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

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ABSTRACT. To determine the effects of timing and extent of regulated deficit irrigation (RDI) on grapevine (Vitis vinifera) canopies, whole-canopy transpiration (TrV) and canopy conductance to water vapor (gc) 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 (RDIs), or weekly replacement of 60% to 70% of estimated evapotranspiration (ET) for well-watered grapevines; 2) early additional deficit (RDIE), or one-half of RDIs applied between fruit set and veraison; and 3) late additional deficit (RDIL), or one-half of RDIs applied between veraison and harvest. Compared with RDIs, the additional deficits (RDIE, RDIL) reduced daily cumulative Tr, by about 45% (RDIE) and about 48% [RDIL (57% by unit leaf area)]. Diurnal patterns of gc indicated consistent moderate water stress in all RDI regimens (gc ~50–150 mmol m−2 s−1). Under RDIs and RDIL, there were transient occurrences of severe water stress, indicated by gc declining below 50 mmol m−2 s−1. Across the day, vines under RDIE and RDIL had lower gc than RDIs. Under all deficit regimens, TrV exhibited opposing hysteretic loops with solar radiation [photosynthetic photon flux (PPF)] and vapor pressure deficit (VPD), with less sensitivity to VPD in RDIE and RDIL. For a given value of VPD, TrV was higher in the morning than in the afternoon. For a given value of PPF, TrV was higher in the afternoon than in the morning. Single-leaf measurements of transpiration overestimated TrV 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 (WUEd) did not differ among regimens during the additional deficits because daily cumulative values of whole-vine net carbon exchange (NCEV) and TrV changed proportionally: by about 43% to 46% in RDIE relative to RDIs. The case was less clear-cut for RDIL, where NCEV declined by 33% and TrV by 48% relative to RDIs. However, WUEd 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 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...
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 (RDIS)] in V. vinifera ‘Cabernet Sauvignon’. Under an early additional deficit [RDIE (fruit set to veraison)], vines fixed about 45% less carbon per day than did vines under RDIE. Under a late additional deficit [RDIE (veraison to harvest)], about 33% less carbon was fixed per day than under RDIE. As a function of cumulative irrigation applied, between fruit set and harvest a total water savings of about 40% accompanied RDIE, whereas about 20% less irrigation was applied to vines under RDIE. 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, gs, 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°55'N, long. 119°45'W, 125 m above sea level). Long-term mean annual rainfall (1990–2013) is 206 mm and reference evapotranspiration (ET0) in V. vinifera ‘Cabernet Sauvignon’. Under an early additional deficit [RDIE (fruit set to veraison)], vines fixed about 45% less carbon per day than did vines under RDIE. Under a late additional deficit [RDIE (veraison to harvest)], about 33% less carbon was fixed per day than under RDIE. As a function of cumulative irrigation applied, between fruit set and harvest a total water savings of about 40% accompanied RDIE, whereas about 20% less irrigation was applied to vines under RDIE. At harvest, there were no consistent differences among irrigation regimens in berry mass, fruit maturity indices, and quality indicators.

To compute RDIE, Kc was multiplied by 0.7 or 0.6. Therefore, RDIE supplied 70% (1999–2002) and 60% (2003) of estimated ETc 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 RDIS vines during specific periods of fruit development. In RDIE, 35% (1999–2002) and 30% (2003) of ETc was applied weekly from shortly after fruit set until veraison, then the vines were returned to RDIS [70% (1999–2002) and 60% (2003) of ETc] until harvest. In RDIL, vines were supplied 70% (1999–2002) and 60% (2003) of ETc (i.e., RDIL) until veraison, then 35% (1999–2002) and 30% (2003) of ETc 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% ETc, then were irrigated to FC in late October. In 2003, all plots were irrigated to FC immediately after harvest. Volumetric soil water content (θe) 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 θe (10% for RDIS, 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 (NCEc; 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 H₂O per second) and daily cumulative Tr (liters H₂O per day) were calculated per vine (Trᵥ) and per unit leaf area (Trᵥ/.LA). The Trᵥ measurements were obtained using framed, open-top, flow-through chambers (≈8 m² 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 ≈16 m³ 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 °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 and 5) postharvest (2 weeks after removal of the fruit). A hypothetical maximum Trᵥ was calculated using only the optimal dᵥ 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 dᵥ).

**Single-leaf transpiration.** To provide context with the preponderance of gas exchange measurements in the literature, rates of single-leaf Tr (TrSL) were measured concurrently with Trᵥ at three developmental stages in 2002 (preveraison, postveraison, preharvest) and at all stages at which Trᵥ was measured in 2003. Repeated measurements (≈0800–1400 hr) of TrSL were recorded four times during the day in 2002 and six times per day in 2003, during each full day that Trᵥ 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-cm² leaf cuvette [PLC6(U), PP Systems]. Air flow through the cuvette was 200 cm³ 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 LAᵥ was measured less frequently in 2002 than in 2003, where data were pooled across years daily cumulative Trᵥ was only assessed on a per vine basis and not per unit LA.

**Water use efficiency.** Whole-canopy daily water use efficiency (WUEᵥ), defined as the ratio of net CO₂ fixed to water transpired, was estimated for the whole canopy and at the leaf level. Values of NCEᵥ are reported in Tarara et al. (2011). The WUEᵥ was calculated using daily total NCE (NCEᵥ) and daily cumulative Trᵥ (Trᵥ). Leaf-level water use efficiency was calculated using daily averages of single-leaf NCE.
(NCESL) and TrSL. To avoid fluctuations in WUE due to VPD (Osmond et al., 1980), intrinsic WUE (WUE\textsubscript{e,\(V\)} and WUE\textsubscript{e,SL}) was calculated from the ratio between NCE\textsubscript{e} and \(g_e\) (whole-canopy) or NCE\textsubscript{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\textsubscript{V} comprises the complete dataset from 2003, where gas exchange and LA\textsubscript{V} data were available at all developmental stages. Instances where Tr\textsubscript{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 \(\approx 1\) 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, \(\theta_v\) declined into early summer until fruit set when RDI was initiated. Thereafter \(\theta_v\) trended according to the RDI regimens. Obvious departures from target \(\theta_v\), 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 \(\theta_v\) than the original target of 10\% v/v. Between fruit set and harvest, 63\% and 79\% of the total water applied to RDIS plots was applied to RDI\textsubscript{E} and RDI\textsubscript{L}, respectively (Table 1). In both years, when RDI\textsubscript{E} plots were under the additional deficit, the vines received 55\% of the cumulative amount of water that had been applied to RDIS, about the target value. Water application was somewhat more variable in RDI\textsubscript{L}: 45\% (2002) and 31\% (2003) of the cumulative RDIS application was delivered when the RDI\textsubscript{L} vines were under the additional deficit. The end-of-season variation in \(\theta_v\) in 2003 reflects the cooperators’ 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\textsubscript{V,LA}. Hence the computation of daily cumulative Tr\textsubscript{v} and Tr\textsubscript{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\textsubscript{v} generally were conserved whether Tr was expressed as Tr\textsubscript{V} or Tr\textsubscript{V,LA}. Daily cumulative Tr\textsubscript{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\textsubscript{V} and Tr\textsubscript{V,LA} did not differ among RDI regimens during fruit set. During preveraison, RDI\textsubscript{E} vines transpired nearly 60\% less per day than RDIS and RDI\textsubscript{L}, whether expressed per vine or per unit leaf area (Tables 2 and 3). During the postveraison stage, across all \(d_m\), RDI\textsubscript{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)* | Precipitation (mm)* | ET\textsubscript{o} (mm*) | Irrigation (mm)* |
|----------|-------------------------|---------------------|----------|--------------------|---------------------------|----------------|
| 2002     | Dormancy                | 8 Nov. to 25 Apr.   | —        | —                  | —                         | —              |
|          | 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     |
|          | Verozai–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.  | —        | —                  | —                         | —              |
|          | 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     |
|          | Verozai–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    |

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

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

*Reference evapotranspiration (ET\textsubscript{o}) calculated from the Penman–Monteith equation for a grass reference crop (Allen et al., 1998).

*RDIS = industry standard regulated deficit irrigation practice of weekly replenishing of 60% to 70% of crop evapotranspiration, RDI\textsubscript{E} = early additional deficit of 50% of RDIS, RDI\textsubscript{L} = late additional deficit of 50% of RDIS.
not appear to have recovered to the $T_{rv}$ values of RDIS (Table 2) because of a missed irrigation set. However, on the optimal $d_m$, $T_{rv}$ did not differ between RDIS and RDIE, and both exceeded RDL. During postveraison, RDIL vines transpired nearly 50% less than RDIS and RDIE on a per vine basis, and nearly 60% less based on $T_{rv,LA}$. Immediately before harvest, cumulative values of $T_{rv}$ in RDIS had declined from pre- and postveraison by about 40% (Tables 2 and 3). At both the pre- and postharvest measurements, daily cumulative $T_{rv,LA}$ did not differ among RDI regimens.

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

After RDI had been imposed for 5 weeks (preveraison stage), maximum $T_{rv,LA}$ values were about 4 to 4.5 mmol m$^{-2}$ s$^{-1}$. The diurnal course of $T_{rv,LA}$ in RDIS and RDIE

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**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 [$T_{rv}$ (top)] and per unit leaf area [$T_{rv,LA}$ (bottom)]. The Tr values are means of six vines averaged across all measurement days ($d_m$) per developmental stage.

| Developmental stage | Sampling period (DOY)$^a$ | RDI regimen$^b$ | $T_{rv}$ (L d$^{-1}$) | $d_m$ | Trt × $d_m$ | $T_{rv,LA}$ (L d$^{-1}$ m$^{-1}$) | $P$ value |
|---------------------|--------------------------|-----------------|---------------------|------|-------------|---------------------------------|--------|
| Fruit set           | 177–184                  | RDIS  11.6      | 11.2                | 13.7 | 0.001       | 0.012                           | 0.182  |
|                     |                          | RDIE  14.1 a$^w$| 7.7 b               | 15.6 a| 0.001       | 0.068                           | 0.030  |
|                     |                          | RDL   11.6 a    | 7.6 b               | 6.0 b| 0.001       | 0.001                           | 0.247  |
| Preveraison         | 212–219                  | RDIS  6.9      | 6.2                | 5.8  | 0.003       | 0.003                           | 0.753  |
|                     |                          | RDIE  4.2      | 4.1                | 5.2  | 0.001       | 0.001                           | 0.341  |
|                     |                          | RDL   6.9      | 6.2                | 5.8  | 0.003       | 0.003                           | 0.247  |
| Preharvest          | 255–262                  | RDIS  0.9      | 0.8                | 0.7  | 0.026       | 0.001                           | 0.092  |
|                     |                          | RDIE  0.7      | 0.7                | 0.7  | 0.004       | 0.004                           | 0.001  |
|                     |                          | RDL   0.9      | 0.8                | 0.7  | 0.026       | 0.001                           | 0.092  |

$^a$DOY = day of the year.

$^b$RDIS = industry standard regulated deficit irrigation practice of weekly replenishing of 60% of crop evapotranspiration, RDIE = early additional deficit of 50% of RDIS, RDL = late additional deficit of 50% of RDIS.

$^c$Trt = treatment.

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

$^d$For pooled data, effect of developmental stage.

$^e$For pooled data, interaction between RDI regimen and developmental stage.
was generally similar to that at fruit set. There was lower Tr V,LA in RDIE vines than in RDIS and RDIL vines after a morning maximum: for example, even following an irrigation (e.g., DOY 213; Fig. 3A), RDIE vines transpired 18% less than RDIS and RDIL 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 RDIE was about 60% less than that in RDIS and RDIL. The lower Tr V,LA in RDIE was reflected in a midday maximum gc of 65 mmol m⁻² s⁻¹, about 60% lower than that of either RDIS or RDIL.

Three weeks after RDIE vines had been returned to RDIS and RDIL was started (postveraison measurements), maximum rates of Tr V,LA in RDIS 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 RDIE vines compared with RDIL and RDIS 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 RDIE vines was 22% less than that of RDIS vines. However, cumulatively there was no difference in Tr V,LA between RDIS and RDIL on this optimal dₚ, indicating that the RDIE vines had essentially recovered from the 5 weeks of additional deficit. The RDIL vines transpired about 77% less than RDIS during the midday hours on the optimal dₚ (DOY 238; Fig. 4B). Concurrent midday gc in RDIL ranged from 21 to 37 mmol m⁻² s⁻¹, indicative of severe water stress according to proposed ranges for gc in grapevine (Lovisolo et al., 2010). By contrast, gc in RDIS and RDIL was between 73 and 135 mmol m⁻² s⁻¹, indicating moderate water stress.

Table 3. Daily cumulative transpiration (Tr) per day in mature, field-grown grapevines under regulated deficit irrigation (RDI) expressed per vine (Trₑ) and per unit leaf area (Trₑ,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) | RDIₑ | RDIₑ D | RDIₑ L |
|---------------------|----------------------|------|--------|--------|
| Fruit set           | 178                  | 14.1 | 15.7   | 19.0   |
| Preveraison         | 218                  | 18.3 a²| 7.8 b | 20.7 a |
| Postveraison        | 238                  | 18.2 a²| 16.2 a | 7.7 b  |
| Preharvest          | 256                  | 8.6  | 7.5    | 6.6    |
| Postharvest         | 278                  | 4.1  | 4.7    | 5.9    |

P value: 0.001* (for pooled data, interaction between regulated deficit irrigation regimen and developmental stage).

*DOY = day of the year.

RDIₑ = industry standard regulated deficit irrigation practice of weekly replenishing of 60% of crop evapotranspiration, RDIₑ D = early additional deficit of 50% of RDIₑ, RDIₑ L = late additional deficit of 50% RDIₑ.

Values followed by different letters within rows are significantly different at P ≤ 0.05 by Tukey–Kramer.

For pooled data, effect of developmental stage.

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

**Fig. 2. Whole-canopy transpiration rate per unit leaf area (Trₑ,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, RDIS = industry standard practice of weekly replenishing of 60% of crop evapotranspiration, RDIE = early additional deficit (preveraison) of 50% of RDIS, RDIL = late additional deficit (postveraison) of 50% of RDIS. ETₑ = reference evapotranspiration, DOY = day of the year. Data were collected before RDIE was imposed.**
indicated continued water stress of varying degrees, where $g_c$ in RDI_I ranged between 40 and 90 mmol·m⁻²·s⁻¹, and that in RDI_S and RDI_E between 60 and 150 mmol·m⁻²·s⁻¹ (e.g., DOY 256). Rates of $T_{V,LA}$ at the end of the measurement run were uniformly low and corresponding midday $g_c$ indicated moderate to severe water stress [24–76 mmol·m⁻²·s⁻¹ (RDI_I), 40–106 mmol·m⁻²·s⁻¹ (RDI_E and RDI_L)]. In the postharvest measurement run the daily pattern of $T_{V,LA}$ 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 $T_V$ 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 $T_V$ (computed from the hypothetical 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 $T_r$. Measurements did reflect the treatment differences that were observed in the whole-vine measurements (data not shown). On the whole, concurrent measurements of $T_{SL}$ overestimated $T_{V,LA}$ (Fig. 6). There was a moderate linear relationship between $T_{SL}$ and $T_{V,LA}$ ($r^2 = 0.34$, $P < 0.001$), consistent with our findings for NCE, albeit the NCE relationship was stronger ($r^2 = 0.61$; Tarara et al., 2011).
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\(_E\) (\(r_s = -0.767\), \(P < 0.0001\)) than for RDI\(_S\) (\(r_s = -0.553\), \(P < 0.0001\)). 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\(_L\) and RDI\(_S\) (data not shown). Around midday in RDI\(_E\), both NCE\(_V\) and \(g_c\) were 59\% less than in RDI\(_S\),
resulting in a constant proportionality. Both regimens exhibited a small decline in WUEi between midmorning and midday. However, the same outcome was not observed during the postveraison measurement run, where RDIL exhibited a large decline in WUEi during midday (data not shown). The average midday WUEi differed between RDIL and RDIS because average NCEV was 85% less in RDIL than in RDIS, whereas midday gc was 75% less in RDIL than in RDIS. Thus the ratio between NCEV and gc changed in response to the additional deficit.

**Discussion**

Vines under additional water deficit (RDIE, RDIL) transpired less than those under RDIS 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 RDIS in RDIE and RDIL, 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 NCEV (Tarara et al., 2011), all vines responded rapidly to irrigation, increasing $T_{rV}$ 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 $T_{r}$ and NCE, mediated by $g_{c}$, change little until about two-thirds of the available soil water is transpired, after which NCE and $T_{r}$ decrease linearly with decreasing $\theta_{w}$. From calculations reported in Tarara et al. (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 $T_{rV}$ differed somewhat from those of NCEV in that rates of $T_{rV}$ approached relatively steady values across midday, whereas NCEV declined steadily from a morning maximum (Tarara et al., 2011). The highest rates of NCEV and the highest rates of change in NCEV occurred earlier in the morning than for $T_{rV}$. Despite these different diurnal patterns, during the additional
Fig. 8. Rate of whole-vine transpiration per unit leaf area (TrV,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 E (A–F)] or under an additional deficit that reduced the standard application by half [RDI L (B–F)] or 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 RDIL in both TrV,d and NCE,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 gs decreased to values of about 50 mmol·m⁻²·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 gs in Vitis sp. have been associated in a general sense with mild water stress (decreasing from about 200–500 mmol·m⁻²·s⁻¹ down to 150 mmol·m⁻²·s⁻¹), moderate water stress (about 50–150 mmol·m⁻²·s⁻¹), and severe water stress (<50 mmol·m⁻²·s⁻¹; Lovisolo et al., 2010). Analogous ranges for gs have not been proposed so we take available values of gs as a starting reference. Based on gs we observed at least transient occurrences of severe water stress in RDI E and RDIL; RDIL 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 TrV,LA values presented here are comparable with others in the literature that evaluated water-stressed vines using whole-canopy gas exchange [e.g., ≈5 mmol·m⁻²·s⁻¹, field-grown (Katerji et al., 1994); ≈3 mmol·m⁻²·s⁻¹, field-grown (Ollat and Tandonnet, 1999); ≈3 mmol·m⁻²·s⁻¹, potted (Palliotti et al., 2014); ≈2–3 mmol·m⁻²·s⁻¹, potted (Poni et al., 2009)]. The lower values of gs that we observed under the additional deficits were in the general range reported for single-leaf measurements (gs) of water-stressed potted vines by Palliotti 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 gs to overestimate gc. Under progressive soil water deficit in other field-grown vines, midday gs declined to values similar to those that we observed (de Souza et al., 2005). Chaves et al. (2007) measured midday gs under water deficit as high as 230 mmol·m⁻²·s⁻¹ in 2 years, but reported a value as low as 80 mmol·m⁻²·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 RDIL, 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)$^*$ | RDI$_{S}$ | RDI$_{E}$ | RDI$_{L}$ | $P$ value |
|---------------------|--------------------------|-----------|-----------|-----------|-----------|
|                      | WUE$_{V,d}$ (g CO$_2$ per vine per day/L H$_2$O per vine per day) |           |           |           |           |
| Fruit set           | 177–184                  | 8.7       | 8.4       | 8.2       | 0.001     |
| Preveraison         | 212–219                  | 8.9       | 8.7       | 8.4       | 0.083     |
| Postveraison        | 233–241                  | 10.3      | 13.8      | 12.2      | 0.001     |
| Preharvest          | 255–262                  | 8.0       | 6.0       | 5.7       | 0.001     |
| Postharvest         | 274–281                  | 12.1 a    | 12.7 a    | 8.6 b     | 0.001     |

$^*$DOY = day of the year.

$^*$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% RDI$_{S}$.

$^*$Tr = treatment

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

For pooled data, effect of developmental stage.

For 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’ (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 $\theta_c$ 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. They found contrasting 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...
confirmed these observations for instantaneous rates of Tr and except the innermost shaded leaves. Medrano et al. (2012) water stress reduced NCE and Tr in all locations of the canopy sunlit exterior to the shaded interior. They found that severe et al., 2003). Drought progressively affected leaves from the canopy section, driven by radiation interception (Escalona et al., 2014). "fruit set," during which all vines were under standard regulated deficit irrigation (RDI), of weekly replenishing of 60% of crop evapotranspiration; (B) "preveraison," during which an early additional deficit was imposed (RDI) that reduced RDI by half; and (C) "postveraison," during which a late additional deficit was imposed (RDI) that reduced RDI 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/$g_c$) allows WUE (NCE/Tr) to be normalized to $g_c$, 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, 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 RDIE than in RDL 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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