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Evaporative demand determines the relative transpirational sensitivity of deficit-irrigated grapevines

Uri Hochberg[1] · Jose Carlos Herrera[1] · Asfaw Degu[2] · Simone Diego Castellarin[3] ·
Enrico Peterlunger[1] · Giorgio Alberti[1] · Naftali Lazarovitch[2]

Abstract A common irrigation strategy is to replenish the soil water reservoir according to evapotranspiration (ET). However, the ET from plants under deficit irrigation is not well explored and is normally assumed to be a constant fraction of their respective well-watered condition. In the current experiment, we hypothesized that the ratio between the ET of well-watered (WW) and water deficit (WD) grapevines is not constant but depends on the reference ET (ET_O). The hypothesis was tested using lysimeters over two consecutive seasons to measure the ET of WD grapevines (*Vitis vinifera* L.) that were irrigated at 35 % of a second set of lysimeters with WW vines. The WD treatment started at veraison and resulted in a quick depletion of the soil water reservoir; thereafter a relatively stable soil water content (θ) and crop coefficient (K_C) were measured. The ET of the WD vines was 20–75 % lower than that of the WW vines, depending on the reference evapotranspiration (ET_O). Under high ET_O, the difference between the treatments was much larger than under low ET_O. The dynamic ratio between the ET of the treatments demonstrates the difficulty in predicting the ET of WD plants and suggests that irrigation according to a constant fraction from a WW plant might result in

either excessive or insufficient irrigation amounts. The high correlation between instantaneous stomatal conductance (g_s) measurements and K_C emphasizes the advantage of utilizing g_s to improve current irrigation models.

Introduction

One of the most practiced irrigation strategies is to replenish the soil's water reservoir based on evapotranspiration (ET) rates. The irrigation volume (IR_V) is usually calculated from the estimations of the crop evapotranspiration (ET_C) since the last time of irrigation; and so, water is supplied to maintain constant water availability for the plant (Allen et al. 1998). ET_C is normally calculated from the measurement of lysimeter evapotranspiration (ET_{lys}; López-Urrea et al. 2012). However, since field-scale lysimeters are expensive and therefore scarce, they are normally used to develop empirical models that link the reference evapotranspiration (ET_O) with ET_C (Evett et al. 2012). The ratio between ET_C and ET_O, normally termed as the crop coefficient (K_C), provides irrigators with a simple method to transform ET_O—available through weather stations data— into ET_C. From a physiological perspective, K_C is a function of the crop's evaporative surface (i.e., leaf area, LA) and its hydraulic resistance. Therefore, the calculation of ET_C for a specific field is valid only under the assumption that the crop hydraulic resistances in that field and in the lysimeter are equal (Annandale and Stockle 1994). Such an assumption is reasonable when both field and lysimeter plants are grown under near optimal conditions, but when field plants are grown under water deficit, the crop resistance is likely to increase and reduce the actual ET.

As many tree crops (e.g., almonds, pistachio, citrus, and others) could benefit from deficit irrigation (Fereres

✉ Jose Carlos Herrera
jc.herrera@uniud.it

[1] Department of Agricultural, Food, Environmental and Animal Sciences, University of Udine, Udine, UD, Italy

[2] The French Associates Institute for Agriculture and Biotechnology of Drylands, Ben-Gurion University of the Negev, Sede Boqer Campus, Midreshet Ben-Gurion, Israel

[3] Wine Research Centre, The University of British Columbia, Vancouver, BC, Canada

and Soriano 2007), it is important to develop methods for deficit irrigation scheduling. Many past studies based the deficit irrigation treatments on multiplying the ET_C of well-watered plants by an irrigation factor (IF), normally ranging between 0.2 and 1:

$$IR_V = ET_C \times IF \qquad (1)$$

For example, using an IF of 0.35, Shellie (2006) down-regulated the irrigation amounts by 65 % to maintain grapevines (*Vitis vinifera* L.) at a leaf water potential of 0.3–0.5 MPa lower than the well-watered control treatment (100 % ET_C). Specifically for grapevines, numerous studies successfully utilized the IF to calculate the IR_V and its influence on berry characteristics (e.g., Intrigliolo and Castel 2010; Romero et al. 2010; Munitz et al. 2016).

However, there are still several fundamental gaps in our understanding of deficit irrigation scheduling according to the IF, especially when it comes to the ET of deficit-irrigated treatments. We know that the IF leads to a constant irrigation ratio between the deficit-irrigated and the well-watered plants. At the same time, it is not clear whether a similar ratio also exists between the ET of these treatments. As a result, it is not clear whether deficit irrigation according to the IF replenishes the soil water reservoir or leads to its gradual depletion. Moreover, the stability of K_C under a deficit irrigation regime, with respect to the environment and plant physiology, requires an in-depth investigation.

While data on the whole plant transpiration are lacking, an examination of water relation studies and models suggests that the ratio of a single leaf ET between deficit-irrigated and well-watered plants depends on the atmospheric demand (Oren et al. 1999; Pou et al. 2008). From a hydraulic perspective, the stomata regulate the transpiration to avoid a critical water potential that would lead to xylem embolism or turgor loss (Tyree and Sperry 1989). Assuming that the soil water potential is high enough, maintaining high stomatal conductance (g_s) would improve the carbon flow into the leaf without reaching this critical water potential. Accordingly, the response function of g_s to stem water potential (Ψ_s) is commonly described as sigmoidal (e.g., Tombesi et al. 2014). Therefore, any reduction of Ψ_s due to high ET_O should lead to a different downregulation of g_s, depending on the soil water potential. This notion is reflected in the recent transpiration model by Sperry and Love (2015) that predicts very similar transpiration rates for both well-watered and water deficit plants under low ET_O, but much lower transpiration rates for water deficit plants under high ET_O.

In the present experiment we used lysimeters to compare the ET_{lys} of well-watered (WW) grapevines with that of water deficit (WD) grapevines that were irrigated at 35 % of ET_{lys} WW (i.e., IF = 35 %). We hypothesized that the ratio between the two treatments depends on ET_O. The two treatments were compared one to another and also to

midday physiological parameters in order to test the feasibility of utilizing these parameters to predict ET.

Materials and methods

Plant material and site description

The study was conducted during the two consecutive seasons of 2014 and 2015, at the University of Udine experimental station "A. Servadei" (46°02′N, 13°13′E; 88 m a.s.l.). The plant material consisted of four-year old *Vitis vinifera* cv. Merlot (clone R3), grafted to SO4 rootstock and potted (40 L) in a mixture of soil (49.0 % sand, 31.5 % silt, and 19.5 % clay) that was supplemented with 20 % perlite. The soil water holding capacity for each pot was 11.6 L. At harvest the vines had on average 1.8 kg of grapes/plant. To prevent natural precipitation, the trial was conducted under a transparent plastic (ethylene-vinyl-acetate) roof (4.5 m in height) that covered the entire experimental plot while the sides of the framing structure remained open (Herrera et al. 2015). The trial consisted of two rows of 16 plants each, spaced 2.5 m apart. Each row was divided into four blocks, for a total of eight plots. The in-row spacing between each vine within the block was 1 m.

The vines were cane pruned to a single Guyot (0.8 m high), with 8–10 nodes per cane, and trained to vertical shoot positioning. Hedging was not performed over the course of the experiment. The plants were provided with mineral nutrition (N-P-K Nitrophoska®), and fungicide was applied as commonly practiced in the area.

Lysimeter setup

Each four-vine plot consisted of three pots buried in the ground and a fourth (served as a lysimeter) that was placed in a hole (50 × 50 × 50 cm), to level with the other pots. The lysimeter was always in a central position within each plot. The outside surfaces of the lysimeter pots were thermally protected through shading, insulating foam, and aluminum foil in an attempt to minimize the effect of soil temperature fluctuation.

A self-constructed balance, based on two-beam single point load cells (©Tedea Huntleigh, Model 1042; maximum mass: 75 kg; accuracy: 0.02 % of rated output), was placed at the bottom of each hole, beneath the lysimeter pot. In 2014, the system was operated manually, starting on July 22. Lysimeters-grown vines were weighed at night, five times per week, both before and after irrigation was applied and drainage had ceased. In this way, it was possible to compute four evapotranspiration (ET_{lys}) values per week for each lysimeter. In 2015, the scales operated automatically and pots' masses were recorded every minute

using a CR1000 data logger (Campbell Scientific, Inc., USA). ET_{lys} was calculated as the difference between the average mass between 04:00 and 05:00 (after irrigation) and the average mass between 22:00 and 23:00 (before irrigation). In 2015, the system was activated in May, resulting in daily ET_{lys} values for the whole season.

Irrigation treatments

Water was supplied by a drip irrigation system with a set of two emitters per pot (PCJ 2 L h^{-1}, Netafim, Israel). Treatments were randomly assigned to each plot and were established at 50 % veraison, on July 24, 2014 and on July 31, 2015, and comprised two irrigation levels: well-watered (120 % of ET_{lys}, WW) and water deficit (IF = 35 % of the WW treatment's ET_{lys}, WD). Irrigation treatments for each week were generally calculated from the average ET_C of the previous week, but were modified in the case of an extraordinary daily ET_O value.

Irrigation volumes were calculated through the linear regression ($R^2 = 0.995$) between irrigation duration and the volume dispensed by the drippers (data not shown). At the beginning of each season, the volume emitted by all drippers was compared to ensure that all drippers were within a 10 % interval. Abnormal drippers were replaced. Irrigation was applied daily and during hours of minimal transpiration (at 21:00 in 2014 and at 00:00 in 2015) to minimize significant effects (ET during the irrigation time was not considered) on the daily ET_{lys} calculation

Following harvest (54 and 60 days after veraison in 2014 and 2015, respectively), the irrigation treatments remained in effect for another 10 days. After this interval, the WD treatment was abandoned, and all vines were irrigated to field capacity.

Weather data

Weather data were collected within the experimental plots to account for the possible impact of the plastic roof. In order to calculate the under-roof potential evapotranspiration according to the Penman–Monteith model (FAO56; ET_O), measurements of temperature and relative humidity (HMP60, Vaisala, Finland), wind speed (Gill Windsonic, Gill Instruments, UK), and global radiation (LI-200SL, LiCor, Inc., USA) were recorded at a frequency of 10 s using a CR1000 data logger (Campbell Scientific, Inc., USA) and then averaged at 30 min.

Soil sensors

Soil volumetric water content (v/v; θ) was monitored in each lysimeter pot using EC-5 sensors (Decagon Devices,

USA) installed at 10–15 cm deep with the waveguides in vertical position. Measurements were recorded every 30 min using the EM50G data logger (Decagon Devices, USA).

Leaf area

Leaf area (LA) for the eight lysimeter-grown vines was calculated six and nine times over the course of the seasons in 2014 and 2015, respectively, based on the number of leaves and their average area (Montero et al. 2000). The latter was computed using a linear model based on the average length of all the leaves in one representative shoot per vine (Rapaport et al. 2014). The model was developed by collecting 60 leaves and measuring their area using a Li-3100 (Li-Cor, Inc., USA; $R^2 = 0.89$).

Evapotranspiration (ET) parameters

Measurements of evapotranspiration from lysimeters (ET_{lys}) are usually normalized to the soil area (Allen et al. 1998), facilitating their implementation for agricultural use. However, the adopted experimental setup (40-L lysimeters not in a field) questions the validity of such normalization. Instead, ET_{lys} values were directly normalized to ET_O (as in Ben-Gal et al. 2010), resulting in K_C (m^2 plant^{-1}):

$$K_C = \frac{ET_{lys}}{ET_0} \tag{2}$$

Physiological parameters

Stem water potential (Ψ_s) and stomatal conductance (g_s) were periodically measured (8–9 times in each year) during the experiment and compared with ET. Both measurements were conducted on all the lysimeter vines (four repetitions per treatment) at midday, during sunny days, on a young fully expanded leaf.

To determine the stem water potential (Ψ_s) the leaves were bagged and covered with aluminum foil for 1 h before they were excised from the shoot using a sharp blade. While still bagged, the leaves were placed into the pressure chamber (Soil Moisture Co., Santa Barbara, CA, USA) with the petiole protruding from the chamber lid. The chamber was pressurized using a nitrogen tank, and Ψ_s was recorded when the initial xylem sap was observed emerging from the cut end of the petiole.

Stomatal conductance (g_s) was measured using an infrared gas analyzer (LI-6400, LiCor, Inc., USA). The measurements were taken at a constant light intensity (1000 µmol m^{-2} s^{-1}) and CO_2 concentration (400 µmol mol^{-1}).

Results

The lysimeter measurements illustrated the large variability in grapevine evapotranspiration (ET_{lys}) throughout the growing season. With respect to the evaporative demand
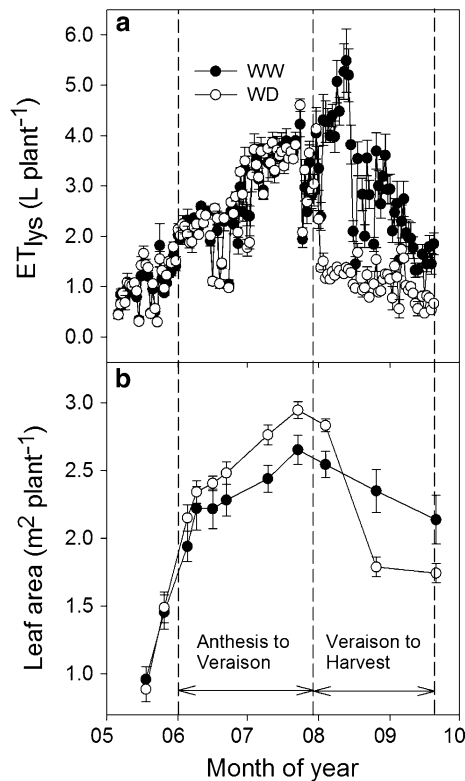

Fig. 1 **a** Seasonal pattern of the lysimeter evapotranspiration (ET_{lys}) and **b** leaf area (LA) of the well-watered (WW) and water deficit (WD) treatments in the 2015 season. Data are the averages of four plants ±SE

and vine physiology, the transpiration ranged between 0 and 6 L plant^{-1} day^{-1} in 2015 (Fig. 1a). The 2014 data collection only began at veraison, when the irrigation treatment started, but the 2015 data shows that the ET_{lys} was minimal shortly after bud break and quickly increased as soon as the canopy developed (Fig. 1), reaching the maximal ET_{lys} on August 13. The application of the WD treatment at veraison resulted in a quick reduction of ET_{lys} to a daily consumption of 0.65–1.3 L.

The irrigation treatments led to significant differences of Ψ_s and g_s (Table 1). The physiological differences were largest between 10 and 20 days after veraison with a difference of ~0.8 MPa in Ψ_s and of ~150 mmol m^{-2} s^{-1} in g_s between the treatments. Surprisingly, in 2014 there was a substantial reduction in g_s of the WW treatment toward harvest to values of 70 mmol m^{-2} s^{-1} (Table 1). The WD treatment led to a fast decline in θ for the first 6–8 days after the initiation of the treatment in both seasons (Fig. 2a, b). Following this short period, there was no further decline of θ, which ranged from 0.05 to 0.2 (v/v), significantly lower than the θ of the WW treatment (0.3–0.5 v/v). While the soil conditions were fairly similar between the two seasons, the evaporative demand (ET_O) was lower in 2014 than in 2015, as it was exceptionally cool and rainy. During the irrigation period, in 2014, the maximal daily ET_O was 3.7 mm, while in 2015, it was 5 mm (Fig. 2a, b). Additionally, a difference between the K_C of the WW treatment was observed between the two seasons. In 2014, an unexpected reduction in K_C during mid-August led to low K_C values (~0.6 m^2 plant^{-1}) in the WW vines until harvest. Conversely, and as expected, in early August of 2014 and throughout the duration of the WD treatment in 2015, K_C was significantly larger in the WW treatment (1 m^2 plant^{-1}) than in the WD treatment (0.4 m^2 plant^{-1}; Fig. 2c, d).

Table 1 Midday stem water potential (Ψ_s, MPa) and stomatal conductance (g_s, mmol m^{-2} s^{-1}) in well-watered (WW) and water deficit (WD) grapevines during the experimental seasons (from veraison to harvest) in 2014 and 2015

	1–10 DAV		10–20 DAV		20–35 DAV		35–50 DAV	
	Ψ_s (MPa)	g_s (mmol m^{-2} s^{-1})	Ψ_s (MPa)	g_s (mmol m^{-2} s^{-1})	Ψ_s (MPa)	g_s (mmol m^{-2} s^{-1})	Ψ_s (MPa)	g_s (mmol m^{-2} s^{-1})
2014								
WW	−0.75	198	−0.68	153	−0.51	85	−0.52	70
WD	−1.21	75	−1.47	15	−1.39	16	−0.93	13
Sign[a]	***	***	***	***	***	***	***	***
2015								
WW	−0.51	249	−0.53	189	−0.47	287	−0.36	187
WD	−0.84	117	−1.36	24	−1.07	62	−0.67	44
Sign	**	**	***	***	***	***	***	***

Data are presented as averages every 10 or 15 days after veraison (DAV). Each value is the average of 4 biological replicates and 2 or 3 dates within the specified interval (DAV)

[a] Within each year, significant differences between treatments are expressed as ** or *** ($P < 0.01$ or $P < 0.001$, respectively) according to ANOVA analysis

Fig. 2 Soil water content (θ; **a**, **b**), reference evapotranspiration (ET_O; **a**, **b**), leaf area (LA; **c**, **d**) and the crop coefficient (K_C; **c**, **d**) of the well-watered (WW) and water deficit (WD) treatments during the application of the water treatment (starting at veraison, *dashed line*) in 2014 (**a**, **c**) and 2015 (**b**, **d**). Data are the averages of four plants ±SE
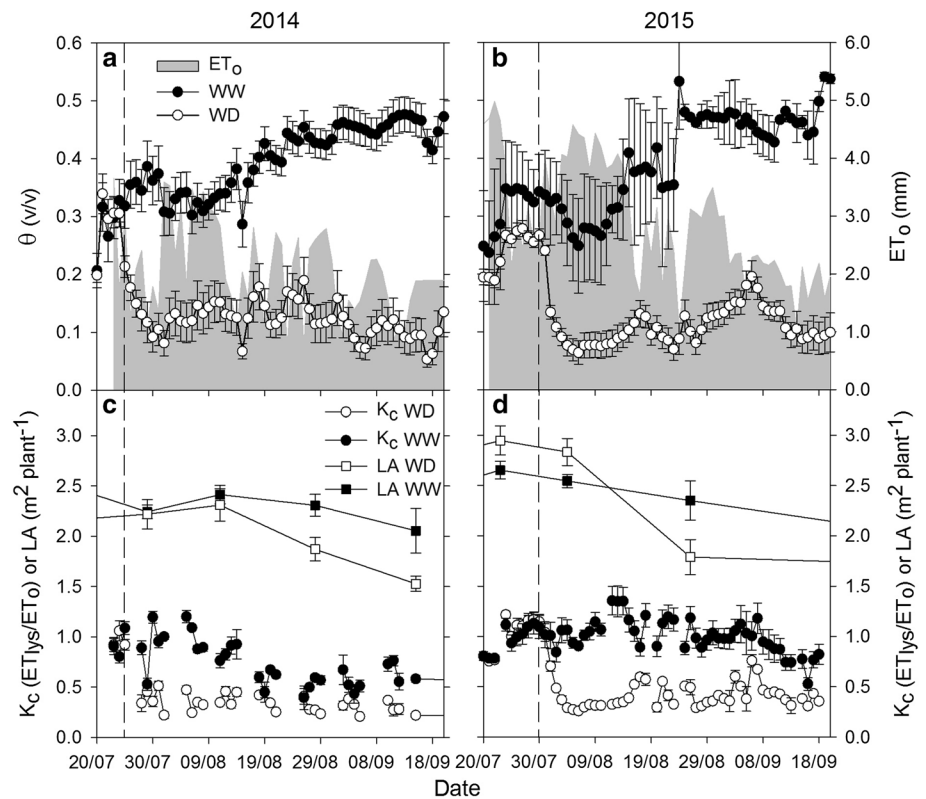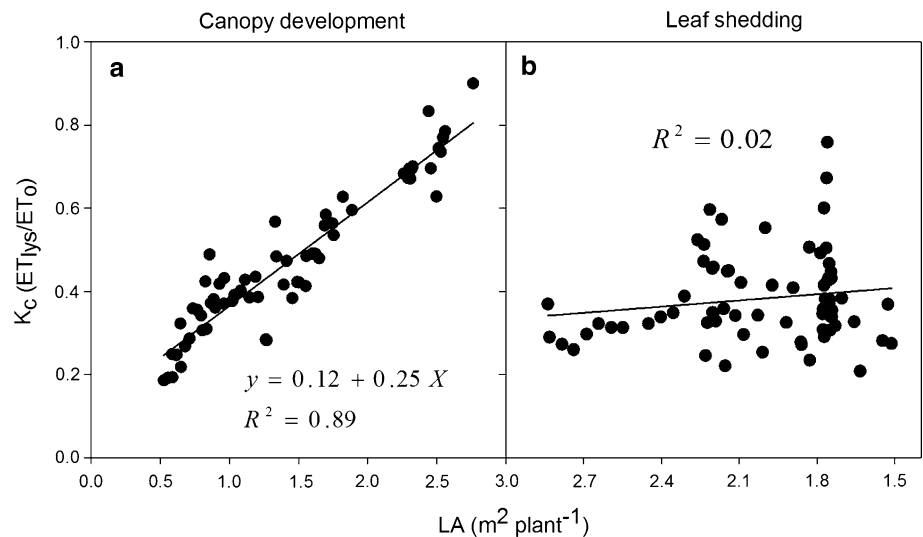

Fig. 3 Crop coefficient (K_C) as a function of leaf area (LA) during canopy development (before treatments were imposed; **a**) and leaf shedding (following the water deficit treatment; **b**). Data are the averages of four plants

During canopy development, there was a strong correlation between LA and K_C ($R^2 = 0.89$; Fig. 3a). However, soon after the application of the WD treatment, since K_C values were significantly reduced (Fig. 2c, d), no correlation between LA and K_C was found (Fig. 3b). The WD treatment did result in a decrease in LA from 2.3 to 1.51 m^2 $plant^{-1}$ in 2014 and from 2.83 to 1.78 m^2 $plant^{-1}$ in 2015 (Fig. 2c, d). However, apparently this decline had a negligible effect on K_C compared with stomatal

regulation, leading to the low correlation between K_C and LA ($R^2 = 0.02$).

To assess whether the irrigation scheduling based on the irrigation factor (IF = 0.35) supplied the actual ET of the WD vines, the ET_{lys} of the two treatments were regressed (Fig. 4). As expected, assuming the regression is linear, the slope (S) was 0.347, a value very close to the scheduled IF (0.35), but with a poor correlation coefficient ($R^2 = 0.343$, $P < 0.001$; data not shown). Instead, the better-fitting
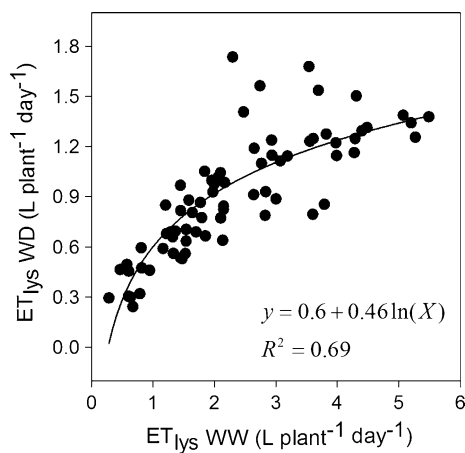
Fig. 4 Lysimeter evapotranspiration (ET_{lys}) of the water deficit treatment (WD) as a function of the ET_{lys} of the well-watered treatment (WW). Data were taken only from post-veraison, during the application of the irrigation treatments. Data are the averages of four plants

logarithmic relationship between the ET_{lys} of the two treatments ($R^2 = 0.69$, $P < 0.001$; Fig. 4) emphasizes that the relation between the treatments' ET is dynamic, possibly depending on environmental conditions and on the degree of water stress developed by the plant during the imposed deficit irrigation conditions.

As hypothesized, ET_{lys} was highly correlated to ET_O, with a very different regression for each of the treatments (Fig. 5a). Under low ET_O (<2 mm), both treatments exhibited similar ET_{lys}, meaning that water limitations had little effect on transpiration in the WD treatment. Conversely, under an ET_O of 3 mm or above, the ET_{lys} of the WD treatment was constant at around 1.2 L plant^{-1} day^{-1}, meaning that under such an ET_O, plant resistance was modified to limit transpiration. At the same time, the response curve of the WW treatment maintained a linear increase of ET_{lys} as a function of ET_O (Fig. 5a). Since both treatments had similar ET_{lys} values under low ET_O, but very different ET_{lys} under high ET_O, the evapotranspiration ratio between the treatments, ranged from 1 (i.e., similar water consumption) under low ET_O down to 0.25 under the high ET_O of 5 mm (Fig. 5b).

In light of the great effect the treatment imposed on K_C, different parameters (θ, Ψ_S and g_s) that could represent the plant limitation to transpiration were compared with K_C. These parameters were correlated with K_C, each with a different response function (Fig. 6). The logarithmic response of K_C to θ flattens at the θ of 0.3, probably since higher θ values do not consist in any water limitation for the plant (Fig. 6a). In addition, the response curve of the Ψ_s flattens at values higher than -0.7 MPa, probably for the same reason (Fig. 6b). Both θ and Ψ_s were not correlated with the unexplained decline of K_C in the WW treatment during
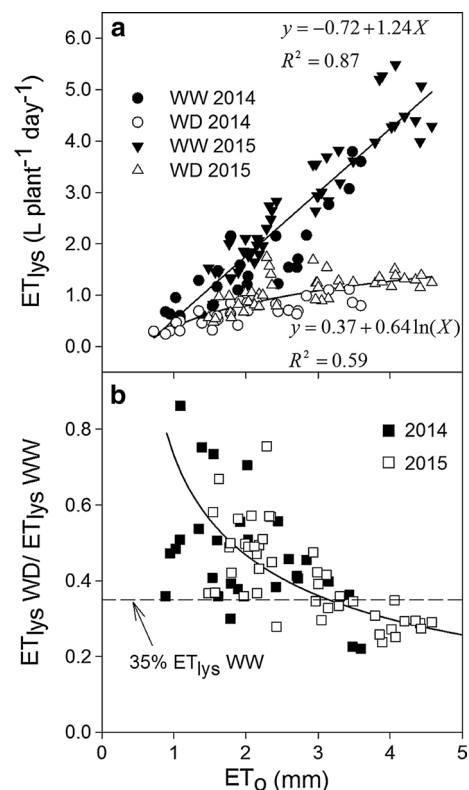

Fig. 5 Lysimeter evapotranspiration (ET_{lys}) as a function of the reference evapotranspiration (ET_O) in the well-watered (WW) and water deficit (WD) treatments (**a**), and the ratio between the two treatments (**b**). Data are the averages of four plants

2014 (in red; Fig. 6). On the other hand, the entire data set of g_s (including WW 2014) was well correlated with K_C, resulting in the highest correlation coefficient ($R^2 = 0.79$). The intercept of the g_s linear regression suggested that even when the transpiration component is 0, soil evaporation will result in a K_C of 0.3.

Discussion

The high correlation between the seasonal ET and the LA, as the one calculated for the measurements during canopy development (Fig. 3a), is supported by previous studies (Williams et al. 2003; Netzer et al. 2009; Picón-Toro et al. 2012). These authors found that under WW conditions, the LA is a good predictor of K_C and suggested practical ideas for its incorporation into irrigation models (Williams and Ayars 2005; Netzer et al. 2009; López-Urrea et al. 2012). It is important to mention that application of deficit irrigation early in the season could lead to a substantial effect on the plant growth (Matthews et al. 1987). Conversely, our results show that under post-veraison WD, restrictions derived from the plant hydraulic resistance were
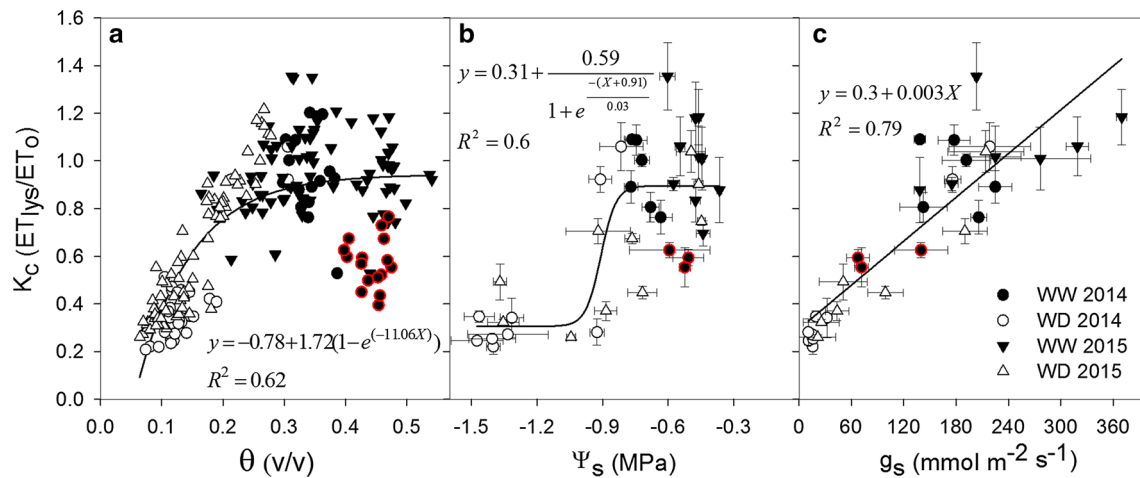
Fig. 6 Crop coefficient (K_C) as a function of the daily average soil water content (θ; **a**), midday stem water potential (Ψ_S; **b**), and stomatal conductance (g_s; **c**) of the well-watered (WW) and water deficit (WD) treatments. Values of unexpected decreases in K_C during the late summer of the WW 2014 treatment are highlighted in *red*. Data are the averages of four plants ±SE

substantially more prominent than LA modification, and led to a significantly lower K_C (Fig. 2). The dominancy of the plant hydraulic resistance over LA was expected, since the downregulation of g_s under WD, up to 40-fold (Fig. 6c), was considerably larger than the modifications of LA. As a consequence, K_C should be modeled with respect to the modifications in plant resistance that the WD imposes. Previous studies have incorporated this "stress factor" (i.e., a fraction that is multiplied with the calculated ET) into their models (Raes et al. 2009; Steduto et al. 2009). Nonetheless, the usage of a constant fraction is probably not accurate, since the stress factor depends on the environmental conditions (Fig. 5).

If deficit irrigation applied through IF provides the plant with its ET ($IR_V = ET_{lys}$), we can expect an apparent steady θ; and indeed, following the initial reduction in θ over the first 6–8 days, the stability of θ suggests that the ET_{lys} of the WD treatment reached an apparent equilibrium with the IR_V. Under field conditions, in which the water holding capacity is much larger than the 40-L lysimeters, the reduction in θ could take a much longer period than 6–8 days (Green et al. 2008). Nonetheless, since the plant hydraulic resistance is expected to grow with the decline in θ, an apparent steady state should be reached once the plant resistance limits the ET to be equal to the IR_V. Accordingly, in the current experiment, after 6–8 days, an apparent steady state was reached, maintaining a relatively constant θ and K_C. The term "apparent" is used to describe the steady state condition, because the change in environmental conditions resulted in a subsequent modification of K_C and θ.

Our results show that the relation between the ET_{lys} of the WW and WD treatments is not linear (Fig. 4).

Therefore, using a constant IF for deficit irrigation scheduling will result in an IR_V that could be lower or higher than the actual ET_{lys}, leading to continuous small fluctuations of θ. The ratio between the ET values in WW and WD conditions depends on ET_O (Fig. 5b), meaning that the evaporative demand determines the relative transpirational sensitivity of deficit-irrigated grapevines. A similar phenomenon was measured by Collins et al. (2010) when comparing the ET of WW and WD plants under different ET_O using sap flow meters. High ET_O will likely drive WD plants to a higher stress degree than WW and as a consequence WD plants will further reduce their transpiration. Therefore, deficit irrigation scheduling according to the IF under high ET_O will probably result in excessive water loads, while under low ET_O, it is probably deficient (compared with the actual ET). The overall ET_{lys} (during long periods) should be equal to the IR_V, but short periods of unusual ET_O might lead to inaccurate irrigation, leaving a margin for optimizing the irrigation volumes. Plants with a large root volume, such as under most field conditions, could probably buffer the deficit or excess irrigation; however, crops that are drip irrigated with high frequency or grown in sandy or shallow soils could be sensitive to several days with extreme ET_O.

The logarithmic behavior of ET_{lys} compared with ET_O in the WD treatment was predicted by Feddes et al. (2001) and is probably the result of stomatal closure under a high vapor pressure deficit (VPD; Pou et al. 2008). High transpiration rates lead to lower Ψ_s and the downregulation of g_s, resulting in a saturation of ET values despite the increased VPD. The differential response of ET_{lys} compared with ET_O in the two treatments is well explained by the model of Sperry and Love (2015). This model assumes that g_s regulation is a function of the "soil-canopy conductance vulnerability

curve," which should be similar in both treatments. Since this function is sigmoidal in nature, increased VPD under WW conditions will maintain Ψ_s close to the upper asymptote, leading to a similar g_s and a linearly growing ET_{lys}. Conversely, increased VPD under WD conditions will drive Ψ_s into the steep slope of the sigmoid, leading to a large reduction in g_s and the saturation of ET_{lys} (Sperry and Love 2015). While the model (Sperry and Love 2015) explains well the qualitative differences between treatments and environments, generalizing it to predict ET_{lys} might prove to be very difficult as g_s regulation largely depends on the soil and genotype (Soar et al. 2006; Tramontini et al. 2014).

This difficulty in calculating reliable estimates of ET based on environmental models highlights the advantage of incorporating direct plant or soil measurements into the models. All of the three measured parameters (θ, Ψ_s, g_s) showed a promising potential for predicting K_C in this study and others (Rana et al. 2004; Williams et al. 2012). Since all three are good indicators for the plant water status (Cifre et al. 2005) and all correspond to one another (Hochberg et al. 2013), the correlation with K_C was expected. However, the nature of the coordination between θ, Ψ_s and g_s highlights the disadvantages of using θ or Ψ_s.

The main control over transpiration—and accordingly over K_C under WD—is the regulation of g_s (van den Honert 1948). Following a water limitation and a reduction of θ and Ψ_s, a combination of hydraulic and chemical signals will downregulate g_s and K_C (Franks 2013). Therefore, we expect K_C to be correlated with θ and Ψ_s as long as water limitation is the key factor in g_s regulation. Previous experiments showed these high correlations in grapevine (Rana et al. 2004; Williams et al. 2012), olives (Ben-Gal et al. 2010) and peach (Mata et al. 1999). However, g_s is not only regulated in response to water limitation, but also by plant development, light, temperature, mesophyll CO_2 concentration, and several other known and possibly unknown factors (Schroeder et al. 2001); accordingly, K_C could be modified without a correspondent change in θ or Ψ_s. Even more so, a reduction of K_C due to factors other than water (for instance, low light) would lead to an increase in both θ and Ψ_s. A good example is the unusual reduction of K_C in the WW treatment during August of 2014 (Fig. 2) that highlighted the potential problem of using θ or Ψ_s to predict K_C (Fig. 6).

On the other hand, the strong linear regression between g_s and K_C (Fig. 6c), even in the 2014 WW treatment, should not come as a surprise. Both parameters are similarly calculated (from ET or transpiration normalized to ET_O or VPD for K_C and g_s, respectively) and physiologically resemble each other. Their good correlation suggests that the instantaneous response of a single leaf at midday provides a good indication of the entire vine daily water use. It is important to mention that in denser canopies with a larger number of shaded leaves, the relationship between g_s and K_C might be different. At the same time, even under denser canopies a strong $K_C \sim g_s$ correlation is expected (Williams et al. 2012). Assuming a similar canopy density, the relation should be similar across genotypes and environments. Conversely, the regression between θ or Ψ_s and transpiration largely varies with soil type, genotype and atmosphere (Rogiers et al. 2009; Tramontini et al. 2014), complicating the ability to generalize transpiration models to different vineyards.

Conclusion

The results provide an insight into the ET of deficit-irrigated grapevines and show their increased relative transpirational sensitivity under high ET_O. Calculating the ET of deficit-irrigated vines as a fraction of the ET of well-watered vines might lead to either over or underestimation of irrigation volumes, and thus, deficit irrigation scheduling should consider its differential response to ET_O. Furthermore, the high correlation between g_s and K_C, and the difficulty in predicting both suggest that the measurement of g_s (both direct and indirect) could provide a reliable estimation for the ET of crops under deficit irrigation regime.

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