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Transpiration efficiency of the grapevine cv. Semillon is tied to VPD in warm climates

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Running Title: Transpiration efficiency in Semillon field vines

Abstract

Water-use efficiency in grapevines is dependent on the aerial and below-ground environment of the plant. Specifically, transpiration efficiency, the ratio of net carbon fixation to water loss, may be influenced by soil moisture and the leaf-to-air vapour pressure deficit (VPD) in the soil-plant-atmosphere continuum. The interactive effect of these abiotic parameters, however, has not been suitably investigated in field-grown grapevines. Accordingly, gas exchange of an anisohydric variety, Semillon, was assessed across a number of vineyards in two warm grape growing regions of NSW to ascertain how soil moisture and VPD interact to affect transpiration efficiency at the leaf level. Leaf gas exchange measurements demonstrated that the rate of transpiration (*E*) was driven by VPD, particularly under high soil moisture. Both high VPD and low soil moisture decreased photosynthesis (*A*) and instantaneous leaf transpiration efficiency (*A/E*). Increased intrinsic leaf transpiration efficiency (*A/g*) in response to drying soil was limited to vines growing in a non-irrigated vineyard. In this site *A/g* was negatively related to vine water status. VPD did not have a substantial influence on *A/g* in any vineyard. While VPD is the main driver for *A/E*, soil moisture is an important determinant of *A/g*. Under high VPD, stomatal closure in Semillon leaves was not substantial enough to suitably curtail transpiration, and as a consequence *A/E* declined. These data indicate that in warm climates, irrigation scheduling of anisohydric varieties must take into account both VPD and soil moisture so that vine water status can be maintained.

Key words: anisohydric, drought responses, evaporative demand, Semillon, stomatal regulation, water relations

Abbreviations: *A*: photosynthesis; ABA: abscisic acid; *A/E*: instantaneous leaf transpiration efficiency; *A/g*: intrinsic leaf transpiration efficiency; *E*: transpiration rate; *g*: stomatal conductance to water vapour; HV: Hunter Valley, MIA: Murrumbidgee Irrigation Area; RAW: readily available water; RH: relative humidity; *Ψ*: plant water status; Ψ_l: leaf water potential; VPD: air vapour pressure deficit.

Introduction

Uncertain and unpredictable water allocations in many warm grape-growing regions has created interest in the development of low water-input irrigation practices (Dry *et al*., 2001; Loveys *et al*., 2004) and the planting of water-use-efficient varieties (Shultz 2003, Gibberd *et al*., 2001; Beis & Patakas, 2010). While plant water uptake is dependent on factors such as rooting profiles and the degree of root-soil contact (McCully & Canny, 1988), transpiration is dependent on atmospheric water demand as well as features such as leaf shading (Cartechini & Palliotti, 1995) and stomatal sensitivity to drying soil through the production of chemical or hydraulic signals (Davies *et al*., 2002; Soar *et al*., 2006). Partial stomatal closure in response to soil water deficit can result in a decrease in transpiration and prevent the formation of embolisms (Tyree & Sperry, 1988). The type and extent of physiological response to drying soils is species and variety dependent and accordingly much research has concentrated on the characterisation and classification of plants in terms of drought tolerance.

While dry soils can result in plant water stress, high VPD can have similar effects (Klepper, 1968; Grantz, 1990) even under conditions of adequate soil moisture. Plant water status often declines around midday, and stomata may close because of the inability of the root system to supply sufficient water to the shoot during periods of high evaporative demand (Tardieu & Davies, 1992; Sperry *et al*., 1993). Stomatal closure is the plant's first line of defence in maintaining its water status. A consequence is that stomatal closure is accompanied with not only decreases in transpiration but carbon assimilation as well, thus affecting transpiration efficiency. Transpiration efficiency at the whole plant level can be defined as the amount of biomass gained per unit of water transpired, while at the individual leaf level it is the ratio of CO_2 assimilation rate (A) per unit of water transpired (E). Intrinsic transpiration efficiency is the ratio between A and stomatal conductance (g) (Condon *et al*., 2002). Because the decline in g and E is often greater than the associated reduction in A (Jones, 1976; Hetherington & Woodward, 2003) an increase in A/E and A/g occurs as g decreases.

Maximal water-use efficiency is a key priority for irrigated viticulture and defining variety specific irrigation strategies is one step towards achieving this aim. It has been established that transpiration efficiency in grapevines is variety dependent (Schultz, 1996; Bota *et al*., 2001, Gibberd *et al*., 2001; Virgona *et al*., 2003; Souza *et al*., 2005). Such varietal differences deserve further exploration because they would be expected to influence the capability of the vine to withstand soil moisture deficits as well as contribute to water saving irrigation techniques such as deficit irrigation and partial rootzone drying.

Understanding how the basic environmental drivers of plant water status, soil moisture and VPD, interact to affect transpiration efficiency is critical to maintaining functional, productive canopies and maximising yield and berry quality with minimal water inputs. Varietal diversity in stomatal control and capability to maintain plant water status under conditions of high evaporative demand and low water availability requires experimentation at the variety level. While genetic variation in instantaneous leaf transpiration efficiency has been studied in regard to soil moisture, little attention has been paid to such variation in response to VPD (Kholova *et al*., 2010) or even more significantly, their interaction.

The focus of this study is *Vitis vinifera* L. grape cv. Semillon, a variety derived from mesic origins with a particular sensitivity to leaf burn when grown in hot, inland regions of Australia. Semillon has high stomatal conductance and transpiration rates compared to a number of other *Vitis vinifera* varieties, and plant water status fluctuates with soil moisture as well as diurnally with VPD (Rogiers *et al*., 2009). Irrigation under high VPD can have inconsistent effects on vine transpiration and in order to develop irrigation strategies for this variety, further information of the interaction of soil moisture and VPD on transpiration efficiency is required. Therefore, the role of VPD on the instantaneous and intrinsic leaf transpiration efficiency of Semillon field vines was surveyed under a range of irrigation systems and soil moistures in the Murrumbidgee Irrigation Area and Hunter Valley, two warm grape-growing regions of NSW.

Materials and Methods

Vineyard sites

The study material encompassed own-rooted Semillon vines grown in four commercial vineyards located in the Murrumbidgee Irrigation Area (34°S, 146°E, Altitude: 119m) and three vineyards in the Hunter Valley (32°S, 151°E, Altitude: 127m). All vines were grown on a double-wire vertical trellis and none were summer-trimmed. Depending on site, the vines were aged from 6 to 60 years. Vineyard characteristics and management practises are outlined in Table 1. Five vineyards were drip irrigated, one was flood irrigated, and one was not irrigated, with irrigation regime during the study following the usual practise of that vineyard. Within each vineyard, three sites were chosen based on an EM 38 survey which delineated a low, intermediate and high EM location. Soil and plant physiological parameters were assessed in the same three sites of each vineyard over three seasons.

At each EM location, Watermark® soil moisture sensors (Irrometer Co., Riverside, CA 92516, USA) were placed at 25, 50, 75 and 100 cm depths directly beneath drippers and wireless resistance block loggers (Model 1H, Hussat, Griffith, NSW) transmitted the outputs to a nearby base station for GSM radiolinking to a central computer that posted real-time data on the web. The soil water content at each depth was used to calculate the proportion of stored readily available water between each measured depth. RAW is defined as the volume of water available to plants in the root zone from field capacity (-10 kPa) to -60 kPa. The proportion of readily available water (%RAW) in the profile was then determined by summing the stored readily available water between each measurement depth and normalizing this value by the RAW.

A screened weather station was placed at canopy height within each vineyard. It was equipped with a humidity and temperature probe (Intercap HMP50, Vaisala, Hawthorn, Vic) and logged at half hourly intervals.

Gas exchange measurements

Midday photosynthesis (*A*), transpiration (*E*) and stomatal conductance (*g*) were measured using a portable LI6400 gas exchange system (Li-Cor Corporation, Lincoln, NE, USA) fitted with a red-blue external light source set at 900 µmol m^{-2} s^{-1}. The equations used to calculate *A* and *E* were those derived from von Caemmerer & Farquhar, 1981). Chamber temperature was not controlled to allow instantaneous measurements under natural conditions and it was covered in shade-cloth to prevent heating by the sun. A fixed, high flow rate with no dessicant scrubbing allowed minimal equilibration time once the leaf was installed into the cuvette. A long tube with a buffer volume was used to achieve steady reference CO_2 concentrations. Net CO_2 assimilation and transpiration rate were monitored continuously and logged when they reached steady state. Measurements were taken on two leaves on each side of the canopy of each of four vines at each location within the vineyard at selected times throughout the annual growth cycle. These same four vines were re-visited over three seasons. Gas exchange measurements were correlated to VPD data obtained from the weather stations within half hour and RAW data within one hour of the gas exchange measurements.

Water potential measurements

Leaf water potential measurements (Ψ_l) were carried out with a Scholander pressure chamber (ICT international, Armidale, NSW) fitted with a Model 3015G4 specimen holder. Two mature leaves were taken from each of four vines within each of the three EM locations within the vineyards and recorded at the same times that gas exchange measurements were taken.

Data analysis

Data were analysed using multiple linear regression with GenStat statistical software, Version 11 (VSN International, UK), and SigmaPlot graphing and statistics software (SPSS Inc., Chicago, Illinois). Results of the statistical analyses are presented in the tables or figure legends.

Results

Cumulative data over seven vineyards and three seasons indicate that photosynthesis, transpiration and instantaneous leaf transpiration efficiency of Semillon vines was affected by VPD and RAW (Figure 1). *A* was highest at low VPD and high RAW, but declined 7-fold when available soil moisture was very low and VPD rose to levels above 4 kPa. VPD explained most of the variance (18%) while RAW contributed less than 1% of the variance. *E* was greatest in vines growing in a full soil moisture profile when VPD was high (Figure 1). The magnitude in response of *E* to VPD was lessened under dry soils. Again, VPD explained most of the variance (14%) in *E* while RAW contributed less than 1%. Similar to *A*, *A/E* was highest at low VPD (10-14 µmol CO_2 mmol H_2O^{-1}) and declined to approximately 2 µmol CO_2 mmol H_2O^{-1} at VPDs of 4 kPa in very dry soils (Figure 1). Despite the significant interaction of VPD and RAW on

A/E, VPD explained nearly all the variance (44%), with less than 1% attributed to RAW.

An analysis of the individual vineyards in both grape growing regions revealed similar curvilinear relationships of *A/E* with VPD (Figure 2). In both the drip irrigated and flood irrigated vineyards of the MIA, instantaneous leaf transpiration efficiency decreased four fold from 8 µmol CO_2 mmol H_2O^{-1} at VPD of less than 1 kPa to 2 µmol CO_2 mmol H_2O^{-1} at 4 kPa. In the drip irrigated and unirrigated vineyards of the Hunter Valley, however, instantaneous leaf transpiration efficiency was higher and reached approximately 12 µmol CO_2 mmol H_2O^{-1}, despite similar VPDs, and declined to 2 µmol CO_2 mmol H_2O^{-1}.

Averaged over the three seasons, *A/E* varied 3.5-fold between the seven sites, ranging from 1.8 to 6.3 µmol CO_2 mmol H_2O^{-1} (Table 2). This was due mostly to differences in VPD. Average VPDs at the time of measurement varied more than two fold (1.3 to 2.9 kPa) across these seven sites and were highly correlated (r^2 = 0.82) with A/E, while RAW ranged from 82% to less than 0% but was not correlated with A/E. It was also apparent there were regional differences in *A* and *A/E* (Table 3). Mean *A* was 1.2 fold higher and *A/E* was almost double in the HV compared with the MIA. These regional differences in gas exchange were accompanied by lower average VPD in the HV (1.5 compared to 2.4 kPa in the HV and MIA, respectively) as well as higher soil moisture (48.6 in the HV as compared to 20.1% RAW in the MIA).

Cumulative data over the three years indicate that photosynthesis was positively correlated to leaf water potential in a linear relationship, however only 24% of the variance was accounted for (Figure 3). Transpiration had a Gaussian-shaped relationship with midday Ψ_l though this only accounted for 10% of the variance, with the greatest range in *E* occurring between -1.0 to 1.5 MPa (Figure 3). *A/E* increased in a curvilinear relationship (Figure 3) with midday Ψ_l increasing three fold as Ψ_l increased from -2.0 MPa to -0.3 MPa and 17% of the variance in *A/E* was accounted for. The variance was particularly extensive at less negative Ψ_l and ranged from nearly 0 to 15 µmol CO_2 mmol H_2O^{-1} at -0.5 MPa.

While there were vineyard differences in intrinsic leaf transpiration efficiency (*A/g*) (1.8-fold, Table 2) as well as regional differences (15% higher in the HV, Table 3), combined data of the seven sites revealed that VPD and soil moisture accounted for only small amounts of variation (less than 1% individually, and less than 5% in combination) on *A/g*. The unirrigated vineyard of the HV was the only site with significant relationships of *A*, *g* and *A/g* with RAW (Figure 4). Compared to the other sites, this unirrigated vineyard was by far the driest (Table 2). *A* doubled to 12 µmol CO_2 $m^{-2}s^{-1}$ and *A/g* halved to 50 µmol CO_2 mol H_2O^{-1} as RAW approached positive values. In this same vineyard there was also a significant linear relationship of leaf water potential with *A*, *g* and *A/g* (Figure 5). Photosynthesis halved over a range of -0.5 MPa to -2.2 MPa while *g* declined six fold. *A/g*, however, increased linearly by five fold (from 20 to 100 µmol CO_2 mol H_2O^{-1}) over this range in Ψ_l.

Discussion

Response of *A/E* to VPD and soil moisture

In this study, gas exchange of Semillon vines was assessed under a range of irrigation strategies in two warm grape growing regions with similar temperatures but differing VPDs. As expected, optimal photosynthesis occurred under ample soil moisture and low evaporative demand, while transpiration tended to be greatest under full moisture and high VPD. Therefore, it was also not surprising to find that *A/E* was most favourable under low VPD. A study of other *V. vinifera* varieties, Riesling and Silvaner, highlighted a similar curvilinear decline in *A/E* to rising VPD (Düring, 1987) and in the drought-tolerant hybrid Richter-110, *A/E* also decreased as VPD increased in well-watered and severely water stressed plants (Pou *et al*., 2008).

When compared to soil moisture, VPD explained a greater proportion of the variance in *A/E*. While declining soil moisture often decreases *A*, *A/E* can increase as has been observed in Tempranillo (Cuevas *et al*., 2006) and Richter-110 (Pou *et al*., 2009), or decrease as in Aleluya vines (Bota *et al*., 2001). The absence of an increase in *A/E* with drier soil in our Semillon vines may be the result of a stomatal limitation or a loss in photosynthetic capacity (Flexas *et al*., 2002). As leaf temperature increases due to a decline in evaporative cooling under reduced *E* in drying soils, photosynthesis can be inhibited through decayed electron transport rate and reduced RuBP regeneration capacity (Medrano *et al*., 2003). The permanent desiccation that occurs around the leaf margins when Semillon vines are grown under dry soil conditions is potentially accompanied by loss in photosynthetic capacity of the entire leaf surface. Further studies, however, are required to verify this.

Based on the strong relationship between *A/E* and VPD, the striking regional differences in *A/E* of our study were most likely due to the lower VPD of the HV relative to the MIA. Even the unirrigated site of the HV, the vineyard with the lowest soil moisture levels in this study, had more favourable *A/E* compared to the MIA vineyards, consistent with the dominance of VPD on the *A/E* response. These regional differences indicate that VPD is an important determinant of leaf transpiration efficiency in Semillon.

Response of *A/g* to VPD and soil moisture

The three-season *A/g* average for all sites varied two-fold between the seven vineyards. *A/g* was highest in the unirrigated site (72 µmol CO_2 mmol H_2O^{-1}) but in the irrigated sites it ranged from 39 to 68 µmol CO_2 mol H_2O^{-1}. A survey of 22 irrigated varieties grown in a semi-arid climate indicated a range in *A/g* of 38 to 74 µmol CO_2 mmol H_2O^{-1} (Bota *et al.*, 2001). Therefore, the range of *A/g* in one variety when grown across different environmental conditions can be as extensive as the range across a number of varieties grown under similar conditions. Furthermore, our data indicate that even within a particular vineyard, *A/g* can vary extensively. In the unirrigated site, for example, instantaneous *A/g* values ranged between 60 to 120 µmol CO_2 mmol H_2O^{-1} and were negatively correlated to soil moisture. A similar extent of variation was evident in the irrigated vineyards.

Because responsiveness of *g* and *A/g* to soil moisture was highest at the unirrigated site in this study, it appears that severely dry soils were required to induce a stomatal response in Semillon vines. This suggests that rather than the aerial microclimate, it is the root environment which has tight control over *g*. Root signal production, in particular ABA, in response to drying soils has been well documented in grapevines (Loveys, 1984 a and b; Correia *et al*., 1995; Stoll *et al*., 2000) and xylem sap ABA concentrations of Semillon vines grown under moderate water stress were comparable to that of other varieties grown under similar conditions (Rogiers *et al*., 2009). Therefore, it is likely that the dry soils of the unirrigated vineyard invoked ABA synthesis in the roots, and after transport to the shoots, resulted in stomatal closure. Consistent with this, the role of ABA in transpiration efficiency was highlighted in a study on transgenic tomatoes where overproduction of ABA increased *A/g* (Thompson *et al*., 2007).

There were no significant relationships between *A/g* and VPD in any of the vineyards in our study. Consistent with this conclusion, *A/g* was lower in the MIA than in the HV, despite nearly twice the VPD at the time of measurement. Under conditions of high soil moisture, high VPD can result in plant water stress if water uptake and transport cannot match transpiration. The lack of correlation between leaf water potential and *g* in irrigated vineyards suggested *g* and *A/g* of Semillon vines were also not particularly responsive to plant water status. By contrast, in the unirrigated vineyard, *g* and *A/g* were highly correlated to plant water status and, therefore, stomatal responses appear to be mediated more by soil moisture through plant water status than by VPD.

Implications for managing Semillon

Maximising irrigation and transpiration efficiency of anisohydric grapevine varieties in warm grape growing regions is not a simple task. Because high VPD and low soil moisture had a negative impact on *A/E* of Semillon in this study, it appears that this variety is better suited to mild climates where extremes in temperatures or extended periods of drought are not common. When grown in warm regions with high evaporative demand, Semillon requires a consistent and reliable water source to aid in leaf cooling and to avoid leaf burn. However, care must be taken to avoid excessive shoot growth which can compete with berry development and, in humid regions, add to disease pressure. Planting in a north-south row orientation can aggravate leaf damage through exposure of the western canopy to the afternoon sun. Vines planted on soils with good water holding capacities, under drip irrigation accompanied with diligent soil moisture monitoring, is highly recommended.

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Tables

Table 1.

Table 1: Block size, row orientation, vine age, average yield, ground cover and soil texture of Semillon sites assessed in the Hunter Valley and MIA.

Vineyard/Region	Block Size (acres)	Row Orien-tation	Vine Age	Average Yield (t/acre)	Ground cover	Soil Texture
Drip A/MIA	4	SW-NE	35	10	Volunteer species	Silty clay to sandy clay
Drip B/MIA	16	N-S	6	18	Volunteer species	Sandy clay loam
Drip C/MIA	14	E-W	10	6	Volunteer species	Sandy clay
Flood/MIA	20	SE-NW	10	7.5	None	Silty clay
Drip A/HV	12	SE-NW	25	5	Volunteer species in alternate rows	Sandy clay or sandy loam
Drip B/HV	10	E-W	60	2.5	Volunteer species in alternate rows	Silty clay or loamy sand to sandy clay
Unirrigated/HV	10	N-S	15	4	None	Loamy sand to sandy loam

Table 2. RAW (%), VPD (kPa), *A* (µmol CO_2 $m^{-2}s^{-1}$), *E* (mmol H_2O $m^{-2}s^{-1}$), *g* (mol H_2O $m^{-2}s^{-1}$), *A/E* (µmol CO_2 mmol H_2O^{-1}) and *A/g* (µmol CO_2 mol H_2O^{-1}) of seven vineyards averaged over three seasons.

Vineyard/Region	RAW	VPD	*A*	*E*	*g*	*A/E*	*A/g*
Drip A/MIA	81.9	2.07	8.93	3.55	0.200	3.16	52.5
Drip B/MIA	32.6	2.86	7.71	4.91	0.212	1.81	38.8
Drip C/MIA	37.7	2.26	8.35	2.75	0.181	3.49	52.2
Flood/MIA	34.0	2.62	7.67	2.49	0.132	3.36	68.0
Drip A/HV	71.0	1.72	9.62	1.33	0.164	6.35	64.5
Drip B/HV	35.0	1.26	10.64	2.20	0.195	5.97	57.1
Unirrigated/HV	-36.3	1.44	9.58	2.03	0.160	5.79	71.4
P<	0.001	0.001	0.001	0.001	0.001	0.001	0.001
SED	3.8	0.08	0.3	0.13	0.008	0.21	2.0

Table 3. Regional differences in RAW (%), VPD (kPa), and Semillon *A* (µmol CO_2 $m^{-2}s^{-1}$), *E* (mmol H_2O $m^{-2}s^{-1}$), *g* (mol H_2O $m^{-2}s^{-1}$), *A/E* (µmol CO_2 mmol H_2O^{-1}) and *A/g* (µmol CO_2 mol H_2O^{-1}) as averaged over three seasons.

Vineyard/Region	RAW	VPD	*A*	*E*	*g*	*A/E*	*A/g*
MIA	48.6	2.44	8.2	3.3	0.178	3.05	54.4
HV	20.1	1.48	10.0	2.1	0.174	6.05	63.9
P<	0.001	0.001	0.001	0.001	ns	0.001	0.001
SED	3.0	0.05	0.2	0.1	0.006	0.14	1.4

Figure Legends

Figure 1. Photosynthesis (*A*) (r^2=0.19, $p<0.001$), transpiration (*E*) (r^2=0.15, $p<0.05$) and instantaneous leaf transpiration efficiency (*A/E*) (r^2=0.45, $p<0.001$) as a function of VPD and RAW. Data represent point measurements in three locations within each of seven vineyards across three seasons in the MIA and Hunter Valley, NSW.

Figure 2. Instantaneous leaf transpiration efficiency (*A/E*) as a function of VPD in a drip or flood irrigated vineyard of the MIA and in a drip or unirrigated vineyard of the Hunter Valley.

Figure 3. Photosynthesis ($p<0.001$, r^2=0.24), transpiration ($p<0.001$, r^2=0.10), instantaneous leaf transpiration efficiency (*A/E*) ($p<0.001$, r^2=0.17) as a function of midday leaf water potential (Ψ_l). Data represent point measurements in three locations within each of seven vineyards across three seasons in the MIA and Hunter Valley, NSW.

Figure 4. Photosynthesis (*A*) ($p<0.001$, r^2=0.65), stomatal conductance (*g*) ($p<0.001$, r^2=0.62) and intrinsic leaf transpiration efficiency (*A/g*) ($p<0.001$, r^2=0.62) as a function of RAW in an unirrigated vineyard of the Hunter Valley.

Figure 5. Photosynthesis (*A*) ($p<0.001$, r^2=0.45), stomatal conductance (*g*) ($p<0.001$, r^2=0.52) and intrinsic leaf transpiration efficiency (*A/g*) ($p<0.001$, r^2=0.56) as a function of midday leaf water potential (Ψ_l) in an unirrigated vineyard of the Hunter Valley.