RESEARCH PAPER

Does night-time transpiration contribute to anisohydric behaviour in a *Vitis vinifera* cultivar?

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Abstract

The hypothesis that vines of the Semillon wine grape variety show anisohydric behaviour was tested, i.e. that tissue hydration is unstable under fluctuating environmental conditions. Stomatal conductance and transpiration rates from leaves were measured during the day and at night. Leaf water potential ($\Psi_l$) in Semillon was negatively correlated to vapour pressure deficit ($VPD$) both predawn and during the day. Furthermore, $\Psi_l$ fell to significantly lower values than in any of the nine other varieties examined. Night-time values of stomatal conductance ($g_n$) and transpiration ($E_n$) in Semillon were up to four times higher than in other varieties; plants enclosed in plastic bags overnight to reduce $E_n$ resulted in better plant–soil equilibration so that predawn $\Psi_l$ in Semillon was the same as in Grenache. These data indicate that the hypothesis is supported, and that night-time transpiration contributes significantly to the low $\Psi_l$ values in Semillon during warm, dry nights. The other contributing factor is daytime stomatal conductance ($g_{day}$), which in Semillon leaves was higher than in other varieties, although the decline in $g_{day}$ with increasing $VPD$ was greater in Semillon than in Shiraz or Grenache. The high values of $g_{day}$ were associated with high rates of transpiration ($E_{day}$) by Semillon through a day when $VPD$ reached 4.5 kPa. When compared to other varieties, Semillon was not unusual in terms of root length density, stomatal density, xylem sap abscisic acid, or leaf electrolyte leakage. Night-time and daytime water loss and insufficient stomatal regulation therefore account for the tendency to anisohydric behaviour shown by Semillon.

Key words: Drought responses, evaporative demand, Semillon, stomatal regulation, water relations.

Introduction

Stomatal regulation of gas exchange is an integral component of plant water relations. Stomata act as regulators of transpiration rates, responding to changes in soil moisture or evaporative demand. Thus, stomatal control regulates plant water status ($\Psi$). Not all species, however, behave similarly in their stomatal control over $\Psi$. Species and varieties with isohydric behaviour are able to maintain tight control of $\Psi$ over a range of environmental conditions, while $\Psi$ in anisohydric plants oscillates in response to environmental changes (Stocker 1956; Tardieu and Simonneau, 1998).

There is increasing evidence that stomata are not always closed at night and that night-time transpiration can affect daytime plant water relations. Night-time conductance ($g_n$) is significant in a diverse range of C3 and C4 species, including crops (Caird et al., 2007; Dawson et al., 2007; Kavanagh et al., 2007) and transpiration ($E_n$) can exceed 30% of daytime values (Caird et al., 2007; Dawson et al.,...
Furthermore, $g_n$ and $E_n$ may contribute to the vulnerability of plants to daytime water deficits. Substantial $E_n$ can result in incomplete predawn equilibration between the water potential of plants and the soil (Donovan et al., 2001; Kavanagh et al., 2007) and reduce the plant’s ability to withstand increases in evaporative demand the following day. Night-time atmospheric conditions can influence $E_n$ and a decrease in $g_n$ in response to increasing night-time VPD has been documented in some species (Oren et al., 2001; Bucci et al., 2004). $E_n$ may occur through stomata or directly through the cuticle. In general, cuticular conductance ($g_c$) is far lower than $g_n$ indicating that stomatal conductance is a more important factor influencing $E_n$ (Caird et al., 2007).

While leaf water status can regulate stomatal conductance, stomatal control over transpiration also involves chemical and/or hydraulic messages (Tardieu and Davis, 1993). Root to shoot signalling, and the importance of abscisic acid (ABA) has been well established (Hartung et al., 1998), including in grapevines (Loveys, 1984; Correia et al., 1995; Stoll et al., 2000; Lovisolo et al., 2002). When roots are exposed to drying soils, ABA concentrations within the xylem sap are increased and this induces stomatal closure in the leaves (Zhang and Davies, 1991). Water stress may result in the formation of embolisms within the xylem vessels and it has been suggested that ABA may also promote embolism repair during rehydration after drought (Lovisolo et al., 2008).

The grapevine is a good model for woody horticultural crops, with a wide range of physiological responses between genotypes. *Vitis vinifera* varieties are particularly diverse in their drought tolerance, traversing the isohydric-anisohydric spectrum (Smart and Coombe, 1983; Carbonneau, 1985; Schultz, 2003). Grenache, for example, of Mediterranean origin, was classified as near-isohydric, while Shiraz, of mesic origin, displayed anisohydric characteristics (Schultz, 1996, 2003). Isohydry is generally attributed to the strong stomatal control of transpiration rate, which results in the observed similarity in midday leaf water potential in droughted and well-watered plants (Tardieu and Simonneau, 1998). Anisohydric plants typically exhibit less stomatal control over evaporative demand and soil moisture, allowing large fluctuations in leaf water potential (Franks et al., 2007). Excessive cavitation in leaf petioles can lead to the death of the entire leaf (Tyree et al., 1993). This comes about when $E_{day}$ exceeds a critical maximum and is accompanied by a loss of hydraulic connection to all or part of a leaf (Sperry et al., 2002). Vessels or tracheids near a leaf margin, however, may be more vulnerable to xylem cavitation than those in leaf petioles or near the centre of a leaf. Leaf margin dieback may be more desirable than the abscission of entire leaves since this minimizes losses of sequestered carbon and photosynthetic capacity.

Semillon is a variety originating from the Bordeaux region of France, which is characterized by a climate with relatively mild average summer temperature, high humidity, and ample precipitation. In vineyards of NSW and other warm, dry grape-growing regions across Australia, Semillon vines exhibit symptoms of wilting and partial dieback of the leaf margins, and this is aggravated by exposure to hot days during ripening. Other varieties grown adjacent to Semillon and managed similarly do not experience foliar dieback to the same severity as Semillon. The present work was aimed at understanding the causes for Semillon’s vulnerability to water stress, to classify this variety as isohydric or anisohydric, and to clarify the contribution of $g_{night}$ and $E_{night}$ to $\Psi$.

**Materials and methods**

**Study site and plant material**

A replicated variety block located at Charles Sturt University, Wagga Wagga, NSW (latitude: –35.1583S, longitude: 147.4573E, elevation: 212 m) was used for most variety comparisons. The block consisted of 6 rows of 10 varieties at a row spacing of 3 m and a vine spacing of 1.5 m. Semillon was compared to seven other wine grape varieties, including Cabernet Sauvignon, Chardonnay, Merlot, Pinot noir, Riesling, Sauvignon Blanc, and Shiraz, and two table grape varieties including Sultana and Flame Seedless. Each variety panel consisted of three vines. The 3-year-old vines were on their own roots and planted in E-W rows in 2005. The double cordon was trained along a single horizontal wire and pruned to 20 buds per vine. Nutrient application was in accordance with recommended best practice for the Australian industry. No soil moisture treatments were imposed and all vines were drip irrigated twice weekly for 3 h during berry development and ripening using 1.7 l h⁻¹ drippers spaced at 50 cm intervals and located 25 cm on either side of the vine trunk. The soil across the block consisted of a sandy loam over very hard medium clay (80+ cm) with the inter-row area consisting of volunteer grass species that were regularly slashed.

A second field site consisting of 35-year-old drip-irrigated Semillon was used for correlations of $VPD$ with leaf water potential. These vines were grown on a silty-clay to sandy-clay soil at a row spacing of 3.6 m and vine spacing of 1.8 m. Vines were irrigated twice weekly during ripening for 8–12 hours with 2.2 l h⁻¹ drippers spaced at 60 cm intervals. Measurements were carried out on three panels each consisting of four vines.

Night-time transpiration rate ($E_n$) comparisons were carried out on 3-year-old Semillon, Grenache, Shiraz, and Chardonnay vines, on their own roots, grown outdoors in 40 l pots in a premium garden mix (60% compost:20% screened loam:20% washed river sand). Vines were pruned to four shoots shortly after budburst and plants were drip irrigated daily for 10 min with 2.0 l h⁻¹ drippers. The potted vines carried berry crops comparable to the field-grown vines at two clusters per shoot. They were used for the bagging treatments (see below) and for the diurnal time-course in gas exchange.
Soil moisture

Soil moisture in the field was measured with Watermark® soil moisture sensors (Irrometer Co., Riverside, CA 92516, USA) placed at 25, 50, 75, and 100 cm depths directly beneath drippers. These sensors measure the tension with which water in the soil in contact with them is held. Microloggers transmitted the outputs to a nearby base station. Outputs were converted to soil water content on the basis of the soil characteristic water release curve, assumed to apply to this soil, obtained from the UNSODA database (USDA-ARS George E Brown Jr, Salinity Laboratory, 450 W Big Springs Road, Riverside, CA 92507-4617, USA) based on a field determination of the soil texture. The soil water contents at each depth were then used to calculate the proportion of stored readily available water between each measured depth. In this analysis the readily available water (RAW) is defined as the volume of water available to plants in the root zone within a specified range of soil tensions, in this case 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.

Soil moisture of potted vines was monitored with an ML2x Theta Probe (Delta-T Devices, Cambridge, England). Readings were taken at a depth of 10 cm from four regions of the pot and averaged.

Physiological measurements

A Scholander pressure chamber (ICT international, Armidale, NSW) fitted with a Model 3015G4 specimen holder was used for leaf water potential (Ψl) measurements and xylem sap collection on field and potted vines. An LI6400 gas exchange system (Li-Cor Corporation, Lincoln, NE, USA) was used to monitor leaf photosynthesis, transpiration, and stomatal conductance. Ψl and gas exchange measurements of field vines were repeated three times during the season, on 18 vines per variety, one leaf per vine, between 11.00 h and 15.00 h on clear days. Night-time measurements were made 1–2 h prior to dawn on six potted vines per variety, three leaves per vine. For both daytime and night-time studies, instantaneous values of E, gs, and A are presented. Canopy temperature of field vines was assessed with an infrared thermometer (Portix D, Keller GMBH, Germany) held 10 cm from the leaf and leaf chlorophyll was assessed with a chlorophyll meter (SPAD-502, Minolta Co., Ltd., Japan). Canopy temperature and leaf chlorophyll measurements were made on three leaves per plant, 18 plants per variety. All the physiological measurements reported here were carried out between November and February, during the period of late berry development and ripening.

Root density

Roots of six vines from each of five varieties from the replicated variety block were sampled immediately after bunches had reached full ripeness. It was expected that these young vines, on drip irrigation since planting, would not have extensive root systems extending far into the inter-row area or to great depths (Stevens and Douglas, 1994). Therefore, root density was assessed directly underneath the drippers. A 30×30×50 cm deep area was excavated under each dripper, the soil was sifted and the roots were dry-extracted. Root density was assessed by fresh weight and by measuring the total length of roots extracted from each vine.

Electrolyte leakage

Leaf electrolyte leakage was measured as an indicator of cell membrane damage. Leaf discs (10) of 1 cm diameter were punched out of each of three leaves per plant with a cork borer, then placed in dH2O within a test tube and shaken overnight. Electrical conductivity of the solution was measured after 1, 3, and 24 h. The discs were then boiled for 30 min, allowed to cool, and the conductivity was measured again. Leakiness was calculated according to Lutts et al. (1996).

Stomatal density

For each variety, one fully-expanded leaf per vine was taken from three vines from each of six rows in the replicated variety block. Nail polish was applied to the central area of the leaf on the right of the mid-vein and allowed to dry for 10 min. Clear adhesive tape was used to peel off the nail polish and this was pressed onto a microscope slide. The image was observed under bright field microscopy (Olympus Provis AX70). Stomata were counted in three 1 mm² sized areas within this central region of the leaf.

Abscisic acid

Xylem sap ABA was quantified using the ELISA technique (Mertens et al., 1983). The xylem sap was passed through a Sep-Pak C18 cartridge (Waters, Inc.) preconditioned with 100% methanol and then dH2O. The sample was loaded in 0.1 M citrate/0.2 M phosphate buffer (pH 2.8). After washing with 10% methanol, the ABA fraction was extracted. Root density was collected in 100% methanol. The sample was reduced to dryness with a centrifugal evaporator (Labconco Corp., Kansas, MO) and reconstituted in 1 ml of TBS buffer (TRIS-buffered saline; 150 mM NaCl, 1 mM MgCl2, and 50 mM TRIS, pH 7.5). The sample was analysed by a competitive ELISA (Phytodetek®, ABA Test Kit, Agdia Inc., Elkhart, Indiana) and processed according to kit instructions. Absorbance was read with a μQuant microplate spectrophotometer (Bio-Tek instruments, VE). An internal ABA standard was used and results compared well with samples that had been analysed with the HPLC method.
Plant bagging

Shortly after the onset of berry ripening, outdoor potted Semillon and Grenache plants were enclosed in clear plastic bags 1 h after sunset (four plants of each variety per treatment) to increase the night-time air humidity around the canopy and decrease $E_n$. One hour before dawn each bag was opened immediately before the excision of leaves for predawn $\Psi_1$ measurements. The bags were then removed and soil moisture was measured immediately. The midday measurements of $\Psi_1$ were made 8 h later.

Data analysis

All data were analysed using either ANOVA with GenStat or generalized linear models with SAS Statistical software. Least squares means and standard errors were determined. Integration of daily transpiration was carried out with Microcal’s Origin software.

Results

VPD effects on leaf water potential

Predawn $\Psi_1$ of well-irrigated commercial Semillon vines was negatively correlated ($R^2=0.92$, $P<0.001$) with predawn air $VPD$, while midday $\Psi_1$ was negatively correlated ($R^2=0.83$, $P<0.001$) with midday $VPD$ (Fig. 1). As predawn $VPD$ increased from 0.1 to 0.8 kPa, predawn $\Psi_1$ decreased from –0.1 to –0.5 MPa. Midday $\Psi_1$ decreased further to less than –1.0 MPa as $VPD$ increased to 3.0 kPa.

Variety survey

Leaf water potential: Predawn values of $\Psi_1$ of Semillon vines grown in the field at moderate water stress ($RAW$ of 25%) and a $VPD$ of 0.6 kPa were –0.43 MPa (Fig. 2): on average about 20% lower than values in the other nine varieties investigated. Midday $\Psi_1$ values under similar soil moisture levels were also significantly lower in Semillon vines (Fig. 3) reaching –1.2 MPa on a moderate day when the air $VPD$ reached a maximum of 2.4 kPa. With the exception of Cabernet Sauvignon, where $\Psi_1$ was reduced to almost the same level as in Semillon, $\Psi_1$ of the other varieties remained at –0.8 to –0.9 MPa.

Daytime transpiration: On a day of moderate vapour pressure deficit (1.25 kPa) and with soil $RAW$ at 55%, a comparison of leaf gas exchange in 10 varieties did not reveal a wide range in $E_{day}$ (Fig. 4; 3.2 to 4.3 mmol H$_2$O m$^{-2}$ s$^{-1}$). Semillon vines were at the high end of this range, however, $E_{day}$ was not significantly different from other varieties such as Pinot Noir and Chardonnay. Stomatal conductance ranged between 0.2 and 0.4 mol H$_2$O m$^{-2}$ s$^{-1}$ and, again rates were high for Semillon (Fig. 4). Across all varieties, there was a highly significant linear relationship between $E_{day}$ and $g_{day}$ ($R^2=0.9425$, $P<0.0001$) indicating that the differences in transpiration were almost fully accounted for by differences in stomatal conductance. The ratio of $E_{day}$ to $g_{day}$ changed between varieties such that those with high $E_{day}$, including Semillon and Pinot Noir, had smaller ratios (11.3) compared with varieties with low $E_{day}$ including Shiraz and Flame Seedless (15.8). This may be related to lower values of $VPD_1$ for Semillon and Pinot Noir (1.2 kPa) compared with Shiraz and Flame Seedless (1.6 kPa). In fact, the markedly higher transpiration rates of both Semillon and Pinot Noir compared with Shiraz and Flame Seedless would have increased the vapour pressure around the leaf during the measurements and would account for the lower $VPD_1$ for these two varieties. Across all varieties, there was a linear correlation ($R^2=0.90$, $P<0.001$) between mean $VPD_1$ and $E$.

Transpiration efficiency: Rates of CO$_2$ assimilation ($A$) of the 10 varieties ranged between 10 and 14 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$;
the rates for Semillon vines were at the high end of the variety range (Table 1). Across all varieties, there was a highly significant ($R^2=0.9287$, $P<0.001$) linear relationship between $A$ and $g_{\text{day}}$ (not shown) indicating that stomatal conductance differences accounted for varietal differences in photosynthesis. Instantaneous transpiration efficiency ($A/E_{\text{day}}$), a measure of the ratio between CO$_2$ assimilation rate and transpiration, ranged from 3.08 to 3.38 mol CO$_2$ mmol$^{-1}$ H$_2$O but was not significantly different between varieties (Table 1), but differences in intrinsic transpiration efficiency ($A/g_{\text{day}}$) were significant. They ranged from 35.7 to 52.5 mol CO$_2$ mmol$^{-1}$ H$_2$O with the lowest values for Semillon (Table 1).

Vine size: Semillon vines in the field were average in size compared with the other varieties (Table 2). Total shoot length per vine, for the varieties monitored in this study, ranged from 6.8 m to 18.5 m and average shoot length per vine ranged from 32.9 cm to 73.8 cm. Semillon total shoot length was 11 m and average shoot length was 47 cm. Root density directly beneath drippers and 30 cm from the vine stem was assessed to a depth of 50 cm (Table 3). Of the six varieties compared, Chardonnay had the highest root biomass density and root length density, at 5.9 g dm$^{-3}$ and 1682 cm dm$^{-3}$. Merlot, Flame Seedless, Semillon, and Shiraz all had fairly similar root biomass densities at about 2–3 g dm$^{-3}$ and root length densities ranging from 300 to 900 cm dm$^{-3}$ of soil. The ratio of trunk cross-sectional area to root fresh weight was not significantly different between varieties, nor was the ratio of total vine shoot length to root fresh weight (Table 3).

Leaf characteristics: Stomata were found only on the underside of the leaf in the 10 varieties. There were no consistent differences in stomatal number between the leaf centre, lobes of the leaf, or the leaf margins. Riesling and Chardonnay had higher stomatal densities at over 225 stomata mm$^{-2}$, and Sultana had the least stomata at 162 stomata mm$^{-2}$ (Table 4). Stomatal density of Semillon leaves was in the middle range at 190 stomata mm$^{-2}$.

Specific leaf area was not significantly different between varieties, although Flame Seedless stood out with the highest specific leaf area at 8.55 mm$^2$ g$^{-1}$ dwt (Table 4). Semillon was similar to most other varieties at around 6.34 mm$^2$ g$^{-1}$ dwt. Leaf chlorophyll concentrations varied between varieties despite equal fertiliser application (Table 4). Of the wine grape varieties, Semillon vines had leaves with the lowest chlorophyll levels (8.70 mg g$^{-1}$ dwt). Leaf cell electrolyte leakage was least for Chardonnay.
While Flame Seedless leaves had the highest rates of leakage (15.0%) (Table 4). All the other varieties, including Semillon, had cell leakage at around 12–13%.

Leaf temperatures, measured with the IR thermometer, of the varieties was measured under water stress conditions (at 20% \( R_A \) W) over a 3 h period during the middle of the day, when ambient temperature reached 27.8 °C and RH dropped to 31%. Daily pan evaporation was 10.6 mm. Each row of 10 varieties was measured sequentially, thus ensuring that the daily rise in temperature did not interfere with variety comparisons. The average canopy temperature for each row increased from 23 °C to 29.2 °C, indicating that the leaves towards the end of the period of measurement were warmer than the air (Fig. 5). As averaged over the 3 h period, leaf temperature was highest for Shiraz and Sauvignon Blanc (27.8 °C) and lowest for Pinot noir (25 °C) and Semillon (25.3 °C).

Despite cooler leaves on moderate days, Semillon vines showed signs of water stress through tendril and leaf wilting at maximum temperatures of 38 °C or warmer. While none of the other varieties in the replicated variety block had complete or partial foliar dieback the following day, Semillon leaf margins were dry and brittle.

**ABA concentrations**: Midday xylem sap ABA concentrations were not significantly different between varieties and ranged from 0.77 to 1.29 nmol ml\(^{-1}\) (Table 1) while Semillon xylem sap concentrations were 1.16 nmol ml\(^{-1}\).

**Correlations of \( \Psi_t \) with other vine parameters**: Predawn and midday \( \Psi_t \) of vines from the experimental variety block were not significantly correlated with stomatal density, specific leaf area, leaf chlorophyll, electrolyte leakage, total shoot length, mean shoot length, root biomass density, root length density, the ratio of trunk cross-sectional area to root fresh weight, or the ratio of total vine shoot length to root fresh weight. Predawn and midday \( \Psi_t \) of these vines were also not significantly correlated with midday xylem sap ABA concentration, or the gas exchange parameters \( A \), \( A/E \), and \( A/g_s \).

**Comparisons with an isohydric variety**

**Diurnal transpiration**: Comparisons of diurnal trends in conductance and \( E \) of Semillon with Grenache under moderate soil-water-deficit conditions indicated that Grenache stomata were quicker to respond to daytime increases in PAR (Fig. 6). Early morning conductance was 1.4-fold higher for Grenache, but by mid-morning, conductance had reached a plateau. Conductance of Semillon leaves, however, continued to increase until midday and remained higher for the rest of the day and night. The large midday drop of conductance in Grenache leaves (by 50%) did not occur in Semillon. \( E_{day} \) did not differ between Semillon and

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**Table 1.** Photosynthesis \( (A) \), transpiration efficiency \( (A/E_{day}) \), intrinsic transpiration efficiency \( (A/g_s) \) and xylem sap ABA concentrations of Semillon and nine other varieties of similar age grown in a replicated variety vineyard block.

\( A \), \( E \), and \( g_s \) data are instantaneous values and were measured as midday VPD reached a maximum of 1.25 kPa, and when readily available water averaged at 55%. Xylem sap samples were collected when VPD reached a maximum of 2.1 kPa and readily available water averaged at 55%.

| Variety            | \( A \) (\( \mu \)mol CO\(_2\) m\(^{-2}\) s\(^{-1}\)) | \( A/E_{day} \) (\( \mu \)mol CO\(_2\) mol\(^{-1}\) H\(_2\)O) | \( A/g_s \) (\( \mu \)mol CO\(_2\) mmol\(^{-1}\) H\(_2\)O) | Xylem sap ABA (nmol ml\(^{-1}\)) |
|--------------------|---------------------------------------------|-------------------------------------------------|---------------------------------|-------------------------------|
| Cabernet Sauvignon | 12.02                                       | 3.17                                            | 41.98                           | 1.29                          |
| Chardonnay         | 12.90                                       | 3.08                                            | 38.70                           | 0.97                          |
| Flame Seedless     | 10.75                                       | 3.37                                            | 52.51                           | 0.78                          |
| Merlot             | 11.39                                       | 3.28                                            | 47.01                           | 0.70                          |
| Pinot Noir         | 13.37                                       | 3.20                                            | 37.84                           | 1.31                          |
| Riesling           | 11.90                                       | 3.10                                            | 43.36                           | 0.77                          |
| Sauvignon Blanc    | 11.17                                       | 3.30                                            | 51.71                           | 0.83                          |
| Semillon           | 14.00                                       | 3.25                                            | 35.71                           | 1.16                          |
| Shiraz             | 10.36                                       | 3.10                                            | 49.56                           | 1.03                          |
| Sultana            | 13.43                                       | 3.20                                            | 40.54                           | 0.80                          |
| \( P \)            | <0.001                                      | ns                                              | <0.001                          | ns                            |
| LSD (5%)           | 1.7                                         | 0.27                                            | 6.5                             | 0.56                          |

**Table 2.** Total and mean shoot length of Semillon compared to nine other varieties of similar age in a replicated variety block within a vineyard.

| Variety            | Total shoot length (m) | Mean shoot length (cm) |
|--------------------|------------------------|------------------------|
| Cabernet Sauvignon | 6.809                  | 32.9                   |
| Sultana            | 8.839                  | 46.0                   |
| Merlot             | 9.765                  | 44.2                   |
| Pinot Noir         | 9.89                   | 38.6                   |
| Flame Seedless     | 10.22                  | 48.4                   |
| Chardonnay         | 11.203                 | 44.3                   |
| Semillon           | 11.305                 | 47.1                   |
| Riesling           | 16.488                 | 73.8                   |
| Shiraz             | 18.135                 | 72.6                   |
| Sauvignon Blanc    | 16.489                 | 62.7                   |
| \( P \)            | <0.001                 | <0.001                 |
| LSD (5%)           | 4.88                   | 16.3                   |
Grenache in the morning but by mid-afternoon it was 1.8-fold greater for Semillon and remained significantly higher for the rest of the day and night. Across the whole day, Grenache vines transpired a total of 22.2 mmol m⁻² while Semillon leaves transpired a total of 28.2 mmol m⁻², thus 27% more water loss, in total.

**VPD effects on transpiration:** Leaf gas exchange in response to a VPD range of 1–4 kPa indicated consistently higher rates of $E_{\text{day}}$ and $g_{\text{day}}$ for Semillon leaves compared to Shiraz or Grenache leaves (Fig. 7). Transpiration ($E_{\text{day}}$) of Semillon ($R^2=0.68$, $P<0.001$), Shiraz ($R^2=0.81$, $P<0.0001$), and Grenache ($R^2=0.19$, $P<0.05$), were all linearly related to VPD with regression slopes, respectively, of $1.66\pm0.24$, $0.61\pm0.05$, and $0.44\pm0.19$ mmol m⁻² s⁻¹ kPa⁻¹. Stomatal conductance ($g_{\text{day}}$) of Semillon ($R^2=0.39$, $P<0.001$), Shiraz ($R^2=0.60$, $P<0.001$), and Grenache ($R^2=0.21$, $P<0.05$) were inversely related to VPD with regression slopes, respectively, of $-0.036\pm0.009$, $-0.011\pm0.001$, and $-0.014\pm0.006$ mol m⁻² s⁻¹ kPa⁻¹. Thus Semillon leaves had steeper responses of both stomatal conductance and transpiration to VPD than the other two varieties. For example, at the lower VPDs, stomatal conductance of Semillon leaves was double that of Shiraz leaves (0.13 compared to 0.25 mol H₂O m⁻² s⁻¹) and 2.5-fold that of Grenache leaves (0.10 mol H₂O m⁻² s⁻¹) while at the higher VPD range, $g_{\text{day}}$ in Semillon leaves was 2-fold greater than Grenache leaves. Thus, Semillon stomata

### Table 3. Root fresh weight, root length density, ratio of trunk cross-sectional area to root fresh weight, and ratio of total vine shoot length to root fresh weight of Semillon and five other varieties of similar age in a replicated variety block within a vineyard

| Variety          | Root fresh weight (g dm⁻³ of soil) | Root length density (cm dm⁻³ of soil) | Trunk area/root fwt (cm² g⁻¹) | Shoot length/root fwt (m g⁻¹) |
|------------------|-----------------------------------|--------------------------------------|-------------------------------|-------------------------------|
| Merlot           | 2.17                              | 347                                  | 0.21                          | 141.1                         |
| Flame Seedless   | 2.54                              | 515                                  | 0.15                          | 68.1                          |
| Semillon         | 2.87                              | 658                                  | 0.16                          | 116.5                         |
| Shiraz           | 2.95                              | 891                                  | 0.22                          | 187.8                         |
| Cabernet Sauvignon | 3.76                          | 798                                  | 0.16                          | 47.1                          |
| Chardonnay       | 5.88                              | 1682                                 | 0.07                          | 42.8                          |
| $P$              | <0.045                            | <0.001                               | ns                            | ns                            |
| LSD (5%)         | 2.32                              | 467                                  | 0.17                          | 146                           |

### Table 4. Leaf abaxial stomatal density, specific leaf area, leaf chlorophyll concentrations, and leaf membrane damage of Semillon and nine other varieties grown in a replicated variety vineyard block

| Variety          | Stomatal density (mm⁻²) | Specific leaf area (mm² g⁻¹ dwt) | Leaf chlorophyll (mg g⁻¹ dwt) | Electrolyte leakage (%) |
|------------------|------------------------|----------------------------------|-------------------------------|-------------------------|
| Cabernet Sauvignon | 180.0                  | 6.58                             | 10.17                         | 12.4                    |
| Chardonnay       | 225.5                  | 6.12                             | 10.42                         | 10.7                    |
| Flame Seedless   | 189.3                  | 8.55                             | 7.85                          | 15.0                    |
| Merlot           | 174.5                  | 7.41                             | 9.92                          | 12.0                    |
| Pinot Noir       | 184.0                  | 6.95                             | 10.12                         | 12.5                    |
| Riesling         | 232.6                  | 6.04                             | 9.25                          | 12.2                    |
| Sauvignon Blanc  | 213.4                  | 6.78                             | 10.24                         | 12.1                    |
| Semillon         | 190.1                  | 6.34                             | 8.70                          | 12.9                    |
| Shiraz           | 167.4                  | 6.70                             | 9.45                          | 12.1                    |
| Sultana          | 162.0                  | 6.25                             | 7.95                          | 12.0                    |
| $P$              | <0.001                 | ns                               | <0.001                        | <0.05                   |
| LSD (5%)         | 13.6                   | 1.6                              | 0.33                          | 1.8                     |

**Fig. 5.** Leaf temperature of Semillon and nine other varieties in a replicated variety vineyard block. The effect of variety on canopy temperature was significant at $P<0.001$. LSD₅% for temperature is 0.57 °C. Readily available water averaged at 20%. Leaf temperatures of the varieties were measured over a 3 h period where ambient temperature reached 27.8 °C at 15.00 h and RH dropped to 31%. Pan evaporation was 10.6 mm.
remained well open at all VPDs in comparison with stomata of the other cultivars.

Across all varieties, $E_{\text{day}}$ tracked $g_{\text{day}}$ quite closely but in an inverse pattern. $E_{\text{day}}$ also nearly doubled with increases in VPD for Semillon vines (3.4 to 6.2 mmol H$_2$O m$^{-2}$ s$^{-1}$), while $E_{\text{day}}$ of Shiraz and Grenache leaves increased by 70%, again conforming with the steeper responses of Semillon to VPD. $A$ was 1.4-fold higher for Semillon leaves than Shiraz and Grenache leaves (data not shown).

Night-time transpiration: $E_n$ rates and $g_n$ values were one-tenth of the daytime rates and values (Figs 4, 8). Despite this, there were strong varietal differences, with both $g_n$ (0.021 mol H$_2$O m$^{-2}$ s$^{-1}$) and $E_n$ (0.32 mmol H$_2$O m$^{-2}$ s$^{-1}$) of Semillon leaves being 4-fold greater than in Grenache leaves, where $g_n$≈0.005 mol H$_2$O m$^{-2}$ s$^{-1}$ and $E_n$≈0.08 mmol H$_2$O m$^{-2}$ s$^{-1}$ (Fig. 8). Across the four varieties, there was a highly significant ($R^2=0.9914$, $P<0.001$) linear relationship between $E_n$ and $g_n$. This indicated night-time differences in stomatal conductance between the cultivars fully accounted for the differences in transpiration.

Night-time bagging: Night-time bagging of potted vines resulted in higher predawn $\Psi_l$ in both Semillon and Grenache (Table 5). Predawn $\Psi_l$ in Semillon was 35% less negative after bagging compared to the control vines without bags, while in Grenache, $\Psi_l$ was 15% less negative than the control. Subsequent midday $\Psi_l$, however, was not significantly different in either Semillon or Grenache after the night-time treatment and the bags had been removed.

Discussion
In a direct comparison with nine other grapevine varieties, Semillon vines stood out with the highest transpiration rates as well as the most negative predawn and midday water potentials and lowest intrinsic transpiration efficiency. To a large extent, the differences in gas exchange rates between these varieties could be accounted for by stomatal conductance, with Semillon vines having the highest values. Our results compare well with other estimates of conductance and transpiration for Semillon (Regina and Carbonneau, 1996; Gibberd et al., 2001; Walker et al., 2005). In addition to Vitis vinifera varieties, the occurrence of genotypic variation in transpiration efficiency is not unusual and is present in other crops such as wheat (Condon et al., 1990) and sunflower (Virgona et al., 1990).
Across the varieties, several groups can be distinguished on the basis of their inherent stomatal conductance, with Semillon and Pinot Noir characterized by high $g_s$, Cabernet Sauvignon and Riesling with moderate $g_s$, and Shiraz and Flame Seedless with low $g_s$. However, these differences in $g_s$ were not related to stomatal density, given that Semillon had moderate stomatal density, Riesling high density, and Shiraz low density. Stomatal density can be influenced by environmental conditions such as light and temperature (Schoch et al., 2001; Casson and Gray, 2008), but there are genetic differences as well (Dillen et al., 2008) as shown here for grapevines.

While $g_{day}$ and $E_{day}$ were substantial in Semillon, further insight into the stomatal behaviour of this variety in a restricted comparison with other varieties, was obtained by carrying out night-time measurements. Again, differences in transpiration during the night between the varieties could be accounted for by stomatal conductance. Further-more, there was a high degree of conformity between daytime conductance and night-time conductance. Semillon with high $g_{day}$ and $g_n$ and Shiraz with low $g_{day}$ and $g_n$. Semillon leaves had significantly higher $g_s$ and $E_{night}$ at 4-fold the rates of Grenache, which has previously been classified as an isohydric variety (Schultz, 1996). Our results compared well with many deciduous trees and shrubs in the range of 0.01–0.02 mol m$^{-2}$ s$^{-1}$ but were lower than a number of other vine species (Caird et al., 2007). Our grapevine $E_{night}$ was 10% of daytime values, imparting a significant loss in the daily water economy of the vine. This is comparable to night:day ratios of $g_s$ ranging between 5% and 20% across a number of tree species in various ecosystems (Dawson et al., 2007).

Given that Semillon vines have intrinsically high $g_s$, both during the day and the night, it may not be surprising that stomata of this variety were more sensitive to changes in leaf $VPD$ than either Grenache or Shiraz. Here the sensitivity of the response to $VPD$ (as defined by Oren et al., 1999) refers to the magnitude of the reduction in $g_s$ with increasing $VPD$. Over a $VPD_l$ range of 1.5–3.5 kPa, Semillon $g_s$, on average, was markedly higher and responded 2.6–3.2-fold more than the other cultivars. The critical point is that, at the highest $VPD$, Semillon stomata remained relatively open. By contrast, Grenache stomata were almost closed across all $VPDs$ and remained un-responsive to $VPD_l$ by comparison, with just a slight decrease in $g_s$ with increasing $VPD_l$. In an intra- and interspecific survey of stomatal sensitivity to $VPD$ it was shown that species with high $g_s$ at low $VPD_l$ had a greater sensitivity to $VPD$ (Oren et al., 1999). Our results on these grape varieties conform with this generalization.

Transpiration of all three grape varieties showed marked responses to $VPD_l$ in contrast with the stomata. Both Shiraz and Grenache increased transpiration at the same rate while Semillon increased at a much higher rate (2.7–3.7-fold) with the increase in $VPD_l$. Consistent with our previous observations, transpiration of Semillon was markedly higher than for the other varieties over all $VPDs$.

It is recognized that stomata of isohydric plants are highly regulatory and prevent fluctuations in $\Psi_l$, particularly during soil drying. Conversely, anisohydric plants typically have large fluctuations in $\Psi_l$ and this is usually attributed to poor stomatal control over evaporative demand or soil moisture (Turner et al., 1984; Schultz, 2003; Franks et al., 2007). Grenache has previously been characterized as isohydric and Shiraz as anisohydric based on their response to slowly developing soil moisture stress (Schultz, 1996, 2003). In our case, vines of both cultivars grew with moderate soil moisture deficit and to changes in evaporative demand indicated relatively low stomatal sensitivity. By contrast, Semillon vines grown in identical conditions were highly responsive to evaporative demand. However, both Shiraz, and particularly Semillon (Grenache was not included), exhibited substantially more negative midday $\Psi_l$ compared with the other varieties under a similar irrigation regime. Furthermore, midday $\Psi_l$ of Semillon vines was strongly influenced by midday $VPD$, an outcome of the
intimate response to evaporative demand. On the basis of these considerations, both Shiraz and Semillon can be classified as anisohydric despite their widely different stomatal sensitivities.

While vine characteristics such as shoot:root ratio and leaf stomatal density were not unusual in Semillon when compared with other grape varieties, substantial daytime and night-time $g$ and $E$ probably contributed to the anisohydric behaviour as applied to $\Psi_t$ characteristics. This is especially so when comparing Semillon with Grenache which has very low night-time conductance. This conclusion was also strengthened by the observation that predawn $\Psi_t$ approached equilibrium to a greater extent in Semillon compared with Grenache when $E_{\text{night}}$ was reduced through canopy bagging.

Low predawn $\Psi_t$ for Semillon vines is indicative of incomplete rehydration and high $E_n$ may have been a contributing factor. Indeed, the negative correlations between predawn $\Psi_t$ and predawn VPD of field vines supports this conclusion, given that high night-time VPD will enhance night-time transpiration water loss. Furthermore, lowering $E_n$ by increasing humidity around the vines through bagging resulted in 35% less negative predawn $\Psi_t$. Under water stress conditions, cavitation embolisms can be repaired by the rehydration of tissues during the night when VPD is low (Smart et al., 2005). If $E$ is substantial during the night then rehydration may be incomplete. As an example, night-time transpiration reduced predawn xylem pressure potential in 16 out of 21 species and the magnitude of the contribution to predawn disequilibrium was large in four woody species (Donovan et al., 2001). The ecological relevance of night-time transpiration may include enhanced nutrient uptake (Donovan et al., 2001) or the delivery of dissolved $O_2$ to woody tissue sinks (Dawson et al., 2007). Significant $E_n$ may, however, reduce the ability of the vine to benefit from hydraulic lift since less water is available for release to the drier upper soil (Caird et al., 2007). $E_n$ may, therefore, be of relevance to the success of partial rootzone drying irrigation strategies. The impact of incomplete rehydration on the vine’s capability to withstand the diurnal increase in VPD is likely to be dependent on a number of environmental factors such as the magnitude of VPD and the level of soil moisture. In our study, lowering $E_n$ did not have a significant effect on subsequent midday values of $\Psi_t$. This indicates that $g_d$ and $E_{\text{day}}$ were the predominant factors affecting daytime $\Psi$ and were able to override the small differences in predawn $\Psi$.

Unlike in drying soils, the mechanism that accounts for stomatal closure in response to humidity is not clear, but it is unlikely that ABA has a role (Assmann et al., 2000). ABA is known to cause daytime stomatal closure in response to drying soil (Loveys, 1984; Loveys and Düring, 1984; Correia et al., 1995) and in our Semillon grown under moderate water deficit, ABA production by the roots appears to be at similar levels to the other varieties. However, while stomatal closure did occur in response to soil water deficit, it was not as complete in Semillon as in other varieties. Factors, such as the alkalization of leaf apoplastic pH (Gollan et al., 2006; Wilkinson and Davies, 1997), may need fine-tuning to ensure complete stomatal closure.

Hydraulic conductance of roots and shoots is another parameter influencing $E$ (Aasamaa et al., 2001; Lovisolo and Schubert, 1998) and differences in stomatal control during water stress may be linked to vulnerability to xylem cavitation (Jones and Sutherland, 1991). In the grapevine, differences in hydraulic architecture within the petioles have been attributed to near-isohydric and anisohydric behaviour in two cultivars (Schultz, 2003). It was suggested that stomata may react to prevent embolism at different levels of $\Psi_t$ (Schultz, 2003). Specifically, lower hydraulic conductance was postulated to lead to lower rates of cavitation in the anisohydric variety, and therefore $g$ and $E$ were not limited. Hydraulic conductance of roots was also found to affect drought tolerance in grapes (Vandeleur et al., 2009). Under water stress, there was a greater reduction in root hydraulic conductance of Grenache compared with Chardonnay, the anisohydric variety. It was postulated that greater stomatal control was required in Grenache to prevent excessively negative xylem water potentials brought about by the lower root hydraulic conductance. While hydraulic conductance of roots, trunk, and shoots were beyond the scope of this study, this aspect of $\Psi$ deserves further attention in Semillon.

Aside from elevated $g_s$, the contribution of various other factors may have resulted in the low water potentials of Semillon. Larger canopies may result in more rapid plant dehydration than smaller canopies, since there is more leaf area for transpirational water loss. For instance, mild deficit irrigation and partial rootzone drying are successfully used to reduce shoot growth (Dry and Loveys, 1998). Similarly, ‘minimal pruning’ is used in hot, irrigated regions of Australia to reduce shoot vigour and increase yield (Clingeleffer, 1984). Our vines were ‘spur pruned’, however, and Semillon canopies were average in size compared with the other varieties. Therefore, lower leaf water potential was not the result of larger vine leaf area.

Along with physiological properties of the roots (e.g., hydraulic conductivity) and properties of the root hair rhizosphere (Segal et al., 2008), root distribution and density are also critical to water uptake rates (Huang, 2000). Of the six varieties that were compared, Chardonnay had the highest root density while Merlot, Flame Seedless, Semillon, and Shiraz all had fairly similar root densities. Similarly, the relative proportion of shoot to root biomass can contribute to plant water status. For example, vigorous canopies on vines with smaller root systems may experience more water stress if water uptake rates are not adequate to meet the transpirational demands of the canopy (Dry and Loveys, 1998). In our study, however, there were no significant differences in the relative proportion of these above- and below ground components.

Leaf characteristics were assessed to understand better the causes of the low leaf water potentials in Semillon. There is extensive variation in leaf morphology,
architecture, hairiness, and venation between *Vitis vinifera* varieties (Kerridge and Antcliff, 1999). Specific leaf area can be an indicator of water storage capacity and was correlated with water use efficiency in peanut (Nageswara Rao and Wright, 1994). In our study, however, Semillon specific leaf area was not unusual, falling within the same range as other varieties. Leaf chlorophyll concentrations can be an indicator of vine stress (Carter and Knapp, 2001). Semillon vines had leaves with the lowest chlorophyll levels when compared with the other wine grape varieties, despite equal fertilizer application rates. The table grapes, however, had even lower chlorophyll levels. Furthermore, water stress can cause membrane damage in leaves (Bajji et al., 2002) and electrolyte leakage from cells increases with membrane damage and so it is regarded as a stress indicator (Lutts et al., 1996). The dried margins of Semillon leaves were not used for this assessment; we were interested in the susceptibility to leaf burn before it occurred. Chardonnay had the least electrolyte leakage while Flame Seedless had the most, and again Semillon was within this range, therefore negating any obvious indicators of vine stress. Thus, none of these factors account for the characteristically low leaf water potentials in Semillon.

In summary, when compared to other varieties grown in similar conditions, Semillon leaves had large stomatal conductances despite high stomatal sensitivity to evaporative demand. Significant transpirational water losses occurred during both the day and the night, resulting in excessive dehydration and low $\Psi_t$. As such, Semillon can be classified as anisohydric. Further work to elucidate attributes and events leading to high daytime and night-time $g_a$ in Semillon across a range of VPDs and soil moistures is required.

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