Moderate Water Stress from Regulated Deficit Irrigation Decreases Transpiration Similarly to Net Carbon Exchange in Grapevine Canopies

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ADDITIONAL INDEX WORDS. water use efficiency, canopy conductance, photosynthesis, whole-canopy gas exchange, *Vitis vinifera*

ABSTRACT. To determine the effects of timing and extent of regulated deficit irrigation (RDI) on grapevine (*Vitis vinifera*) canopies, whole-canopy transpiration (Tr_v) and canopy conductance to water vapor (g_c) were calculated from whole-vine gas exchange near key stages of fruit development. The vines were managed under three approaches to RDI: 1) standard industry practice (RDI_s), or weekly replacement of 60% to 70% of estimated evapotranspiration (ET) for well-watered grapevines; 2) early additional deficit (RDI_E), or one-half of RDI_s applied between fruit set and veraison; and 3) late additional deficit (RDI_L), or one-half of RDI_s applied between veraison and harvest. Compared with RDI_s , the additional deficits (RDI_E , RDI_L) reduced daily cumulative Tr_v by about 45% (RDI_E) and about 48% [RDI_L (57% by unit leaf area)]. Diurnal patterns of g_c indicated consistent moderate water stress in all RDI regimens ($g_c \approx 50\text{--}150 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Under RDI_E and RDI_L , there were transient occurrences of severe water stress, indicated by g_c declining below $50 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Across the day, vines under RDI_E and RDI_L had lower g_c than RDI_s . Under all deficit regimens, Tr_v exhibited opposing hysteretic loops with solar radiation [photosynthetic photon flux (PPF)] and vapor pressure deficit (VPD), with less sensitivity to VPD in RDI_E and RDI_L . For a given value of VPD, Tr_v was higher in the morning than in the afternoon. For a given value of PPF, Tr_v was higher in the afternoon than in the morning. Single-leaf measurements of transpiration overestimated Tr_v by an average of 45%. Instantaneous water use efficiency (WUE) declined during midday at the pre- and postveraison measurements for all RDI regimens. Whole-canopy daily integrated WUE (WUE_d) did not differ among regimens during the additional deficits because daily cumulative values of whole-vine net carbon exchange (NCE_v) and Tr_v changed proportionally: by about 43% to 46% in RDI_E relative to RDI_s . The case was less clear-cut for RDI_L , where NCE_v declined by 33% and Tr_v by 48% relative to RDI_s . However, WUE_d did not differ significantly between the two. More substantial water deficits than those are currently practiced in the industry through RDI could be used for potential water savings in semiarid climates.

Regulated deficit irrigation is used to manage soil water content to impose predetermined periods of plant water stress or soil water deficit that may elicit a desirable response in the plants (see reviews by Behboudian and Singh, 2001; Chaves et al., 2010; Lovisolo et al., 2010). Concomitant with this plant-based objective, RDI is a management tool that is relevant to concerns about water scarcity and the competition for water among agriculture, industry, and domestic use (Intergovernmental Panel

on Climate Change, 2014). Regulated deficit irrigation has become widely adopted in the production of wine grapes in arid and semiarid areas. About two-thirds of the major grape-producing regions of the world may be subjected to moderate or severe drought in any given year (Flexas et al., 2010). Irrigation timing and frequency are used to control canopy size (Loveys et al., 2004) and to influence berry size and change berry composition (see reviews by Chaves et al., 2010; Lovisolo et al., 2010), which are particularly pertinent in red wine grapes. The effects of water deficits on vegetative growth, vine productivity, and fruit quality vary based on their timing, and results have not been entirely consistent among studies (e.g., Castellarin et al., 2007; Intrigliolo et al., 2012; Tarara et al., 2011).

Regulated deficit irrigation affects both net carbon exchange (NCE) and transpiration (Tr), which are coupled processes. The ratio between NCE and Tr is referred to as instantaneous WUE. Under RDI, the physiological regulation of WUE is not fully understood (Schultz and Stoll, 2010). For example, under moderate water stress, WUE was not different between irrigated and nonirrigated plants, but WUE decreased under more severe water stress (Schultz and Stoll, 2010). Whole-vine WUE (Poni et al., 2014) under moderate water stress (irrigated to 70% of full-vine ET) did not differ from that of well-watered vines, but whole-vine WUE was substantially lower for more severely

Received for publication 18 May 2015. Accepted for publication 7 July 2015. Funding for this project was provided by USDA-ARS CRIS no.5358-21000-025-D, USDA-ARS Northwest Center for Small Fruits Research, USDA-CSREES-Viticulture Consortium, WSU Department of Horticulture and Landscape Architecture, American Vineyard Foundation, and Washington Wine Advisory Committee.

We thank Ste Michelle Wine Estates for generously allowing use of the vineyard site and Mimi Nye for vineyard management. We also thank INTA for support of the sabbatical of J.E. Perez Peña.

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water stressed vines (irrigated to 50% of full-vine ET). Variation in WUE under drought occurs across cultivars and within a cultivar depending upon the conditions in which the vines were grown (Lovisolo et al., 2010). There is a paucity of information on WUE at the whole-vine level, but recently WUE was investigated under various deficit irrigation regimens using concurrent single-leaf and whole-vine methods (Merli et al., 2015), the single-leaf measurements providing a link to the bulk of data in the literature.

We reported (Tarara et al., 2011) the consequences on NCE of different timing (pre- vs. postveraison) and degree of RDI [additional deficits of 50% of the industry standard RDI (RDI_S)] in *V. vinifera* ‘Cabernet Sauvignon’. Under an early additional deficit [RDI_E (fruit set to veraison)], vines fixed about 45% less carbon per day than did vines under RDI_S . Under a late additional deficit [RDI_L (veraison to harvest)], about 33% less carbon was fixed per day than under RDI_S . As a function of cumulative irrigation applied, between fruit set and harvest a total water savings of about 40% accompanied RDI_E , whereas about 20% less irrigation was applied to vines under RDI_L . At harvest, there were no consistent differences among irrigation regimens in berry mass, fruit maturity indices, and quality indicators.

The objective of this report is to demonstrate how the timing and extent of water restrictions greater than that of standard industry RDI alter whole-vine transpiration, g_c , and whole-vine WUE in field-grown, mature grapevines in a semiarid climate. The additional deficits were each imposed independently during one of two main periods of fruit development that have been implicated in affecting fruit quality: 1) shortly after fruit set to the onset of veraison and 2) veraison to commercial maturity. These two stages of berry development were selected to investigate the ultimate effect on yield and fruit quality—critical variables for the wine industry—and to contribute to the body of knowledge on physiological responses to deficit irrigation regimens. At key developmental stages, whole-vine measurements of gas exchange were made to minimize the scaling-up limitations of the single-leaf technique.

Materials and Methods

SITE DESCRIPTION. The experiment was conducted during 2002 and 2003 in a commercial vineyard (4 ha) ≈ 15 km west of Paterson, WA (lat. $45^{\circ}53'N$, long. $119^{\circ}45'W$, 125 m above sea level). Long-term mean annual rainfall (1990–2013) is 206 mm and reference evapotranspiration (ET_o) is ≈ 1075 mm [Washington State University AgWeatherNet (AWN), 2015]. The vineyard was located on a 14% south-facing slope on a uniformly deep (≈ 1 m) Burbank loamy fine sand (sandy-skeletal, mixed mesic Xeric Torriorthents) with an estimated field capacity (FC) of 14.6% v/v and permanent wilting point of 7.1% v/v (U.S. Department of Agriculture, 2015). The vineyard had been planted in 1992 to own-rooted grapevines (‘Cabernet Sauvignon’) in rows oriented north–south, with 2.7 m between rows and 1.8 m between vines for an average plant density of ≈ 2000 vines/ha. Vines were trained to a bilateral cordon (permanent, horizontal extension of the trunk) at a height of ≈ 1 m aboveground. Shoots were loosely trained vertically between two foliage wires spaced 0.25 m apart at 0.2 m above the cordon, allowing a “sprawl” architecture above that height. Vines were winter pruned annually to two-bud spurs. All other horticultural practices were according to commercial convention for red wine grapes grown in the area. Fertilizer and pest

management interventions were applied uniformly across plots. Irrigation was delivered by drip through a single line per row using $1.8 \text{ L}\cdot\text{h}^{-1}$, pressure-compensated emitters spaced 1.2 m apart (three emitters for every two vines).

Meteorological variables were measured on-site (Tarara et al., 2011) or where applicable, reference data were obtained from the Alderdale AWN station [≈ 10 km west of site (2002, 2003)] and Paterson West [≈ 15 km east of site (long-term normals)]. Thermal time expressed as degree-days [DD ($^{\circ}C$)] was computed in daily increments from the daily maximum and minimum temperatures using a lower threshold of $10^{\circ}C$ and no upper threshold. The daily values were summed arithmetically from 1 Apr. [day of year (DOY) 91] to 31 Oct. (DOY 304) according to local convention for grape production.

RDI REGIMENS. A complete description of the experimental methods is given in Tarara et al. (2011) and is briefly summarized below. The RDI regimens were applied to plots consisting of five rows each within which the middle two rows were used for data collection. All were irrigated to FC just after budbreak (early April). Irrigation was then withheld until shoots were ≈ 1 m long to minimize the rate of growth in main shoots. Regulated deficit irrigation was imposed from shortly after fruit set until harvest. All RDI regimens were based on estimated crop evapotranspiration (ET_c) derived from ET_o (Allen et al., 1998) and a crop coefficient (K_c) for drip irrigated ‘Cabernet Sauvignon’ in eastern Washington (Evans et al., 1993). The RDI regimens had been imposed since 1999 as part of a larger experiment. The treatments were based on regional knowledge of water limitations and published data on the consequences of the timing of water stress on fruit quality in red wine cultivars.

To compute RDI_S , K_c was multiplied by 0.7 or 0.6. Therefore, RDI_S supplied 70% (1999–2002) and 60% (2003) of estimated ET_c on a weekly basis from shortly after fruit set until harvest. The “early” and “late” deficits received 50% of the irrigation that was applied to RDI_S vines during specific periods of fruit development. In RDI_E , 35% (1999–2002) and 30% (2003) of ET_c was applied weekly from shortly after fruit set until veraison, then the vines were returned to RDI_S [70% (1999–2002) and 60% (2003) of ET_c] until harvest. In RDI_L , vines were supplied 70% (1999–2002) and 60% (2003) of ET_c (i.e., RDI_S) until veraison, then 35% (1999–2002) and 30% (2003) of ET_c was applied weekly between veraison and commercial maturity.

Irrigation was delivered in two to four applications (sets) per week to achieve the weekly target. Actual water applied was estimated using the nominal flow rate of the drip emitters and the duration of water delivery as detected by pressure transducers in the drip line. For 4 to 5 weeks after harvest (2002) all plots were irrigated to replace 70% ET_c , then were irrigated to FC in late October. In 2003, all plots were irrigated to FC immediately after harvest. Volumetric soil water content (θ_v) was measured using the neutron scattering method (HydroProbe 503 DR; CPN, Concord, CA) at 0.15-, 0.45-, and 0.75-m depths ($n = 3$ per plot; in-row and equidistant from emitters). The average of these values was used to represent a 0.9-m deep soil unit for which the grower-cooperator’s irrigation engineer adjusted upward or downward the scheduled irrigation amount in response to deviations from target θ_v (10% for RDI_S , 8.3% for additional deficit).

WHOLE-VINE TRANSPIRATION. In 2002 and 2003, whole-vine rates of transpiration were measured concurrently with whole-vine rates of NCE (NCE_v ; Tarara et al., 2011) during

five periods corresponding to key developmental stages in grape berries: 1) fruit set (before initiation of the additional deficit); 2) preveraison (about the end of stage I of berry growth); 3) postveraison (early in stage III of berry growth); 4) preharvest (just as the fruit approached commercial maturity); and 5) postharvest (≈ 2 weeks after removal of the fruit). Instantaneous rates (millimoles H_2O per second) and daily cumulative Tr (liters H_2O per day) were calculated per vine (Tr_V) and per unit leaf area ($\text{Tr}_{V,LA}$). The Tr_V measurements were obtained using framed, open-top, flow-through chambers ($\approx 8 \text{ m}^3$ volume) that fully enclosed one vine each without modification of the canopy or trellis. Details of chamber design, operation, and calibration are provided in Perez Peña and Tarara (2004) and Tarara et al. (2011). Briefly, six chambers operated simultaneously, with an in-house-built gas multiplexer switching sample streams among chambers. The rate of airflow through the chambers was $\approx 16 \text{ m}^3 \cdot \text{min}^{-1}$ for an air exchange rate of about two chamber volumes per minute. Maximum differences in air temperature between ambient and that at canopy height in the chamber were 2.5 to 3.0 $^\circ\text{C}$ (Perez Peña and Tarara, 2004). All analog signals were recorded at 2.5-s intervals and averaged every 2 min by datalogger (CR7; Campbell Scientific, Logan, UT) so that a mean was recorded for each chamber every 12 min. Measurements were collected continuously for 36 to 48 h on six vines (two per regimen) after which the chambers were moved to a second set of replicate vines in each RDI regimen, the process was repeated, and again for a third set of replicate vines. Vines were paired across rows so that on any one measurement day (d_m), the two vines within an RDI regimen were not along the same drip irrigation line. Replication was addressed by repeated measurements across days within a developmental stage ($n = 6$ vines). The same 18 experimental vines were retained for both years. Data were analyzed only for complete 24-h measurements.

Concentrations of water vapor [H_2O_v] in air drawn from the chamber inlet and outlet were measured with an IR gas analyzer (IRGA; CIRAS-DC, PP Systems, Amesbury, MA) with a measurement range from 0 to 75 mb and a precision of 0.02 mb at 10 mb. Instantaneous rates of $\text{Tr}_{V,LA}$ (millimoles H_2O per square meter per second) were calculated from the difference in [H_2O_v] between the air exiting and that entering the chamber, adjusted for the rate of air flow through the chamber (von Caemmerer and Farquhar, 1981):

$$\text{Tr}_{V,LA} = \frac{u_o w_o - u_e w_e}{\text{LA}_V} \quad [1]$$

where u_e and u_o are air flows (moles per second), w_e and w_o are the mole fractions of H_2O_v (moles per mole) entering and exiting the chamber, respectively, and LA_V is the foliage area per vine (square meters). Because of distance limitations for drawing gas samples, all experimental vines were within 60 m of the mobile laboratory that housed the IRGA, gas handling units, and data acquisition system. Daily total Tr_V was calculated by integrating instantaneous rates of Tr_V over 24 h and is expressed as liters per day (per vine basis), and liters per square meter per day (per unit leaf area basis).

Complete measurement runs consumed 8 to 9 d, during which there were d_m with clear skies and d_m with cloudy skies, and during which two to four irrigation sets were applied, varying with season (i.e., ET_o and K_c) and the RDI regimen. Therefore, two sets of analyses for Tr_V were conducted to

address this variation in weather and in the days of the week on which irrigation was applied: 1) data were pooled across all d_m in a developmental stage ($n = 6$ vines) and 2) data were extracted for the “optimal” measurement day in each run ($n = 2$ vines), which we defined as d_m with clear skies and the lowest likelihood of an RDI regimen being confounded by irrigation scheduling (i.e., the timing of multiple irrigation sets to apply the required amount of water).

A bulk g_c that combines stomatal and boundary layer conductances (Campbell and Norman, 1998) was calculated by

$$g_c = \frac{\text{Tr}_{V,LA}}{\text{VPD}} \times P_a \quad [2]$$

where g_c is expressed in millimoles per square meter per second; VPD is vapor pressure deficit of the air entering the chamber (kilopascals); and P_a is atmospheric pressure (kilopascals). The VPD was calculated by

$$\text{VPD} = e_s(T_{in}) - e_a \quad [3]$$

where $e_s(T_{in})$ is the saturation vapor pressure at the temperature of the air entering the chamber and e_a is the actual vapor pressure.

A hypothetical maximum Tr_V was calculated using only the optimal d_m from each measurement run to scale the values between developmental stages. Integration periods were defined by the duration of the interval between RDI treatments. Estimates were calculated using linear interpolation. This variable is not intended to represent an actual cumulative water use for the season but to indicate relative differences among irrigation regimens using the available data that were least confounded by irrigation sets and weather (i.e., optimal d_m).

SINGLE-LEAF TRANSPIRATION. To provide context with the preponderance of gas exchange measurements in the literature, rates of single-leaf Tr (Tr_{SL}) were measured concurrently with Tr_V at three developmental stages in 2002 (preveraison, postveraison, preharvest) and at all stages at which Tr_V was measured in 2003. Repeated measurements (≈ 0800 – 1400 HR) of Tr_{SL} were recorded four times during the day in 2002 and six times per day in 2003, during each full day that Tr_V was recorded. Measurements were collected from fully expanded, sunlit leaves ($n = 9$ vines per RDI regimen at each developmental stage; Tarara et al., 2011). Gas exchange was measured under ambient irradiance with a portable photosynthesis system (CIRAS-2, PP Systems) using a 2.5- cm^2 leaf cuvette [PLC6(U), PP Systems]. Air flow through the cuvette was $200 \text{ cm}^3 \cdot \text{min}^{-1}$. For the single-leaf measurements, VPD was calculated using leaf temperature and vapor pressure in the cuvette.

LEAF AREA. Leaf area per vine was estimated twice during 2002 (veraison and preharvest) and four times during 2003 (fruit set, veraison, preharvest, and postharvest) using the indirect methods detailed in Tarara et al. (2011). Because LA_V was measured less frequently in 2002 than in 2003, where data were pooled across years daily cumulative Tr_V was only assessed on a per vine basis and not per unit LA .

WATER USE EFFICIENCY. Whole-canopy daily water use efficiency (WUE_d), defined as the ratio of net CO_2 fixed to water transpired, was estimated for the whole canopy and at the leaf level. Values of NCE_V are reported in Tarara et al. (2011). The WUE_d was calculated using daily total NCE (NCE_d) and daily cumulative Tr_V ($\text{Tr}_{V,d}$). Leaf-level water use efficiency was calculated using daily averages of single-leaf NCE

(NCE_{SL}) and Tr_{SL} . To avoid fluctuations in WUE due to VPD (Osmond et al., 1980), intrinsic WUE ($WUE_{i,V}$ and $WUE_{i,SL}$) was calculated from the ratio between NCE_V and g_c (whole-canopy) or NCE_{SL} and stomatal conductance (g_s).

STATISTICAL ANALYSES. Data were tested for normality using the Kolmogorov–Smirnov test and for homogeneity of variance using Brown–Forsythe test. A general linear model procedure was used for analysis of variance. Means were compared by Tukey or Tukey–Kramer ($P < 0.05$) as appropriate. Where data were normally distributed, correlations between plant response variables were assessed using the Pearson product moment correlation coefficient (R). Otherwise, the Spearman Rank correlation coefficient was used (r_s). For linear regression analyses, data were transformed as needed to adjust for heterogeneous variances and for distributions that deviated from normal. All statistical analyses were performed using SAS (version 8.2; SAS Institute, Cary, NC). The data collected at fruit set in 2002 were excluded from the analysis because of technical difficulties with the whole-canopy system. Hereafter for conciseness, graphical presentation of Tr_V comprises the complete dataset from 2003, where gas exchange and LA_V data were available at all developmental stages. Instances where Tr_V values differed significantly between years are noted in the text.

Results

ENVIRONMENTAL SUMMARY. Thermal time was below the long-term mean (1702 DD) in 2002 and above average in 2003 (Table 1; Tarara et al., 2011). Key developmental stages (budbreak, anthesis, veraison) occurred ≈ 1 week earlier in 2003 than in 2002. Annual rainfall during the study was 28% (2002) and 7% (2003) below the long-term mean, and was consistent with the seasonal pattern of rainfall in eastern Washington: 25% (2002) and 18% (2003) of the annual total fell between budbreak and leaf fall. No rain was detected between early June (prebloom) and early August (about veraison) in 2003.

Soil water content reflected the timing and intensity of the RDI regimens (Fig. 1; Schreiner et al., 2007). Per grower practice, θ_v declined into early summer until fruit set when RDI was initiated. Thereafter θ_v trended according to the RDI regimens. Obvious departures from target θ_v are indicative of the inherent limitations in the posthoc soil water balance approach, particularly under drip irrigation (Stevens and Douglas, 1994). Standard RDI resulted in consistently higher θ_v than the original target of 10% v/v. Between fruit set and harvest, 63% and 79% of the total water applied to RDI_S plots was applied to RDI_E and RDI_L , respectively (Table 1). In both years, when RDI_E plots were under the additional deficit, the vines received 55% of the cumulative amount of water that had been applied to RDI_S , about the target value. Water application was somewhat more variable in RDI_L : 45% (2002) and 31% (2003) of the cumulative RDI_S application was delivered when the RDI_L vines were under the additional deficit. The end-of-season variation in θ_v in 2003 reflects the cooperator's attempt to immediately rewater the plots to FC (Fig. 1).

DAILY CUMULATIVE TRANSPIRATION. Across the experiment, d_m were significantly different from one another (Table 2). There was a significant interaction between RDI regimen and d_m during the periods of additional deficit, except during preveraison and preharvest if Tr was expressed as $Tr_{V,LA}$. Hence the computation of daily cumulative Tr_V and $Tr_{V,LA}$ both as a mean across all d_m within a developmental stage and for the optimal d_m in each stage (i.e., clear skies and the least confounding effect of an irrigation set; Table 3). Treatment differences in daily cumulative Tr_V generally were conserved whether Tr was expressed as Tr_V or $Tr_{V,LA}$. Daily cumulative Tr_V differed between RDI regimens during the periods of additional deficit (Tables 2 and 3) but the differences were not always the same based on all d_m or only the optimal d_m .

Daily cumulative Tr_V and $Tr_{V,LA}$ did not differ among RDI regimens during fruit set. During preveraison, RDI_E vines transpired nearly 60% less per day than RDI_S and RDI_L , whether expressed per vine or per unit leaf area (Tables 2 and 3). During the postveraison stage, across all d_m , RDI_E vines did

Table 1. Developmental stages, summary meteorological variables, and irrigation applied to mature grapevines under three regimens of regulated deficit irrigation (reprinted from Tarara et al., 2011).

Yr	Developmental stage	Dates	DD (°C) ^z	Precipitation (mm) ^y	ET _o (mm) ^x	Irrigation (mm) ^w		
						RDI_S	RDI_E	RDI_L
2002	Dormancy	8 Nov. to 25 Apr.	—	114	—	—	—	—
	Budbreak–bloom	25 Apr. to 11 June	262	17	301	11	9	11
	Bloom–veraison	11 June to 9 Aug.	771	13	499	140	78	134
	Veraison–harvest	9 Aug. to 19 Sept.	462	4	252	60	48	27
	Harvest–frost	19 Sept. to 25 Oct.	128	4	104	46	41	42
	Growing season total	—	1,623	38	1,156	257	176	214
2003	Dormancy	25 Oct. to 15 Apr.	—	170	—	—	—	—
	Budbreak–bloom	15 Apr. to 3 June	232	12	269	0	0	0
	Bloom–veraison	3 June to 5 Aug.	832	1	512	158	87	143
	Veraison–harvest	5 Aug. to 13 Sept.	486	19	233	42	40	13
	Harvest–frost	13 Sept. to 21 Oct.	284	5	148	48	45	48
	Growing season total	—	1,834	37	1,162	248	172	204

^zCumulative thermal time expressed as degree days (DD) above 10 °C base air temperature.

^yDormant season rainfall was summed between the dates of the first frost of the preceding year and budbreak of the current year.

^xReference evapotranspiration (ET_o) calculated from the Penman–Monteith equation for a grass reference crop (Allen et al., 1998).

^w RDI_S = industry standard regulated deficit irrigation practice of weekly replenishing of 60% to 70% of crop evapotranspiration, RDI_E = early additional deficit of 50% of RDI_S , RDI_L = late additional deficit of 50% of RDI_S .

Fig. 1. Volumetric soil water content (θ_v) in mature, field-grown grapevines during 2002 (A) and 2003 (B) for three regimens of regulated deficit irrigation (RDI): RDI_S = industry standard practice of weekly replenishing of 60% of crop evapotranspiration, RDI_E = early additional deficit of 50% of RDI_S, RDI_L = late additional deficit of 50% of RDI_S. Arrows from left to right denote fruit set, veraison, and harvest, respectively. Redrawn by permission from Schreiner et al. (2007).

not appear to have recovered to the Tr_V values of RDI_S (Table 2) because of a missed irrigation set. However, on the optimal d_m , Tr_V did not differ between RDI_S and RDI_E, and both exceeded RDI_L. During postveraison, RDI_L vines transpired nearly 50% less than RDI_S and RDI_E on a per vine basis, and nearly 60% less based on $Tr_{V,LA}$. Immediately before harvest, cumulative values of Tr_V in RDI_S had declined from pre- and postveraison by about 40% (Tables 2 and 3). At both the pre- and postharvest measurements, daily cumulative $Tr_{V,LA}$ did not differ among RDI regimens.

TRANSPIRATION DYNAMICS. Before the imposition of an additional deficit (i.e., fruit set), the diurnal course of $Tr_{V,LA}$ was similar among RDI regimens (Fig. 2). The magnitude and diurnal course of $Tr_{V,LA}$ between d_m reflected a response to both irrigation application and rapid soil dry-down. Maximum $Tr_{V,LA}$ values were about 3 to 3.5 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Following 15 mm of irrigation (DOY 178), the diurnal course of $Tr_{V,LA}$ largely followed that of solar radiation, with a slight lag in $Tr_{V,LA}$ under decreasing solar radiation because of sensitivity to VPD (Fig. 2A). Between irrigation sets (e.g., DOY 181; Fig. 2B), daytime rates of $Tr_{V,LA}$ were relatively flat between 0800 and 1300 hr following a maximum of about 2 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Vines in RDI_E (Fig. 2C) were erroneously irrigated at 40% of the scheduled water on one d_m (DOY 183), causing lower rates of $Tr_{V,LA}$ compared with RDI_S and RDI_L. Despite this error, across all d_m , daily cumulative $Tr_{V,LA}$ did not differ among RDI regimens (Table 2).

After RDI_E had been imposed for 5 weeks (preveraison stage), maximum $Tr_{V,LA}$ values were about 4 to 4.5 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The diurnal course of $Tr_{V,LA}$ in RDI_S and RDI_L

Table 2. Daily cumulative transpiration (Tr) by mature, field-grown grapevine canopies under three regimens of regulated deficit irrigation (RDI) near key developmental stages in 2003. Data are expressed per vine [Tr_V (top)] and per unit leaf area [$Tr_{V,LA}$ (bottom)]. The Tr values are means of six vines averaged across all measurement days (d_m) per developmental stage.

Developmental stage	Sampling period (DOY) ^z	RDI regimen ^y			<i>P</i> value	
		RDI _S	RDI _E	RDI _L		
		Tr _V (L·d ⁻¹)			<i>d</i> _m	Trt ^x × <i>d</i> _m
Fruit set	177–184	11.6	11.2	13.7	0.001	0.182
Preveraison	212–219	14.1 a ^w	7.7 b	15.6 a	0.001	0.030
Postveraison	233–241	11.6 a	7.8 b	6.0 b	0.001	0.001
Preharvest	255–262	6.9	6.2	5.8	0.003	0.247
Postharvest	274–281	4.2	4.1	5.2	0.001	0.341
<i>P</i> value			0.001 ^v		0.001 ^u	
Developmental stage	Sampling period (DOY) ^z	Tr _{V,LA} (L·d ⁻¹ ·m ⁻¹)			<i>P</i> value	
		RDI _S	RDI _E	RDI _L		
		Tr _{V,LA} (L·d ⁻¹ ·m ⁻¹)			<i>d</i> _m	Trt ^x × <i>d</i> _m
Fruit set	177–184	1.3	1.3	1.4	0.001	0.202
Preveraison	212–219	1.6 a	0.9 b	1.6 a	0.001	0.068
Postveraison	233–241	1.4 a	0.9 b	0.6 c	0.001	0.001
Preharvest	255–262	0.9	0.8	0.7	0.026	0.592
Postharvest	274–281	0.7	0.7	0.7	0.004	0.753
<i>P</i> value			0.001 ^v		0.001 ^u	

^zDOY = day of the year.

^yRDI_S = industry standard regulated deficit irrigation practice of weekly replenishing of 60% of crop evapotranspiration, RDI_E = early additional deficit of 50% of RDI_S, RDI_L = late additional deficit of 50% RDI_S.

^xTrt = treatment.

^wValues followed by different letters within rows are significantly different at the $P \leq 0.05$ level by Tukey-Kramer.

^vFor pooled data, effect of developmental stage.

^uFor pooled data, interaction between RDI regimen and developmental stage.

Table 3. Daily cumulative transpiration (Tr) per day in mature, field-grown grapevines under regulated deficit irrigation (RDI) expressed per vine (Tr_V) and per unit leaf area ($Tr_{V,LA}$). Data are means of two vines from days with clear skies and the least confounding effect of irrigation application (the “optimal” measurement day) in 2003.

Developmental stage	Sampling period (DOY) ^z	RDI regimen ^y		
		RDI _S	RDI _E	RDI _L
		Tr _V (L·d ⁻¹)		
Fruit set	178	14.1	15.7	19.0
Preveraison	218	18.3 a ^x	7.8 b	20.7 a
Postveraison	238	18.2 a	16.2 a	7.7 b
Preharvest	256	8.6	7.5	6.6
Postharvest	278	4.1	4.7	5.9
<i>P</i> value			0.001 ^w	0.001 ^v
		Tr _{V,LA} (L·m ⁻¹ ·d ⁻¹)		
Fruit set	178	1.6	1.9	1.9
Preveraison	218	2.2 a	0.9 b	2.1 a
Postveraison	238	2.2 a	1.9 a	0.7 b
Preharvest	256	1.2	1.1	0.7
Postharvest	278	0.7	0.7	0.8
<i>P</i> value			0.001 ^w	0.001 ^v

^zDOY = day of the year.

^yRDI_S = industry standard regulated deficit irrigation practice of weekly replenishing of 60% of crop evapotranspiration, RDI_E = early additional deficit of 50% of RDI_S, RDI_L = late additional deficit of 50% RDI_S.

^xValues followed by different letters within rows are significantly different at $P \leq 0.05$ by Tukey–Kramer.

^wFor pooled data, effect of developmental stage.

^vFor pooled data, interaction between regulated deficit irrigation regimen and developmental stage.

was generally similar to that at fruit set. There was lower $Tr_{V,LA}$ in RDI_E vines than in RDI_S and RDI_L vines after a morning maximum: for example, even following an irrigation (e.g., DOY 213; Fig. 3A), RDI_E vines transpired 18% less than RDI_S and RDI_L vines during midday (1000–1400 HR). The $Tr_{V,LA}$ in all RDI regimens converged during the latter part of the day when VPD was high. This convergence was not the case under cloudy skies and lower VPD (e.g., DOY 215; Fig. 3B). The largest differences among RDI regimens were apparent at the end of the irrigation cycle (DOY 218; Fig. 3C), where midday $Tr_{V,LA}$ in RDI_E was about 60% less than that in RDI_S and RDI_L. The lower $Tr_{V,LA}$ in RDI_E was reflected in a midday maximum g_c of 65 mmol·m⁻²·s⁻¹, about 60% lower than that of either RDI_S or RDI_L.

Three weeks after RDI_E vines had been returned to RDI_S and RDI_L was started (postveraison measurements), maximum rates of $Tr_{V,LA}$ in RDI_S were about 4 to 4.5 mmol·m⁻²·s⁻¹ (Fig. 4). The general course of $Tr_{V,LA}$ was generally similar to that observed earlier in the season except for lower $Tr_{V,LA}$ in RDI_L vines compared with RDI_E and RDI_S after about 0800 HR. Under cloudy skies, RDI regimen appeared to have had no effect on $Tr_{V,LA}$ (DOY 234; Fig. 4A). Under nearly clear skies (DOY 238; Fig. 4B) and at the end of the irrigation cycle, midday $Tr_{V,LA}$ in RDI_E vines was 22% less than that of RDI_S vines. However, cumulatively there was no difference in $Tr_{V,LA}$ between RDI_S and RDI_E on this optimal d_m , indicating that the

Fig. 2. Whole-canopy transpiration rate per unit leaf area ($Tr_{V,LA}$) in mature, field-grown grapevines, photosynthetic photon flux (PPF), and air vapor pressure deficit (VPD) during the “fruit set” developmental stage in 2003. Symbols represent the mean of two vines; RDI = regulated deficit irrigation, RDI_S = industry standard practice of weekly replenishing of 60% of crop evapotranspiration, RDI_E = early additional deficit (preveraison) of 50% of RDI_S, RDI_L = late additional deficit (postveraison) of 50% of RDI_S, ET_0 = reference evapotranspiration, DOY = day of the year. Data were collected before RDI_E was imposed.

RDI_E vines had essentially recovered from the 5 weeks of additional deficit. The RDI_L vines transpired about 77% less than RDI_S during the midday hours on the optimal d_m (DOY 238; Fig. 4B). Concurrent midday g_c in RDI_L ranged from 21 to 37 mmol·m⁻²·s⁻¹, indicative of severe water stress according to proposed ranges for g_s in grapevine (Lovisolo et al., 2010). By contrast, g_c in RDI_S and RDI_E was between 73 and 135 mmol·m⁻²·s⁻¹, indicating moderate water stress. An irrigation scheduling error (DOY 239) that omitted irrigation from RDI_E plots induced enough cumulative water stress that on the subsequent day (DOY 240; Fig. 4C) both the instantaneous rates of $Tr_{V,LA}$ and the daily cumulative Tr_V (data not shown) fell below those of RDI_L plots.

At the preharvest developmental stage, maximum $Tr_{V,LA}$ in RDI_S was about 2.5 mmol·m⁻²·s⁻¹ (Fig. 5). The $Tr_{V,LA}$ in RDI_L was below that of RDI_E and RDI_S by as much as 40% in midafternoon, but this difference was not reflected in daily cumulative $Tr_{V,LA}$ (Tables 2 and 3). Midday values of g_c

Fig. 3. Whole-canopy transpiration rate per unit leaf area ($Tr_{V,LA}$) in mature, field-grown grapevines, photosynthetic photon flux (PPF), and air vapor pressure deficit (VPD) during the “preveraison” developmental stage in 2003. Symbols represent the mean of two vines; RDI = regulated deficit irrigation, RDI_S = industry standard practice of weekly replenishing of 60% of crop evapotranspiration, RDI_E = early additional deficit (preveraison) of 50% of RDI_S , RDI_L = late additional deficit (postveraison) of 50% of RDI_S , ET_0 = reference evapotranspiration, DOY = day of the year. Data were collected 3 weeks after RDI_E had been imposed.

indicated continued water stress of varying degrees, where g_c in RDI_L ranged between 40 and 90 $mmol \cdot m^{-2} \cdot s^{-1}$, and that in RDI_S and RDI_E between 60 and 150 $mmol \cdot m^{-2} \cdot s^{-1}$ (e.g., DOY 256). Rates of $Tr_{V,LA}$ at the end of the measurement run were uniformly low and corresponding midday g_c indicated moderate to severe water stress [24–76 $mmol \cdot m^{-2} \cdot s^{-1}$ (RDI_L), 40–106 $mmol \cdot m^{-2} \cdot s^{-1}$ (RDI_E and RDI_S)]. In the postharvest measurement run the daily pattern of $Tr_{V,LA}$ was similar to that during preharvest (data not shown). During both pre- and postharvest measurements, canopies showed some senescence.

Across the entire duration of measurements (fruit set to postharvest), a hypothetical cumulative Tr_V differed by about 20% between RDI_S and RDI_E (Table 4). Between RDI_S and RDI_L , the difference was only 2.6%. During the early additional deficit period, the hypothetical maximum difference between RDI_S and RDI_E was estimated at about 28%. About half of the measurement season’s Tr_V (computed from the hypothetical

Fig. 4. Whole-canopy transpiration rate per unit leaf area ($Tr_{V,LA}$) in mature, field-grown grapevines, photosynthetic photon flux (PPF), and air vapor pressure deficit (VPD) during the “postveraison” developmental stage in 2003. Symbols represent the mean of two vines; RDI = regulated deficit irrigation, RDI_S = industry standard practice of weekly replenishing of 60% of crop evapotranspiration, RDI_E = early additional deficit (preveraison) of 50% of RDI_S , RDI_L = late additional deficit (postveraison) of 50% of RDI_S , ET_0 = reference evapotranspiration, DOY = day of the year, PP = precipitation. Data were collected 3 weeks after RDI_L had been imposed and RDI_E had been returned to RDI_S .

maximum values) was between fruit set and veraison in RDI_S and RDI_E , whereas in RDI_L about three-quarters of the hypothetical maximum water was transpired. Between veraison and harvest, about the same percent of the hypothetical seasonal maximum was transpired in RDI_S and RDI_E ; absolute values were within 11%, supporting the notion that vines under RDI_E recovered well from the additional deficit. The hypothetical maximum was low between preharvest and postharvest regardless of RDI regimen.

We were not able to conduct hourly single-leaf measurements of gas exchange late enough in the day to sufficiently capture the diurnal pattern of Tr . Measurements did reflect the treatment differences that were observed in the whole-vine measurements (data not shown). On the whole, concurrent measurements of Tr_{SL} overestimated $Tr_{V,LA}$ (Fig. 6). There was a moderate linear relationship between Tr_{SL} and $Tr_{V,LA}$ ($r^2 = 0.34$, $P < 0.001$), consistent with our findings for NCE, albeit the NCE relationship was stronger ($r^2 = 0.61$; Tarara et al., 2011).

Fig. 5. Whole-canopy transpiration rate per unit leaf area ($Tr_{V,LA}$) in mature, field-grown grapevines, photosynthetic photon flux (PPF), and air vapor pressure deficit (VPD) during the “preharvest” developmental stage in 2003. Symbols represent the mean of two vines; RDI = regulated deficit irrigation, RDI_S = industry standard practice of weekly replenishing of 60% of crop evapotranspiration, RDI_E = early additional deficit (preveraison) of 50% of RDI_S, RDI_L = late additional deficit (postveraison) of 50% of RDI_S, ET_0 = reference evapotranspiration, DOY = day of the year.

Henceforth for brevity, only fruit set, preveraison, and postveraison data are shown, and for the optimal d_m . The NCE_V was strongly related to g_c at fruit set and at the pre- and postveraison measurements, whether the vines were under RDI_S or an additional deficit (Fig. 7). Under RDI_S, $Tr_{V,LA}$ was a curvilinear function of solar radiation (expressed as PPF) and of VPD , exhibiting hysteresis between morning and afternoon (Fig. 8). The hysteretic loop was smaller as a function of solar radiation, indicative of the tighter coupling between Tr_V and solar radiation. Under the additional deficit, both relationships ($Tr_{V,LA}$ vs. PPF , $Tr_{V,LA}$ vs. VPD) were weak. The hysteresis was clockwise as a function of VPD (Fig. 8A–C) and counter clockwise as a function of PPF (Fig. 8D–F). In other words, under RDI_S more water was transpired per unit VPD in the morning than in the afternoon; the contrary was the case as a function of PPF . At a given VPD or a given PPF , $Tr_{V,LA}$ under RDI_S was higher than that of vines under the additional water deficit (except

Table 4. Estimated hypothetical maximum transpiration per vine (Tr_V) by mature, field-grown grapevine canopies under three regimens of regulated deficit irrigation (RDI) near key developmental stages in 2003.

Period	Duration (d)	Hypothetical cumulative Tr _v ^z		
		RDI _S	RDI _E	RDI _L
		[H ₂ O (L per period per vine)]		
Fruit set to veraison	46	745 (58) ^y	540 (52)	913 (72)
Veraison to harvest	32	428 (33)	379 (37)	229 (18)
Harvest to postharvest	19	121 (9)	116 (11)	119 (9)
Total	97	1,294 (100)	1,035 (100)	1,261 (99)

^zThe hypothetical, or potential maximum per period was estimated by linear interpolation between developmental stages using data from the “optimal” measurement day during the respective measurement run, which was defined as having clear skies and the least likelihood of confounding effects from irrigation application; RDI_S = industry standard regulated deficit irrigation practice of weekly replenishing of 60% of crop evapotranspiration, RDI_E = early additional deficit of 50% of RDI_S, RDI_L = late additional deficit of 50% of RDI_S.

^yNumbers in parentheses are percent of total.

at either end of the day), consistent with the diurnal curves presented above.

WATER USE EFFICIENCY. Daily water use efficiency did not differ among RDI regimens during the periods of additional deficit when considered either as a mean across all d_m or under the optimal d_m per measurement run (Table 5). The diurnal curves of WUE were synchronized among treatments during fruit set (Fig. 9A). The diurnal pattern of WUE at preveraison did not differ between RDI_S and RDI_E (Fig. 9B). However, under the late deficit, midday WUE in RDI_L dropped below that of RDI_S (Fig. 9C). Despite variation in diurnal patterns among RDI regimens and between NCE_V and Tr_V , on a daily basis under RDI_E, NCE_V and Tr_V declined about proportionally from RDI_S (44% less carbon fixed; 45% less water transpired). On average during the postveraison measurements, 48% less water was transpired and 33% less carbon was fixed under RDI_L than under RDI_S. When only the optimal d_m was considered, the values of both Tr_V and NCE_V for RDI_E (preveraison) and RDI_L (postveraison) were about 57% less than RDI_S. Relative differences in WUE_d from single-leaf estimates were consistent with treatment differences in whole-vine data (data not shown). Absolute values of single-leaf WUE_d tended to be lower than those from the whole-vine estimates (data not shown). At all measurement periods, g_c reached a daily maximum value before noon.

Using the optimal d_m per measurement run, WUE_i (NCE_V/g_c) at fruit set and preveraison was negatively correlated with g_c (data not shown); i.e., WUE_i generally rose as g_c declined. This relationship is in contrast to WUE . Before the imposition of the additional deficits, the correlation between WUE_i and g_c was nearly identical among regimens ($r_s = -0.631$ to -0.663 , $P < 0.0001$). During the early additional deficit, the relationship between WUE_i and g_c was stronger for RDI_S ($r_s = -0.767$, $P < 0.0001$) than for RDI_E ($r_s = -0.553$, $P < 0.0001$). The case differed during the postveraison run, where WUE_i was significantly correlated with g_c in neither RDI_S nor RDI_L [$r_s = -0.173$, $P = 0.182$ (RDI_S); $r_s = 0.053$, $P = 0.697$ (RDI_L)]. During the early additional deficit, the average midday WUE_i did not differ between RDI_E and RDI_S (data not shown). Around midday in RDI_E, both NCE_V and g_c were 59% less than in RDI_S,

Fig. 6. Linear association between rate of transpiration in mature, field-grown grapevines at the single leaf level (Tr_{SL}) and at the canopy level expressed per unit leaf area ($Tr_{V,LA}$), for vines under an industry standard practice of regulated deficit irrigation of weekly replenishing of 60% of crop evapotranspiration, or under an additional deficit that reduced the standard application by half. Symbols represent means over 1 h of simultaneous measurement ($n = 6$ for Tr_{SL} , $n = 10$ for $Tr_{V,LA}$). Data are from all developmental stages in 2003 except harvest, when there were no coincident measurements.

resulting in a constant proportionality. Both regimens exhibited a small decline in WUE_i between midmorning and midday. However, the same outcome was not observed during the postveraison measurement run, where RDI_L exhibited a large decline in WUE_i during midday (data not shown). The average midday WUE_i differed between RDI_L and RDI_S because average NCE_V was 85% less in RDI_L than in RDI_S , whereas midday g_c was 75% less in RDI_L than in RDI_S . Thus the ratio between NCE_V and g_c changed in response to the additional deficit.

Discussion

Vines under additional water deficit (RDI_E , RDI_L) transpired less than those under RDI_S during the specific periods of additional deficit, as we observed in carbon fixation (Tarara et al., 2011). Because of the duration of the respective additional deficits, cumulative irrigation applied over the course of the season was about 40% and 20% less than RDI_S in RDI_E and RDI_L , respectively. Therefore, under increased demand for water resources, growers may consider the interaction between the effect of various RDI regimens on fruit quality goals and total irrigation water applied. As with the response that we observed in NCE_V (Tarara et al., 2011), all vines responded rapidly to irrigation, increasing Tr_V within 24 h or less. This response is similar to response rates of three cultivars evaluated by Pou et al. (2012). In the present study, the response to soil drying occurred over 2 to 3 d. Sinclair (2005) suggested for a wide range of soils that Tr and NCE , mediated by g_c , change little until about two-thirds of the available soil water is transpired, after which NCE and Tr decrease linearly with decreasing θ_v . From calculations reported in Tarara et al.

Fig. 7. Whole-vine net carbon exchange (NCE_V) in mature, field-grown grapevines as a function of bulk canopy conductance (g_c) before noon (AM) and after noon (PM), for vines under an industry standard practice of regulated deficit irrigation or under an additional deficit that reduced the standard application by half in 2003. Symbols represent the mean of two vines; RDI = regulated deficit irrigation, RDI_S = industry standard practice of weekly replenishing of 60% of crop evapotranspiration, RDI_E = early additional deficit (preveraison) of 50% of RDI_S , RDI_L = late additional deficit (postveraison) of 50% of RDI_S .

(2011), during midsummer more than 50% of available water could have been transpired in 2 d.

Under the additional water deficits, the diurnal patterns of Tr_V differed somewhat from those of NCE_V in that rates of Tr_V approached relatively steady values across midday, whereas NCE_V declined steadily from a morning maximum (Tarara et al., 2011). The highest rates of NCE_V and the highest rates of change in NCE_V occurred earlier in the morning than for Tr_V . Despite these different diurnal patterns, during the additional

Fig. 8. Rate of whole-vine transpiration per unit leaf area ($Tr_{V,LA}$) in mature, field-grown grapevines as a function of vapor pressure deficit [VPD (A–C)] and photosynthetic photon flux [PPF (D–F)] before noon (AM) and after noon (PM), for vines under an industry standard practice of regulated deficit irrigation [RDI_S (A–F)] or under an additional deficit that reduced the standard application by half [RDI_E (B,E)], RDI_L (C,F) in 2003. Symbols represent the mean of two vines; RDI = regulated deficit irrigation, RDI_S = industry standard practice of weekly replenishing of 60% of crop evapotranspiration, RDI_E = early additional deficit (preveraison) of 50% of RDI_S , RDI_L = late additional deficit (postveraison) of 50% of RDI_S .

deficit periods there were similar relative cumulative differences from RDI_S in both $Tr_{V,d}$ and $NCE_{V,d}$. This outcome substantiates the notion that stomatal and not photochemical limitation dominated the response in NCE (Tarara et al., 2011). Flexas et al. (2002) found that under slowly induced water stress in field-grown vines, as g_s decreased to values of about $50 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, NCE decreased progressively with almost no change in photosynthetic efficiency. Below this approximate threshold, nonstomatal limitations may be dominant (Medrano et al., 2002), but in our case this situation would not have occurred extensively. Ranges of g_s in *Vitis* sp. have been associated in a general sense with mild water stress (decreasing from about $200\text{--}500 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ down to $150 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), moderate water stress (about $50\text{--}150 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), and severe water stress ($<50 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; Lovisolo et al., 2010). Analogous ranges for g_c have not been proposed so we take available values of g_s as a starting reference. Based on g_c we observed at least transient occurrences of severe water stress in RDI_E and RDI_L ; RDI_S consistently would have been classified as under

moderate water stress. All vines were under at least moderate water stress for the entire period of fruit set to harvest.

The daily maximum $Tr_{V,LA}$ values presented here are comparable with others in the literature that evaluated water-stressed vines using whole-canopy gas exchange [e.g., $\approx 5 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, field-grown (Katerji et al., 1994); $\approx 3 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, field-grown (Ollat and Tandonnet, 1999); $\approx 3 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, potted (Pallioti et al., 2014); $\approx 2\text{--}3 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, potted (Poni et al., 2009)]. The lower values of g_c that we observed under the additional deficits were in the general range reported for single-leaf measurements (g_s) of water-stressed potted vines by Pallioti et al. (2014), but much lower than those reported for field-grown, deficit-irrigated vines elsewhere (de Souza et al., 2003). In context, we found g_s to overestimate g_c . Under progressive soil water deficit in other field-grown vines, midday g_s declined to values similar to those that we observed (de Souza et al., 2005). Chaves et al. (2007) measured midday g_s under water deficit as high as $230 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in 2 years, but reported a value as low as $80 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in the third year of the study, the driest year.

One indicator of vine water stress that would have been valuable to include, for example, are measurements of midday stem water potential. Unfortunately, stem water potential measurements that had been recorded by the commercial

grower-cooperator could not be included in this data set because they had not been recorded at a consistent time of day and thus were not comparable over time. Future work would clearly benefit from such measurements, with the caveat that they are single-leaf measurements and subject to the same sampling bias of single-leaf measurements of gas exchange. Furthermore, a limited number of samples can be collected during the short midday window. Nonetheless, an independent indicator of vine water stress is useful in context.

There may be other physiological implications from the deficit regimens. Under water stress that was indicated by both photosynthesis and transpiration behavior, the additional water deficits could have generated more extensive hydraulic and chemical signals than RDI_S , for example root water transport mediated by aquaporins; reduced root water potential; increased xylem sap pH; and/or increased abscisic acid (ABA) concentrations in the leaf, xylem, or root, all implicated in the control of stomatal aperture. However, there is yet to be consensus on the relative importance of each factor (see

Table 5. Daily water use efficiency (WUE_d) for mature, field-grown grapevine canopies under three regimens of regulated deficit irrigation (RDI) near key developmental stages in 2003. Data are a mean of six vines across all measurement days [d_m (top)] and means of two vines on days with clear skies and no confounding irrigation sets [the “optimal” d_m (bottom)].

Developmental stage	Sampling period (DOY) ^z	RDI regimen ^y			<i>P</i> value	
		RDI _S	RDI _E	RDI _L		
		WUE _{V,d} (g CO ₂ per vine per day/L H ₂ O per vine per day)			<i>d</i> _m	Trt ^x × <i>d</i> _m
Fruit set	177–184	8.7	8.4	8.2	0.001	0.001
Preveraison	212–219	8.9	8.7	8.4	0.083	0.910
Postveraison	233–241	10.3	13.8	12.2	0.001	0.001
Preharvest	255–262	8.0 a ^w	6.0 b	5.7 b	0.001	0.045
Postharvest	274–281	12.1 a	12.7 a	8.6 b	0.001	0.064
<i>P</i> value			0.001 ^v	0.167 ^u		
Fruit set	178	7.9	7.6	7.4		
Preveraison	218	7.6	7.7	7.2		
Postveraison	238	8.0	7.6	7.8		
Preharvest	256	9.4	8.8	7.4		
Postharvest	278	13.2	12.6	9.7		
<i>P</i> value			0.002 ^v	0.318 ^u		

^zDOY = day of the year.

^yRDI_S = industry standard practice of weekly replenishing of 60% of crop evapotranspiration, RDI_E = early additional deficit of 50% of RDI_S, RDI_L = late additional deficit of 50% RDI_S.

^{*}Trt = treatment

^wValues followed by different letters within rows are significantly different at the $P \leq 0.05$ level by Tukey–Kramer.

^vFor pooled data, effect of developmental stage.

^uFor pooled data, interaction between RDI regimen and developmental stage.

reviews by Chaves et al., 2010; Lovisolo et al., 2010; Schultz and Stoll, 2010), not least because of observed differences in responses among cultivars, for example to ABA (e.g., Beis and Patakas, 2010; Rogiers et al., 2011a; Tramontini et al., 2014). In field-grown ‘Cabernet Sauvignon’ (Speirs et al., 2013), gene expression for ABA synthesis was highest under their more severe deficit irrigation regimen. In potted ‘Cabernet Sauvignon’ (Tramontini et al., 2014), g_s was strongly related to leaf ABA.

Under very high g_c (little if any water stress), Tr_v is proportional to g_c and the coupling of the leaf or canopy to the atmosphere is strong (Jones, 1990). For example, in well-watered grapevines in the field, g_c was mostly a function of VPD once stomates fully opened in response to solar radiation (in their case $>200 \text{ W} \cdot \text{m}^{-2}$; Lu et al., 2003). In a sparse crop like grapevine, one would expect the plants to be well coupled to the atmosphere, but this coupling can be modified by water stress. For example, Chaves et al. (2002) proposed that under progressive water stress in field-grown vines, g_s declines beginning in midmorning and for increasingly longer portions of the day as stress intensifies. We observed that g_c reached a daily maximum value in the morning, generally earlier for the vines under the additional deficit than for those under RDI_S, indicating that under more severe water deficits Tr_v may be less coupled to the atmosphere (i.e., VPD). Rogiers et al. (2011b) found that the magnitude of the response of Tr to VPD was smaller under dry soils (lower g_s) than under well-watered conditions. Responses are not necessarily cultivar-specific. In ‘Cabernet Sauvignon’ (Collins and Loveys, 2010), which is thought of as displaying anisohydric behavior (delayed stomatal closure), longer term and increasing water deficits resulted in higher sensitivity of g_c to VPD, eliciting what are considered isohydric responses (earlier stomatal closure). In other

water stressed vines, Tr became limited as VPD increased (Patakas et al., 2005), leading to the proposition that under water stress, stomates are more sensitive to VPD. Our data from the additional water deficits appear to support these observations.

We found contrasting (clockwise vs. counterclockwise) hysteretic loops in the relationship between Tr_v and VPD, and between Tr_v and PPF . Zhang et al. (2014) proposed that the phase angle difference, or kinetic lag, between radiation and VPD prompts asymmetric responses of Tr to VPD and of Tr to net radiation (solar radiation as proxy). Because Tr is more in phase with solar radiation than with VPD, the hysteretic loop between Tr and radiation is smaller than that between Tr and VPD. The same was the case under both RDI_S and the additional deficits. The hysteretic responses can be modulated by abiotic factors like soil water potentials and by biotic factors like leaf water potential, which are particularly relevant under water deficit. That Tr can be less correlated with VPD under low θ_v is evident in the compressed hysteretic loops of the additional deficits. As in the grapevines in this study, in trees growing under water stress (Zeppel et al., 2004) there was a clockwise hysteretic pattern between Tr and VPD, meaning that for a given VPD, more water was transpired in the morning than in the afternoon. They reported a counterclockwise hysteretic pattern between Tr and solar radiation, meaning that for a given value of solar radiation, less water was transpired in the morning than in the afternoon, as we also observed. The same patterns in Tr were reported for *Ziziphus jujuba* (Chen et al., 2014), a shrubland meadow (Zheng et al., 2014), and for prairie forbs and *Zea mays* (Matteos-Remigio, 2015). Postulated abiotic and biotic causes of the phenomenon include an increase in stomatal sensitivity to VPD in the afternoon, thereby prompting lower g_c ; decreasing soil water potential, leading

Fig. 9. Whole-vine instantaneous water use efficiency (WUE) and canopy conductance (g_c) of mature, field-grown grapevines during three measurement periods: (A) “fruit set,” during which all vines were under standard regulated deficit irrigation (RDI_s) of weekly replenishing of 60% of crop evapotranspiration; (B) “preveraison,” during which an early additional deficit was imposed (RDI_E) that reduced RDI_s by half; and (C) “postveraison,” during which a late additional deficit was imposed (RDI_L) that reduced RDI_s by half in 2003.

to decreased hydraulic conductance; and reduced leaf water potential in the afternoon, also eliciting reduced g_c (Zeppel et al., 2004).

That our values of g_s and Tr_{SL} were higher than g_c and $Tr_{V,LA}$ is substantiated elsewhere by experiments in which the grapevine canopy was divided into sections: interior, exterior, and aspect of the vine row. Both Tr and NCE varied with leaf position in the canopy and cardinal direction of the canopy section, driven by radiation interception (Escalona et al., 2003). Drought progressively affected leaves from the sunlit exterior to the shaded interior. They found that severe water stress reduced NCE and Tr in all locations of the canopy except the innermost shaded leaves. Medrano et al. (2012) confirmed these observations for instantaneous rates of Tr and

NCE (expressed as WUE and WUE_i) as functions of incident solar radiation at a specific section of the canopy. One known limitation of leaf-level measurements is the propensity for selecting sunlit, fully-exposed leaves on the canopy exterior. Difficulties in “scaling up” leaf level measurements to canopy or larger scales are ubiquitous both empirically (Medrano et al., 2012; Merli et al., 2015; Poni et al., 2009; Tomás et al., 2014) and in the modeling community (e.g., Launiainen et al., 2011).

An optimization theory of stomatal aperture (e.g., Cowan, 1982) predicts that daytime variation in g_s minimizes Tr while maximizing NCE ; changes in g_s theoretically maintain a constant ratio of $\Delta Tr:\Delta NCE$, “conserving” so to speak, WUE (Bacon, 2004). We found that the relative decline in Tr_V under the additional deficits was similar to the relative decline in NCE_V , resulting in no differences in WUE_d among RDI regimens during the respective periods of additional deficit. This result is in contrast to other findings where the decline in net photosynthesis under water deficit was less than that of Tr [leaf-level (Bowen et al., 2011)], indicating an increase in WUE . In other leaf-level measurements (Pou et al., 2008), WUE increased with increasing water stress but became more independent of VPD. In whole-vine measurements (Poni et al., 2014), deficit irrigation limited NCE_V more than Tr_V and thus WUE was dramatically reduced during the second half of a deficit period.

There is a general hypothesis that Tr_V is more sensitive to changes in g_c than is NCE_V (e.g., Jones, 2014) because of differences in $[H_2O_v]$ and $[CO_2]$ gradients, respectively. However, water deficits potentially alter this relationship. For example, if leaf temperature diverges from air temperature (leaf > air), which is plausible under water deficit, Tr_V may not be proportional to g_c , resulting in a change in g_c not necessarily leading to a change in WUE (Jones, 2004). For fully sunlit leaves in field-grown vines (Medrano et al., 2012), WUE did not differ between moderate and severe water stress for instantaneous midday WUE or WUE_d . They postulated that stomatal closure during water stress resulted in increased leaf temperature which in turn increased VPD, counteracting the effect of reduced g_s on Tr . Similar to our observations, WUE decreased during the day (Merli et al., 2015) with a maximum limitation around solar noon, under a caveat that their vines received a second daily irrigation application in midafternoon. Apparent inconsistencies in the literature on WUE under water deficits undoubtedly are compounded by the dependence of WUE on cultivar and on the environmental conditions under which the vines are grown (Tomás et al., 2014).

The use of WUE_i (NCE/g) allows WUE (NCE/Tr) to be normalized to g , allowing the near exclusion of the confounding effect of VPD on Tr (Schultz and Stoll, 2010). Most studies of grapevine NCE report WUE_i , undoubtedly a consequence of an emphasis on leaf-level measurements of photosynthesis. Chaves et al. (2010) mention the importance of tracking WUE_i throughout the day to adequately estimate an integrated WUE_d , although this integration is difficult (Schultz and Stoll, 2010). However, physiologically it can be argued that the ratio of interest is $NCE:Tr$, on short- and long-term bases (e.g., Merli et al., 2015). Furthermore, measurements conducted under high VPD and water deficit, as in this study, may show opposite tendencies in WUE and WUE_i : VPD negatively affects WUE over wide range of plant

water status but there is no obvious relationship between VPD and WUE_i (Schultz and Stoll, 2010). This study was conducted in a semiarid climate with high evaporative demand: in midseason, we calculated maximum daily VPD up to about 5.5 kPa.

Conclusion

The daily cumulative relative decline in Tr_v under additional water deficits was similar to that of NCE_v , resulting in no differences in WUE_d among RDI regimens during the respective periods of additional deficit. In the case of single-leaf measurements, relative differences among treatments may support that conclusion. However, whole-canopy measurements provide a powerful tool for identifying integrated absolute differences in NCE and Tr that are free from the scaling-up uncertainties of leaf-level measurements. In terms of irrigation management, there was greater water savings in RDI_E than in RDI_L because the majority of water that was transpired during the season occurred between fruit set and veraison. The previous report of this study showed that nonetheless there was no apparent loss of yield or compromise in fruit quality.

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