This indicates that altering the A/g_s ratio may not provide a useful means to increase vineyard WUE, especially if environmental conditions (temperature and vapor pressure deficit (VPD)) have more of an impact on g_s than A and if yield is not directly related to A. Lastly, diurnal gas exchange of vines in the 1.0 irrigation treatment receiving applied water amounts equal to that of ET_c measured with a weighing lysimeter provided values of Ψ_l, A and g_s for a truly 'well-watered' irrigation treatment.

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References

Araujo, F., Williams, L.E., Grimes, D.W. and Matthews, M.A. (1995) A comparative study of young 'Thompson Seedless' grapevines under drip and furrow irrigation. I. Root and soil water distributions. Scientia Horticulturae **60**, 235–249.

Chaves, M.M., Santos, T.P., Souza, C.R., Ortuño, M.F., Rodriques, M.L., Lopes, C.M., Maroco, J.P. and Pereira, J.S. (2007) Deficit irrigation in grapevine improves water-use efficiency while controlling vigour and production quality. Annals of Applied Biology **150**, 237–252.

Cifre, J., Bota, J., Escalona, J.M., Medrano, H. and Flexas, J. (2005) Physiological tools for irrigation scheduling in grapevine (*Vitis vinifera* L.). An open gate to improve water-use efficiency. Agriculture, Ecosystems & Environment **106**, 159–170.

Correia, M.J., Chaves, M.M. and Pereira, J.S. (1990) Afternoon depression in photosynthesis in grapevine leaves – evidence for a high light stress effect. Journal of Experimental Botany **41**, 417–426.

Correia, M.J., Pereira, J.S., Chaves, M.M., Rodriques, M.L. and Pacheco, C.A. (1995) ABA xylem concentrations determine maximum daily leaf conductance of field-grown *Vitis vinifera* L. plants. Plant, Cell & Environment **18**, 511–521.

Cuevas, E., Baeza, P. and Lissarrague, J.R. (2006) Variation in stomatal behavior and gas exchange between mid-morning and mid-afternoon of north-south oriented grapevines (*Vitis vinifera* L. cv. Tempranillo) at different levels of soil water availability. Scientia Horticulturae **108**, 173–180.

Daane, K.M. and Williams, L.E. (2003) Manipulating vineyard irrigation amounts to reduce insect pest damage. Ecological Applications **13**, 1650–1666.

Downton, W.J.S., Grant, W.J.R. and Loveys, B.R. (1987) Diurnal changes in the photosynthesis of field-grown grape vines. New Phytologist **105**, 71–83.

Fereres, E. and Soriano, M.A. (2007) Deficit irrigation for reducing agricultural water use. Journal of Experimental Botany **58**, 147–159.

Flexas, J., Galmés, J., Gallé, A., Gulías, J., Pou, A., Ribas-Carbo, M., Tomàs, M. and Medrano, H. (2010) Improving water use efficiency in grapevines: potential physiological targets for biotechnological improvement. Australian Journal of Grape and Wine Research **16**, 106–121.

Gollan, T., Turner, N.C. and Schulze, E.D. (1985) The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. III. In the sclerophyllous woody species *Nerium oleander*. Oecologia **65**, 356–362.

Greenspan, M.D., Schultz, H.R. and Matthews, M.A. (1996) Field evaluation of water transport in grape berries during water deficits. Physiologia Plantarum **97**, 55–62.

Grimes, D.W. and Williams, L.E. (1990) Irrigation effects on plant water relations and productivity of 'Thompson Seedless' grapevines. Crop Science **30**, 255–260.

Jacobs, C.M.J., van den Hurk, B.J.J.M. and de Bruin, H.A.R. (1996) Stomatal behavior and photosynthetic rate of unstressed grapevines in semi-arid conditions. Agricultural and Forest Meteorology **80**, 111–134.

Kriedemann, P.E. and Smart, R.E. (1971) Effects of irradiance, temperature, and leaf water potential on photosynthesis of vine leaves. Photosynthetica **5**, 6–15.

Lebon, E., Dumas, V., Pieri, P. and Schultz, H.R. (2003) Modelling the seasonal dynamics of the soil water balance in vineyards. Functional Plant Biology **30**, 699–710.

Liu, W.T., Wenkert, W., Allen, L.H. Jr and Lemon, E.R. (1978) Soil-plant water relations in a New York vineyard: resistances to water movement. Journal of the American Society for Horticultural Science **103**, 226–230.

Lovisolo, C., Perrone, I., Carra, A., Ferrandion, A., Flexas, J., Medrano, H. and Schubert, A. (2010) Drought-induced changes in development and function of grapevine (*Vitis* spp.) organs and in their hydraulic and nonhydraulic interactions at the whole-plant level: a physiological and molecular update. Functional Plant Biology **37**, 98–116.

Marsal, J., Mata, M., del Campo, J., Arbones, A., Vallverdú, X., Girona, J. and Olivo, N. (2008) Evaluation of partial root-zone drying for potential field use as a deficit irrigation technique in commercial vineyard according to two different pipeline layouts. Irrigation Science **26**, 347–356.

Matthews, M.A. and Anderson, M.M. (1989) Reproductive development in grape (*Vitis vinifera* L.): responses to seasonal water deficits. American Journal of Enology and Viticulture **40**, 52–60.

McCarthy, M.G., Loveys, B.R., Dry, P.R. and Stoll, M. (2000) Regulated deficit irrigation and partial rootzone drying as irrigation management techniques for grapevines. In: Deficit irrigation practices. FAO Water Report No. 22. (FAO: Rome, Italy) pp. 79–87.

Medrano, H., Escalona, J.M., Cifre, J., Bota, J. and Flexas, J. (2003) A ten-year study on the physiology of two Spanish grapevine cultivars under field conditions: effects of water availability from leaf photosynthesis to grape yield and quality. Functional Plant Biology **30**, 607–619.

Moutinho-Pereira, J.M., Correia, C.M., Goncalves, B.M., Bacelar, E.A. and Torres-Pereira, J.M. (2004) Leaf gas exchange and water relations of grapevines grown in three different conditions. Photosynthetica **42**, 81–86.

Mullins, M.G., Bouquet, A. and Williams, L.E. (1992) Biology of the grapevine (Press Syndicate of the University of Cambridge: Cambridge).

Naor, A. and Wample, R.L. (1994) Gas exchange and water relations of field-grown Concord (*V. labruscana* Bailey) grapevines. American Journal of Enology and Viticulture **45**, 333–357.

Naor, A., Bravdo, B. and Gelobter, J. (1994) Gas exchange and water relations in field-grown Sauvignon blanc grapevines. American Journal of Enology and Viticulture **45**, 423–428.

Ojeda, H., Deloire, A. and Carbonneau, A. (2001) Influence of water deficits on grape berry growth. Vitis **40**, 141–145.

Olivo, N., Girona, J. and Marsal, J. (2009) Seasonal sensitivity of stem water potential to vapour pressure deficit in grapevine. Irrigation Science **27**, 175–182.

Patakas, A., Noitsakis, B. and Chouzouri, A. (2005) Optimizations of irrigation water use in grapevines using the relationship between transpiration and plant water status. Agriculture, Ecosystems & Environment **106**, 253–259.

Pellegrino, A., Lebon, E., Voltz, M. and Wery, J. (2004) Relationships between plant and soil water status in vine (*Vitis vinifera* L.). Plant and Soil **266**, 129–142.

Pellegrino, A., Gozé, E., Lebon, E. and Wery, J. (2006) A model-based diagnosis tool to evaluate the water stress experienced by grapevine in field sites. European Journal of Agronomy **25**, 49–59.

Poni, S., Bernizzoni, F., Civardi, S., Gatti, M., Porro, D. and Camin, F. (2009) Performance and water-8se efficiency (single-leaf vs. whole-canopy) of well-watered and half-stressed split-root Lambrusco grapevines grown in the Po Valley (Italy). Agriculture, Ecosystems & Environment **129**, 97–106.

Romero, P., Fernandez-Fernandez, J.I. and Martinez-Cutillas, A. (2010) Physiological thresholds for efficient regulated deficit-irrigated management winegrapes grown under semiarid conditions. American Journal of Enology and Viticulture **61**, 300–312.

Schultz, H.R. (2003) Differences in hydraulic architecture account for near-isohydric and anisohydric behaviour of two field-grown *Vitis vinifera* L. cultivars during drought. Plant, Cell & Environment **26**, 1393–1405.

Schultz, H.R. and Stoll, M. (2010) Some critical issues in environmental physiology of grapevines: future challenges and current limitations. Australian Journal of Grape and Wine Research **16**, 4–24.

Shackel, K.A. (2007) Water relations of woody perennial plant species. Journal International des Sciences de la Vigne et du Vin **41**, 121–129.

Soar, C.J., Collins, M.J. and Sadras, V.O. (2009) Irrigated Shiraz vines (*Vitis vinifera*) upregulate gas exchange and maintain berry growth in response to short spells of high maximum temperature in the field. Functional Plant Biology **36**, 801–814.

Soar, C.J., Speirs, J., Maffei, S.M., Penrose, A.B., McCarthy, M.G.M. and Loveys, B.R. (2006) Grape vine varieties Shiraz and Grenache differ in their stomatal response to VPD: apparent links with ABA physiology and gene expression in leaf tissue. Australian Journal of Grape and Wine Research **12**, 2–12.

de Souza, C.R., Maroco, J.P., dos Santos, T.P., Rodrigues, M.L., Lopes, C., Pereira, J.S. and Chaves, M.M. (2005) Control of stomatal aperture and carbon uptake by deficit irrigation in two grapevine cultivars. Agriculture, Ecosystems & Environment **106**, 261–274.

Steduto, P., Hsiao, T.C. and Fereres, E. (2007) On the conservative behavior of biomass water productivity. Irrigation Science **25**, 189–207.

Tardieu, F. and Simonneau, T. (1998) Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. Journal of Experimental Botany **49**, 419–432.

Turner, N.C. and Long, M.J. (1980) Errors arising from rapid water loss in the measurement of leaf water potential by the pressure chamber technique. Australian Journal of Plant Physiology **7**, 527–537.

Turner, N.C., Schulze, E.D. and Gollan, T. (1985) The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content II. In the mesophytic herbaceous species *Helinathus annuus*. Oecologia **65**, 348–355.

Vandeleur, R.K., Mayo, G., Shelden, M.C., Gilliham, M., Kaiser, B.N. and Tyerman, S.D. (2009) The role of plasma membrane intrinsic protein aquaporins in water transport through roots: diurnal and drought stress responses reveal strategies between isohydric and anisohydric cultivars of grapevine. Plant Physiology **149**, 445–460.

Williams, L.E. (2010) Interaction of rootstock and applied water amounts at various fractions of estimated evapotranspiration (ET_c) on productivity of Cabernet Sauvignon. Australian Journal of Grape and Wine Research **16**, 434–444.

Williams, L.E. and Araujo, F. (2002) Correlations among predawn leaf, midday leaf, and midday stem water potential and their correlations with other measures of soil and plant water status in *Vitis vinifera* L. Journal of the American Society for Horticultural Science **127**, 448–454.

Williams, L.E. and Baeza, P. (2007) Relationships among ambient temperature and vapor pressure deficit and leaf and stem water potentials of fully irrigated, field-grown grapevines. American Journal of Enology and Viticulture **58**, 173–181.

Williams, L.E. and Matthews, M.A. (1990) Grapevine. In: Irrigation of agricultural crops – Agronomy Monograph No. 30. Eds. B.A. Stewart and D.R. Nielson (ASA-CSSA-SSSA: Madison, WI, USA) pp. 1019–1059.

Williams, L.E. and Trout, T.J. (2005) Relationships among vine and soil based measures of water status in a Thompson Seedless vineyard in response to high frequency drip irrigation. American Journal of Enology and Viticulture **56**, 357–366.

Williams, L.E., Grimes, D.W. and Phene, C.J. (2010a) The effects of applied water at various fractions of measured evapotranspiration on water relations and vegetative growth of Thompson Seedless. Irrigation Science **28**, 221–232.

Williams, L.E., Grimes, D.W. and Phene, C.J. (2010b) The effects of applied water at various fractions of measured evapotranspiration on reproductive growth and water productivity of Thompson Seedless. Irrigation Science **28**, 233–243.

Williams, L.E., Baeza, P. and Vaughn, P. (2011) Midday measurements of leaf water potential and stomatal conductance are highly correlated with daily water use of Thompson Seedless grapevines. Irrigation Science. (DOI 10.1007/s00271-011-0276-2).

Williams, L.E., Phene, C.J., Grimes, D.W. and Trout, T.J. (2003a) Water use of young Thompson Seedless grapevines in California. Irrigation Science **22**, 1–9.

Williams, L.E., Phene, C.J., Grimes, D.W. and Trout, T.J. (2003b) Water use of mature Thompson Seedless grapevines in California. Irrigation Science **22**, 11–18.

Williams, L.E., Retzlaff, W.A., Yang, W., Biscay, P.J. and Ebisuda, N. (2000) Effect of girdling on leaf gas exchange, water status and non-structural carbohydrates of field-grown *Vitis vinifera* L. (cv. Flame Seedless). American Journal of Enology and Viticulture **51**, 49–54.

Winkel, T. and Rambal, S. (1993) Influence of water stress on grapevines growing in the field: from leaf to whole plant response. Australian Journal of Plant Physiology **20**, 143–157.

van Zyl, J.L. (1987) Diurnal variation in grapevine water stress as a function of changing soil water status and meteorological conditions. South African Journal of Enology and Viticulture **8**, 45–52.

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