Modelling leaf photosynthetic and transpiration temperature-dependent responses in Vitis vinifera cv. Semillon grapevines growing in hot, irrigated vineyard conditions

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Abstract

Background and aims
Grapevines growing in Australia are often exposed to very high temperatures and the question of how the gas exchange processes adjust to these conditions is not well understood. The aim was to develop a model of photosynthesis and transpiration in relation to temperature to quantify the impact of the growing conditions on vine performance.

Methodology
Leaf gas exchange was measured along the grapevine shoots in accordance with their growth and development over several growing seasons. Using a general linear statistical modelling approach, photosynthesis and transpiration were modelled against leaf temperature separated into bands and the model parameters and coefficients applied to independent datasets to validate the model.

Principal results
Photosynthesis, transpiration and stomatal conductance varied along the shoot, with early emerging leaves having the highest rates, but these declined as later emerging leaves increased their gas exchange capacities in accordance with development. The general linear modelling approach applied to these data revealed that photosynthesis at each temperature was additively dependent on stomatal conductance, internal CO2 concentration and photon flux density. The temperature-dependent coefficients for these parameters applied to other datasets gave a predicted rate of photosynthesis that was linearly related to the measured rates, with a 1:1 slope. Temperature-dependent transpiration was multiplicatively related to stomatal conductance and the leaf to air vapour pressure deficit and applying the coefficients also showed a highly linear relationship, with a 1:1 slope between measured and modelled rates, when applied to independent datasets.

Conclusions
The models developed for the grapevines were relatively simple but accounted for much of the seasonal variation in photosynthesis and transpiration. The goodness of fit in each case demonstrated that explicitly selecting leaf temperature as a model parameter, rather than including temperature intrinsically as is usually done in more complex models, was warranted.

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Introduction

Models of photosynthesis have been in vogue since Farquhar et al. (1980) first published their biochemical model and much progress in the biochemical understanding of photosynthesis has followed (von Caemmerer 2000; Farquhar et al. 2001). Photosynthesis is recognized to be limited by the two processes of ribulose 1,5-bisphosphate (RuBP) carboxylation and RuBP regeneration, and many models of photosynthesis incorporate these limitations as an intrinsic part (Amthor 1994; Hikosaka 1997; Le Roux et al. 1999; Bown et al. 2007). Other photosynthetic models are based on the photosynthetic light response curve for individual leaves (Battaglia et al. 1996; Pachepsky and Acoc 1996; Thornley 1998; Gómez et al. 2005) while other models are extended to the whole canopy using the physics of light attenuation to extend the photosynthetic light responses (Reynolds et al. 1992; Sands 1995; Cannell and Thornley 1998; Kull and Krujlt 1998; Rauller et al. 1999). Further still, the canopy has been partitioned into sun and shade leaves for some models (De Pury and Farquhar 1997; Dai et al. 2004; Greer et al. 2004). Although the effect of temperature is usually inherent in these models, it is less common for the effect of leaf temperature over the wide range that plants can experience to be explicitly investigated in the models.

The processes of photosynthesis are intrinsically related to temperatures, photon flux densities (PFD) and CO₂ concentrations (both ambient and internal) prevailing at the time and including stomatal conductance, these parameters have been incorporated into some dynamic models of photosynthesis (Lieth and Pasian 1990; Kim and Lieth 2003; Noe and Giersch 2004; Caballé et al. 2011). These models often also couple photosynthesis with stomatal conductance and transpiration (Collatz et al. 1991; von Stamm 1994; Kim and Lieth 2003; Keenan et al. 2010). In turn, there are various ways to model stomatal conductance, notably that of Ball et al. (1987) relating stomatal conductance to assimilation, relative humidity (RH) and the CO₂ mole fraction of the air, and the modification by Leuning (1995) involving replacing the RH term with a hyperbolic function of vapour pressure deficit (VPD). In addition, a multiplicative model relating stomatal conductance to RH, water status, PFD and air temperature has also been proposed (Fernández et al. 2006; Op de Beeck et al. 2010b) and to PFD and VPD (Noe and Giersch 2004). In contrast, transpiration is simply modelled as a function of stomatal conductance and leaf-to-air VPD and the effect of leaf temperature is essentially encapsulated in determining the saturated vapour pressure of the leaf (Kim and Lieth 2003; Yu et al. 2004).

Semillon grapevines are grown in many parts of Australia and are an economically important crop for the different regions (Australian Bureau of Statistics (ABS) 2005). This cultivar is known to have high rates of transpiration (Rogiers et al. 2009) and, therefore, irrigation is sometimes required for growth of the vines. The vines are also grown in climates where summer air temperatures readily exceed 35 °C (Gladstones 1992). These high-temperature exposures, sometimes >40 °C, are known to reduce photosynthesis of grapevine leaves (Kriedemann 1968; Ferrini et al. 1995; Yu et al. 2009; Zsófi et al. 2009). In part, these reductions in photosynthesis are related to stomatal limitation and, generally, photosynthetic recovery occurs within a few days after a heat treatment (Sepúlveda and Kliwer 1986; Ferrini et al. 1995; Soar et al. 2009). A pot trial on Semillon vines (Greer and Weston 2010) showed a reduction in photosynthesis after a heat event was caused by stomatal limitation but photosynthesis also recovered over a 10- to 12-day period. However, it is not known if stomatal limit photosynthesis to the same extent in vineyard conditions, especially at the high temperatures to which the vines are exposed.

Thus, the objective of the present study was to measure gas exchange of Semillon leaves throughout the growing season under the prevailing high-temperature conditions and then to model photosynthesis and transpiration in relation to stomatal conductance, internal CO₂ concentration, PFD, VPD and leaf temperature. The approach adopted was to use a statistical general linear model to assess which of these effects, as well as physical and biological effects such as time of day, day of season, leaf position, shoot position and vine, were significant. Temperature-dependent coefficients derived from the model for each parameter were then applied to independent datasets to assess the goodness of fit and validation of the model over a range of leaf temperatures.

Materials and methods

Plant material and growth conditions

This project was undertaken in a commercial vineyard in the Riverina, NSW, Australia, over the growing season of 2008/09. Some additional measurements were collected in the 2007/08 and 2009/10 growing seasons. The vines (Vitis vinifera L. cv. Semillon) were not grown on a rootstock and were planted in north–south rows with 3.5 m spacing between rows and 1.8 m spacing between the vines. The vines were grown with a vertical shoot position trellis and catch wires were lifted from about canopy closure to constrain the shoots semi-vertically. Apart from a fungicide spray programme, the
selected vines had no other management practices imposed. Drip irrigation was used, with drippers at 0.6-m spacing supplying water and nutrients at a rate of 2.4 L h\(^{-1}\) for 12 h per week prior to ripening and 24 h per week after ripening started. Midday water potentials in midsummer averaged \(-1.6 \pm 0.3\) MPa and no indications of water stress were evident. Budbreak occurred at about 25 September and harvest of the grapes occurred on 12 February.

**Gas exchange measurements**

Throughout the growing season, commencing on 9 October 2008 (14 days after budbreak, DAB) and finishing on 18 March 2009 (174 DAB), photosynthesis and associated gas exchange measurements (stomatal conductance, \(g_s\); transpiration, \(E\); internal CO\(_2\) concentration, \(c_i\)) were made at 7- to 14-day intervals with an open gas exchange system (LCA4, ADC BioScientific, Hoddesdon, UK). On each occasion, measurements were conducted on all leaves of each of two selected shoots of three vines in each of six whole panels (three vines per panel), totalling 36 shoots. In each case, all leaves present that were >25 mm were measured on each occasion; thus, an increasing number of leaves were measured, starting with about five leaves and finishing with over 30 leaves at the end of the measurements. In all cases, gas exchange was measured between 0900 and 1600 h on the leaves in their natural orientation, and the PFD, leaf temperature and leaf-to-air vapour pressure deficit (VPDL) were measured concurrently. Leaf temperature was measured with a thermocouple appressed to the lower leaf surface within the gas exchange chamber.

**Modelling procedure**

Once all the data were collected and assembled into a spreadsheet, leaf temperatures and all associated data were selected using a sorting procedure with SAS 9.13 (SAS Institute, Inc., Cary, NC, USA) into 5 \(\pm\) 2.5 \(^\circ\)C bands from 20 to 45 \(^\circ\)C. Photosynthesis (\(A\)) was modelled as a function of stomatal conductance (\(g_s\)), internal CO\(_2\) concentration (\(c_i\)) and PFD for each temperature band. A general linear modelling approach using the GLM procedure of SAS 9.1 (SAS Institute) was used to model photosynthesis to equation (1):

\[
A = f\left(g_s, c_i, \text{PFD}\right)
\]

Similarly, transpiration (\(E\)) was modelled as a function of stomatal conductance and VPD\(_L\) as:

\[
E = f\left(g_s, \text{VPD}_L\right)
\]

The models were fitted to all data across the growing season and coefficients for each parameter \((T_p, T_g, T_c)\), including an intercept term \((T_o)\), were derived from these analyses for each temperature band. These coefficients were then analysed as a function of leaf temperature, using the GLM procedure in SAS.

A second dataset of photosynthetic and transpiration rates, stomatal conductances, internal CO\(_2\) concentrations, PFDs, VPDs and leaf temperatures were measured over the 2009/10 growing season from 22 October 2009 until 2 February 2010. The same numbers of vines and shoots (although different plants) were used and the same methods of measuring gas exchange. These data were then used to independently evaluate the model in equations (3) and (4) using the model parameters and encompassing their specific temperature coefficients derived from the comparable dataset in 2008/09.

**Results**

**Seasonal changes in gas exchange along the shoot**

Early in the growing season, photosynthesis, transpiration and stomatal conductance (Fig. 1) all increased in leaves along the shoot, at least to position 10–12, where
net photosynthesis was maximal at \( \sim 15 \text{ mmol m}^{-2} \text{s}^{-1} \)
while conductance peaked at \( \sim 0.16 \text{ mol m}^{-2} \text{s}^{-1} \) and
transpiration at 8–9 mmol m\(^{-2}\) s\(^{-1}\) at similar shoot
positions. Reduced rates in each leaf at the higher shoot positions up to about position 17 probably reflected
leaves not being completely developed. This was con-
firmed later in the season (Fig. 2), when leaves up to
about this same position had the highest rates, although
in all cases these had declined to about 12 \( \mu\text{mol m}^{-2} \text{s}^{-1} \)
of CO\(_2\) fixation, 0.10 mol m\(^{-2}\) s\(^{-1}\) of stomatal conduct-
ance and 4 mmol m\(^{-2}\) s\(^{-1}\) of water transpired.

Again, rates in leaves at higher positions (20–25)
declined because of incomplete development and yet
again, later in the season, this same cohort of leaves
now had the highest rates (Fig. 3). Nevertheless, the
maximum rates of photosynthesis in these leaves were
lower than in the mid-season and across the whole
shoot rates had declined markedly, presumably from
some senescence now occurring. In contrast, stomatal conductance and transpiration, especially, did not show
a comparable decline in these late-emerging leaves
and, in fact, had the highest rates for the whole shoot.

Temperature dependency of gas exchange attributes

Averaged net photosynthesis over all leaves from
throughout the growing season but divided into the six
leaf temperature bands (Fig. 4A) showed an optimum
between 25 and 30°C. With further increases in leaf
temperature, there was a linear decline in rates such
that at 45°C, net photosynthesis was reduced by 30%.
It was also notable that a sharper decrease in photosyn-
thesis occurred when the leaf temperature decreased to
20°C and, at 35% reduction, was greater than occurred
with the high temperatures.

By contrast, mean transpiration rates increased expo-
nentially with increasing leaf temperature (Fig. 4B),
particularly above 35°C, and the increase in rates of
transpiration between 20 and 45°C was \( > 4 \)-fold. Thus,
transpiration was strongly temperature dependent.
However, it was not related to mean stomatal conduct-
ance, which was not especially temperature dependent
(Fig. 4C) over the whole temperature range. Neverthe-
less, there were significant differences in stomatal conductance between the different leaf temperatures.
Internal CO₂ concentration did vary with temperature (Fig. 4D) and highest at the low temperatures and lowest at 30–35 °C (by 30 %) with a slight (16 %) increase thereafter at the highest temperatures. Thus, the internal CO₂ concentration was also strongly temperature dependent.

Assessing the model: assimilation

From the GLM procedure, neither leaf position along the shoot, shoot position on the vine, vine number, time of day nor day of season was significant in any of the analyses. Consequently, all these were excluded from further analyses and the full fit to equation (1) but with leaf temperature initially included indicated a highly significant temperature effect \( P < 0.0001 \). Thus, the data were re-analysed by fitting equation (1) to each cohort of data in the separate leaf temperature bands. In all cases, stomatal conductance, internal CO₂ concentration and PFD were all highly significant where the \( r^2 \) for the fit to an additive model for each leaf temperature ranged from 0.75 to 0.90 (Table 1). By contrast, a multiplicative model, assuming interactions between all parameters, gave \( r^2 \) from 0.15 to 0.58. Though all highly significant, the model accounted for much less of the variance in assimilation than the additive model and, therefore, was not adopted. Similarly, a model incorporating the non-linear hyperbolic tangent relationship between photosynthetic assimilation and PFD (Greer and Halligan 2001) gave no additional account of the variance in assimilation. Thus, the simpler additive model was adopted:

\[
A_{\text{fit}} = f(T_i + g_s \times T_g + c_i \times T_c + \text{PFD} \times T_P)
\] 

where \( A_{\text{fit}} \) was the fitted rate of photosynthetic assimilation to the temperature-dependent function.

The coefficients, including an intercept term, for each parameter in the model across the different leaf temperatures (Fig. 5) were not uniform in their response.
The intercept coefficient declined in a general linear pattern with increasing leaf temperature. The coefficient for stomatal conductance increased in a more or less linear pattern to leaf temperature, with a slight drop at 35 °C but significantly (P < 0.001) higher at high than low temperatures. The coefficient for internal CO₂ concentration decreased from 20 to 25 °C (become less negative) and varied only slightly up to 40 °C but then increased sharply at 45 °C and again there were significant differences between temperatures. In contrast, the coefficient for PFD was the most responsive to temperature, increasing markedly between 20 and 30 °C, but thereafter declining more or less consistently with increasing leaf temperature and differences were significant.

### Model fitting: assimilation

The application of the additive assimilation model and coefficients to a separate dataset from the 2009/10 growing season indicated that a highly significant (P < 0.0001) linear relationship occurred between the measured and modelled rates (Fig. 6). This relationship accounted for 80% of the variance in modelled assimilation. The fitted line had a slope of 1.104 ± 0.008 μmol μmol⁻¹, thus very close to a 1:1 relationship, suggesting a good fit to the model. A smaller dataset from the 2007/08 growing season was also evaluated and the fitted line had a slope of 0.981 ± 0.019 μmol μmol⁻¹ and an r² of 0.817 (not shown), thus a comparable fit of the model to the 2009/10 dataset. These analyses suggest that the overall fit was very good, demonstrating that the parameters and temperature coefficients were readily translatable to independent datasets.

### Assessing the model: transpiration

The GLM procedure was applied to all the transpiration data from the 2008/09 growing season and no effect of leaf position, time of day or day of year was significant. There was, however, a significant effect of temperature (P < 0.001) and, therefore, a separate fitting of the model was applied to each temperature. An additive model fitting stomatal conductance and VPD₈ to the transpiration data was highly significant in all cases and accounted for 96–98% of the variance. However, an interactive model, whereby transpiration was modelled with the product of stomatal conductance and VPD₈, gave an r² > 0.99 in all cases and was, therefore, adopted. The specific model used was as follows:

\[
E_{\text{fit}} = f(T_i + g_s \times T_{sv} \times \text{VPD}_8)
\]

where \(E_{\text{fit}}\) was the fitted estimate of transpiration and \(T_{sv}\) was the coefficient for an interaction between stomatal conductance and VPD₈ in the model.

The coefficients, including the intercept term, were strongly affected by leaf temperature (Fig. 7), both increasing in a generally linear pattern as leaf temperature increased.

### Model fitting: transpiration

The application of the interactive transpiration model to the 2009/10 dataset indicated a highly significant (P < 0.0001) linear relationship between the measured and modelled rates (Fig. 8), with an overall slope of 0.981 ± 0.002 mmol mmol⁻¹, that is close to 1:1 and accounting for 97% of the variance. Thus, the model appeared to account extremely well for the changes in transpiration across the 2009/10 growing season.

### Discussion

The present study of gas exchange of Semillon leaves over the growing season revealed that both photosynthesis and transpiration varied along the shoots in accordance with their expansion and development. Earliest emerging leaves had the highest rates of photosynthesis and transpiration, and these were achieved early in the growing season. As the season progressed, rates of photosynthesis declined in the basal leaves and increased in leaves towards the apical meristem. It was notable, however, that the leaves appearing in the mid- and late season did not reach the highest rates of photosynthesis and transpiration that were observed in the early emerging leaves. This suggested that some ontogenetic factor might have been at play, where the early-forming leaves are photosynthetically most active because of vines being heterotrophic at this stage and
dependent on carbon reserves (Goffinet 2004; Field et al. 2009). A similar conclusion was reached for the early-emerging leaves on Actinidia deliciosa vines and elsewhere (Catský and Šesták 1996; Greer and Jeffares 1998; Suriyagoda et al. 2010). Although transpiration followed a pattern similar to photosynthesis, it is much harder to suggest a reason for this except that high transpiration rates might support transport of carbon assimilates from the roots to the leaves and shoot apical meristem. However, it was also clear that all changes in photosynthesis and transpiration were highly correlated with stomatal conductance. Stomatal conductance is also known to change with leaf development, increasing initially but generally declining with leaf age (Bogaert and Lemeur 1994; Suriyagoda et al. 2010; Salmon et al. 2011) as shown here for the Semillon leaves.

However, from the modelling of photosynthesis it was uncertain in statistical terms that there was a role of leaf development in photosynthetic capacity of the leaves. Leaf position, time of day and day of season were not significant terms in the model, which suggested that differences in photosynthesis along the shoot and during the season were almost entirely accounted for by leaf temperature, stomatal behaviour, internal CO₂ concentration and PFD. The model generally accounted for 80–90 % of the variance in photosynthesis across the various temperature bands, but it was noteworthy that stomatal conductance accounted for ≏ 55 % of the variance at lower temperatures but 80 % at very high temperatures. This conforms to the well-established linear dependence of photosynthesis on stomatal conductance (Wunsche et al. 2000; Caballé et al. 2011), although at high gs the response can be non-linear (Williams 2012). In contrast, although photosynthesis was negatively correlated with internal CO₂ concentration (see also Caballé et al. 2011), the percentage of the variance accounted for declined from ≏ 35–45 % at 20–25 °C to 15–20 % at 40–45 °C. Across all leaf temperatures, the
PFD accounted for <10 % of the variance in the model and suggesting that the leaves were generally exposed to saturating PFDs during measurements, even though basal leaves were exposed to PFDs of ~200–400 mu;mol m^-2 s^-1 from mid-season. This might also explain why a more complex model incorporating the non-linear relationship between photosynthesis and PFD did not improve the fit of the model. Nevertheless, the simple three-parameter model was successfully applied to the independent datasets of the 2007/08 and 2009/10 growing seasons, and the fit accounted for 80 % of the variance. Furthermore, the slope of the line fitted between the measured and modelled rates of photosynthesis gave a slope close to 1:1, which was another indication of the goodness of fit. This compares with the multiplicative PFD model of Fernández et al. (2006) for Festuca pallescens, which accounted for 86.5 % of the variance, and the PFD-based model of Caballé et al. (2011) for the same species and which accounted for 82 % of the variance. Similarly, the more extensive biochemical model of Kim and Lieth (2003) for rose leaves gave a similar slope and accounted for 96 % of the variance, while for a range of crops, shrubs and trees, both more extensive biochemical and leaf models gave variances from 50 to 85 % (Gao et al. 2004). The biochemical-leaf model of Gouasmi et al. (2009) and Op de Beeck et al. (2010a) also had a 1:1 slope between measured and predicted photosynthesis. Thus, the simple model presented here gave consistent results with the more complex models.

Photosynthesis of Semillon grape leaves is sensitive to temperature with an optimum around 25–30 °C and rates declining by 30 % with leaf temperatures around 40–45 °C, consistent with that for other grapevine varieties (Kriedemann 1968). The response is also well in keeping with the generally understood effect of temperature on photosynthesis (Berry and Björkman 1980). Underlying this temperature response are those of the stomata, internal CO₂ concentration and PFD and their response to temperature. Although there were effects of temperature on stomatal conductance, across the whole temperature range, there was only a small overall change. This is in contrast to stomatal conductance of Eucalyptus leaves, which were markedly affected...
by temperature (Battaglia et al. 1996), especially towards the higher temperatures where the VPD increases markedly and thus closed the stomata (Reynolds et al. 1992; Battaglia et al. 1996). In contrast, for a range of warm- and cool-climate herbaceous species (Bunce 2000), stomatal conductance increased with increasing temperatures, which may be the response when the increase in VPD is prevented from occurring. Similar results were observed by Fischer et al. (1998) and Lu et al. (1994). In contrast, in a simulation, Reynolds et al. (1992) have suggested that stomatal conductance peaks at \( \sim 12–15 \, ^\circ \text{C} \) and declines markedly at higher temperatures. A similar response was observed for spinach (Yamori et al. 2006). Stomatal conductance of two cool-temperature Poa species also declined with an increase in temperature from 7 to 12 \(^\circ\text{C}\) (Medek et al. 2010), while in *Pisum sativum*, *g*\textsubscript{s} increased from 15 to 25 \(^\circ\text{C}\) and in *Chenopodium album*, *g*\textsubscript{s} remained about constant between 20 and 30 \(^\circ\text{C}\) (Hamilton et al. 2008).

Relative to other grapevine cultivars such as Campbell Early and Kyoho (Yu et al. 2009), Kékfrancos (Zsőfi et al. 2009), Zinfandel and White Reisling (Schultz 2003), Temperanillo (Maroco et al. 2002) and Thompson Seedless (Williams 2012), the average stomatal conductances for the Semillon vines in the present study were towards the lower end of the reported ranges. In addition, the values reported here are lower than those reported for this variety in a cultivar comparison (Rogiers et al. 2009). This reflects the fact that many leaves and days of measurements were used to determine the overall gas exchange response to temperature in the present study. It does appear, however, that the temperature response of stomatal opening in other grapevine cultivars has not been assessed.

For the Semillon leaves, the internal \( \text{CO}_2 \) concentration \((c)\) varied strongly with temperature, especially below 30 \(^\circ\text{C}\) where the concentration increased markedly in a trend opposite to photosynthesis. In contrast, over a near similar range of temperatures, \( c \) of *Eucalyptus* leaves changed only slightly, rising at high and low temperatures (Battaglia et al. 1996). Similarly, Caballé et al. (2011), Yamori et al. (2006) and Eamus et al. (2008) found no effect of temperature on \( c \), but Caballé et al. (2011) suggested that \( c \) should change in the same direction as photosynthesis when stomata are dominating photosynthesis. The coupled changes in photosynthesis and stomatal conductance accompanied by an increase in \( c \) that occurred in *Coffea arabica* plants (Gómez et al. 2005) conforms with this hypothesis. For the present study, however, the temperature dependency of \( c \) was close to a mirror image of the temperature dependency of photosynthesis and, given that stomatal conductance was not strongly temperature dependent, suggests that non-stomatal limitations also played a part in regulating Semillon leaf photosynthesis (Greer and Weedon 2012).

The model of photosynthesis of Semillon leaves was constructed with three parameters, namely stomatal conductance, internal \( \text{CO}_2 \) concentration and PFD, but determined separately for the different leaf temperatures. This model was similar to that of Kim and Lieth (2003), who used PFD, \( c \) and leaf temperature to determine photosynthesis, and to that of Caballé et al. (2011), who used leaf temperature, \( c \) and \( g \) in a multiplicative model. A multiplicative model was also used by Fernández et al. (2006), involving RH, air temperature and \( g \) and PFD-dependent responses. Thus, it would appear that the model used in the present study was one of a few to focus on leaf temperature explicitly and to ascertain the specific effect of temperature on each parameter of the model. In fact, all the coefficients of the parameters were temperature dependent although all varied in different ways, but the differences in the coefficients at the different temperatures were significant and warranted the approach. When combined, and taking into account the coefficients at the different temperatures, the model applied to new datasets gave an excellent fit and this confirmed the approach of determining the temperature sensitivity of the parameters of the model and indeed validated the model.

Transpiration of the Semillon leaves more than doubled when leaf temperatures increased from 20 to 45 \(^\circ\text{C}\), in keeping with the need for increased evaporative cooling at the higher temperatures (Bunce 2000; Keenan et al. 2011).
et al. 2010). This cultivar is known to have high transpiration rates among common wine grape cultivars (Rogiers et al. 2009) and this cooling capacity can maintain leaf temperatures several degrees cooler than air temperature (Greer et al. 2010). In contrast, transpiration rates of the grape variety Trincadeira preta declined markedly above about 35 °C (Correia et al. 1995) and similarly transpiration rates of Eucalyptus haemastoma leaves declined markedly above about 35 °C (Eamus et al. 2008). For Vigna unguiculata, however, rates were maximal between 36 and 40 °C (Hall and Schulze 1980). There are clearly differences in the temperature dependency of transpiration and the response may well depend on the growth conditions of each species.

The modelling of transpiration over the growing season indicated that a multiplicative model of stomatal conductance and VPDl (leaf to air) gave the best fit, and accounted for almost 100% of the variance in transpiration (Cowan and Farquhar 1977; Hall and Schulze 1980; Meinzer et al. 1995; Zhu et al. 2011). Using a similar relationship, Op de Beeck et al. (2010a) had comparable results between measured and modelled transpiration, with 93% of the variance accounted for and a 1 : 1 slope. The same multiplicative model used here was also used by Meinzer et al. (1995), but compared with whole tree transpiration. It is noteworthy that an additive model in the present study, where g, and VPDl were included separately in the model, accounted for 93–98% of the variance in transpiration over all temperatures, but significantly, g, accounted for most of the variance even though the effect of VPDl was highly significant. Transpiration has been commonly reported to be linear function of stomatal conductance, as has been shown for V. vinifera x V. labrusca cv. Campbell’s Early and Kyoho (Yu et al. 2009) and sugarcane (Meinzer and Grantz 1989). Likewise, from diurnal changes in transpiration and stomatal conductance, a linear function was evident for Anacardium excelsium leaves (Meinzer et al. 1993). In contrast, Bunce (1997) showed an inverse relationship between stomatal conductance and transpiration for Abutilon leaves.

The role of temperature in transpiration is explicitly in the determination of VPDl and calculating the saturated vapour pressure of the leaf (Collatz et al. 1991), but also through the effect of temperature on g,. Fredeen and Sage (1999) have shown for white spruce seedlings that g, increased with increasing leaf temperature but only if the VPD was 2–3 kPa. Hall and Schulze (1980) had observed a similar response, except that the temperature effect on conductance was greatest at low rather than at high VPDs. For well-watered grapevines, in contrast, g, declined with increasing leaf temperature (Correia et al. 1995). However, Peak and Mott (2011) concluded that a direct effect of temperature on g, is relatively small when the VPDl is kept constant. With the approach adopted in the present study, it was not possible to exclude a direct temperature effect on g, in relation to transpiration from that of the effect on VPDl. Nevertheless, the model including leaf temperature responses of the g, × VPDl interaction was warranted, given the extremely high-quality fit of the model prediction of the independent datasets and, therefore, validated the approach.

Conclusions and forward look

The modelling of photosynthesis and transpiration from measurements made over whole growing seasons using a statistical regression approach successfully accounted for much of the seasonal variation that occurred. The model was underpinned by the temperature response of the various parameters, including stomatal conductance, internal CO2 concentration, leaf-to-air water vapour difference and PFD. In contrast to other more complex biochemically based models, the present model was relatively simple and accounted for a high percentage of the variance in independent datasets. It is common to include temperature in various photosynthetic models but more typically as an intrinsic property of various biochemical processes (Farquhar et al. 1980), whereas the temperature responses in the present study were explicitly encapsulated by the parameter coefficients and central to the model. This focus on temperature is related to the high-temperature climate in which the vines are grown and these models will contribute to more extensive models of vine growth and development in relation to the climate that are currently under development.

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Conflict of interest statement

None declared.

References


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