Title: Incorporating non-stomatal limitation improves the performance of leaf and canopy models at high vapour pressure deficit

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Abstract

Vapour pressure deficit ($D$) is projected to increase in the future as temperatures rise. In response to increased $D$, stomatal conductance ($g_s$) and photosynthesis ($A$) are reduced, which may result in significant reductions in terrestrial carbon, water, and energy fluxes. It is thus important for gas exchange models to capture the observed responses of $g_s$ and $A$ with increasing $D$.

We tested a series of coupled $A$-$g_s$ models against leaf gas exchange measurements from the Cumberland Plain Woodland (Australia), where $D$ regularly exceeds 2 kPa and can reach 8 kPa in summer. Two commonly used $A$-$g_s$ models (Leuning 1995 and Medlyn et al. 2011) were not able to capture the observed decrease in $A$ and $g_s$ with increasing $D$ at the leaf scale. To explain this decrease in $A$ and $g_s$, two alternative hypotheses were tested: hydraulic limitation (i.e., plants reduce $g_s$ and/or $A$ due to insufficient water supply) and non-stomatal limitation (i.e., downregulation of photosynthetic capacity). We found that the model that incorporated a non-stomatal limitation captured the observations with high fidelity and required the fewest number of parameters. While the model incorporating hydraulic limitation captured the observed $A$ and $g_s$, it did so via a physical mechanism that is incorrect.

We then incorporated a non-stomatal limitation into the stand model, MAESPA, to examine its impact on canopy transpiration and gross primary production. Accounting for a non-stomatal limitation reduced the predicted transpiration by ~19%, improving the correspondence with sap flow measurements, and gross primary production by ~14%. Given the projected global increases in $D$ associated with future warming, these findings suggest that models may need to incorporate non-stomatal limitation to accurately simulate $A$ and $g_s$ in the future with high $D$. Further data on non-stomatal limitation at high $D$ should be a priority, in order to determine the generality of our results and develop a widely applicable model.

**Keywords:** Vapour pressure deficit, stomatal conductance, non-stomatal limitation, hydraulic limitation, model-data assimilation, photosynthesis
**Introduction**

Vapour pressure deficit \((D)\) is the difference between the amount of water vapour that the air can hold at saturation \((e_s)\) and the actual amount of water vapour in the air \((e_a)\; (\text{Monteith and Unsworth}, 2013)\). With rising air temperatures, \(e_s\) increases exponentially and as a result, \(D\) is projected to increase strongly into the future (Ficklin and Novick, 2017). At the leaf level, as \(D\) increases and plant water supply becomes limiting, a direct reduction in stomatal conductance \((g_s)\) occurs to limit transpiration, which inevitably also affects photosynthesis \((A)\; (\text{Cowan and Farquhar}, 1977)\). The reduction of \(A\) and potentially transpiration due to increasing \(D\) has important implications for global carbon-climate predictions (Reichstein et al., 2013; Will et al., 2013). Thus, it is crucial to understand the response of vegetation to the projected increase in \(D\) (Novick et al., 2016).

The challenges involved in modelling \(g_s\) responses to high \(D\) have been discussed since the late 1970’s (Cowan, 1978; Farquhar, 1978). Monteith (1995) characterised the response of \(g_s\) to \(D\) as consisting of two different regimes: (i) regime A—where \(g_s\) gradually declines with \(D\), but transpiration \((E)\) increases with \(D\); (ii) regime B—where \(g_s\) declines non-linearly with \(D\), resulting in a peak and then decline in \(E\). Regime A is the most commonly observed pattern and occurs at intermediate \(D\) (0.5-2 kPa). It also represents the range of leaf level measurements most commonly used to parameterise models of \(g_s\) (e.g., Ball et al., 1987; Leuning, 1995; Medlyn et al., 2011). Regime B takes place at higher \(D\) \((D > 2 \text{ kPa})\), which is typically rare in humid ecosystems but common in hot and dry ones (e.g., Franks et al., 1997; Thomas and Eamus, 1999; MacFarlane et al., 2004; Whitley et al., 2013; Gimeno et al., 2018; Renchon et al., 2018).

Current representations of \(g_s\) in terrestrial biosphere models (TBMs) differ in their sensitivity to \(D\), especially at \(D > 2 \text{ kPa}\) (i.e., regime B; De Kauwe et al., 2015; Knauer et al., 2015; Franks et al., 2017), which has carry-over effects on TBM predictions at high \(D\). The \(g_s\) model of Leuning (1995) has a strong \(D\) dependence \((g_s\) depends on the reciprocal of \(D\)), which yields a reduction in \(E\) at high \(D\). However, it can be difficult to parameterise the Leuning model such that it can fit data at both high and low \(D\) (Duursma et al., 2014). The parameter values most commonly used are biased towards low \(D\) (e.g., those used in the Community Atmosphere Biosphere Land Exchange (CABLE) land surface model (Kowalczyk et al., 2015) or the Sheffield Dynamics Global Vegetation Model (Woodward et al., 1995)). Alternatively, Medlyn et al. (2011) proposed an optimality model, in which \(g_s\)
depends on $D^{-0.5}$. Due to this lower sensitivity of $g_s$ to $D$ compared to the Leuning model, the Medlyn model does not predict a reduction in $E$ at high $D$ (i.e., regime B).

The reduction of $E$ at high $D$ in regime B could result from a hydraulic limitation (Buckley, 2005). Experimental observations show that $g_s$ is strongly linked to guard cell and epidermal turgor (e.g., Franks et al., 1997; Franks, 2004) and not simply to environmental conditions (i.e., $D$). Tuzet et al. (2003) proposed a model coupling $g_s$ to leaf water potential ($\psi_L$). The $\psi_L$ term in the Tuzet model is determined by the balance of plant water use via stomata and the water supply, which is calculated as the product of hydraulic conductance and the difference between leaf and soil water potentials. In the Tuzet model, $\psi_L$ is solved iteratively by balancing the demand and supply. If the hydraulic conductance is held constant, the Tuzet model will not yield a decline in transpiration at high $D$ because a reduction in $\psi_L$ cannot occur at the same time as a reduction in transpiration (Farquhar 1978). However, reductions in hydraulic conductance can occur within the xylem by cavitation (Tyree and Sperry, 1989) or in the outside xylem component of the pathway via a variety of mechanisms (Scoffoni et al., 2017). A very negative $\psi_L$ leads to a large pressure difference but low conductance, the net effect of which can lead to a reduction in water supply and thus a decrease in $g_s$. Although theoretically plausible, the hydraulic limitation hypothesis has not been extensively tested against observations.

An alternative hypothesis to explain the coupled $A$-$g_s$ response at high $D$ is a non-stomatal limitation of $A$ (Dewar et al. 2018; Gimeno et al. 2019). The mechanism for such a non-stomatal limitation is not clear, but it could potentially involve biochemical regulation or a reduction in mesophyll conductance. For example, Duursma et al. (2014) proposed that the reduction of $E$ at high $D$ is driven by a decrease in apparent carboxylation capacity ($V_{\text{cmax}}$) at the high temperatures (>30°C) that accompany high $D$. This hypothesis was supported by leaf and canopy scale measurements in a whole tree chamber experiment (Duursma et al., 2014). Low leaf water potential at high $D$ could also reduce apparent photosynthetic capacity via a downregulation of the capacity of photosynthetic biochemistry or a reduction in mesophyll conductance (Tezara et al., 1999; Lawlor and Cornic, 2002; Lawlor and Tezara, 2009), which would subsequently drive a coupled reduction in $g_s$. Such an effect is increasingly reported in soil drought studies (e.g., Zhou et al., 2013, 2014; Verhoef and Egea, 2014; Drake et al., 2017). Incorporating a non-stomatal limitation into TBMs has led to improved predictions of soil drought responses (Keenan et al., 2010, Verhoef and Egea, 2014; De Kauwe et al., 2015; Drake et al., 2017). Although these studies have shown the importance of non-stomatal
limitation under soil drought (i.e., via reduced photosynthetic capacity), it is unclear whether high $D$ can cause the same non-stomatal limitation.

Here, we evaluate alternative stomatal modelling approaches at a woodland site where $D$ reaches high levels every summer (mean daily maximum = 2.7 kPa; maximum = 8 kPa). We first test leaf-scale models against in situ observations which showed a reduction in $g_s$ and $A$ with increasing $D$ (Gimeno et al., 2016). We then implement the best model into a canopy scale model against whole-tree-scale sap flow data that showed a decrease in transpiration at high $D$ (Gimeno et al., 2018). We aim to quantify how well the alternative gas exchange models captured the high $D$ responses of both $g_s$ and $A$.

**Methods**

We tested five leaf-scale $g_s$ models in this study (Table 1): (i) the Medlyn model (Medlyn et al., 2011), which is derived from optimal stomatal theory and assumes that $g_s$ depends on the reciprocal of $D^{0.5}$; (ii) the Leuning model (Leuning, 1995), which has a similar functional form to the Medlyn model but assumes a stronger $g_s$ sensitivity to $D$; (iii) the Tuzet stomatal model (Tuzet et al., 2003), which assumes a $g_s$ sensitivity to $\psi_L$, incorporating a reduction of hydraulic conductance with low $\psi_L$ (hereafter referred as Tuzet K-PSI); (iv) the Tuzet stomatal model incorporating a non-stomatal limitation at low $\psi_L$ (hereafter referred as Tuzet V-PSI); and (v) the Medlyn model, incorporating a non-stomatal limitation that increases with increasing $D$ (hereafter referred as Medlyn V-D). The comparison between the performance of Medlyn and Leuning model tests whether increasing the sensitivity of $g_s$ to $D$ improves model performance. The Tuzet K-PSI model was chosen to test whether considering a hydraulic limitation improved model performance. The comparison between the Tuzet V-PSI and Medlyn V-D models was designed to test whether this assumption was necessary to improve predictions at high $D$ and to explore the best way to represent non-stomatal limitation.

**Sites**

Data were obtained from two sites in the Cumberland Plain Woodland. The first site is the *Eucalyptus* Free-air-CO2-Enrichment site (EucFACE) in Richmond, Western Sydney, Australia (33.62°S, 150.73°E). The site is a natural mature woodland, dominated by *Eucalyptus tereticornis*. EucFACE consists of six circular plots (referred to as “rings”
hereafter), each of which has a diameter of 25 m (Gimeno et al., 2016). The rings receive two CO₂ concentrations: ambient (rings 1, 4, 5; ambient CO₂ ≈ 400 μmol mol⁻¹) and elevated (rings 2, 3, 6; ambient CO₂+150 μmol mol⁻¹). The data from the elevated CO₂ rings were included in this study to increase the number of observations for statistical testing, but responses to elevated CO₂ are not a focus of the study (see Gimeno et al., 2016, 2018 for analysis of effects of elevated CO₂). Meteorological data measured at EucFACE during the measurement period of the year 2013 are shown in Figure S1. The second site is 10 km south of EucFACE in the Castlereagh Nature Reserve, Sydney, Australia (33.39°S, 150.46°E) (Zeppel et al., 2008). This site is also a mature natural woodland with E. parramattensis as the dominant species, a local species closely related to E. tereticornis.

**Measurements**

This study used three types of data: leaf gas exchange (Zeppel et al., 2008; Gimeno et al., 2016), xylem vulnerability curves, and sap flow (Zeppel et al., 2008; Gimeno et al., 2018). Leaf gas exchange and xylem cavitation data were used in parameterization as well as evaluation of the gs models. Sap flow data were used in whole-tree scale evaluations to test transpiration predictions of the canopy scale model.

Diurnal leaf gas exchange measurements were made throughout the day under prevailing field conditions using LiCOR 6400XT at EucFACE in 2013 (Gimeno et al., 2016) and a LCpro+ system (ADC BioScientific, Hoddesdon, UK) at Castlereagh in 2006 (Zeppel et al., 2008). Canopy access at EucFACE was provided by a crane (canopy height = 20m) whereas canopy access at Castlereagh was provided by a portable rising work platform (canopy height = 2-8 m), both suitable to reach the upper canopy. The EucFACE data were measured at saturating photosynthetically active radiation (1800 μmol m⁻² s⁻¹). The Castlereagh data were measured at ambient light levels, so we only used data with saturating light (>1200 μmol m⁻² s⁻¹). At EucFACE, leaf water potential measurements at pre-dawn, morning (9:30-11:30), and afternoon (13:00-15:00) were also made by Gimeno et al. (2016).

In addition to the four diurnal gas exchange campaigns at EucFACE, repeated light- and temperature-controlled photosynthesis-CO₂ response (A-Cᵢ) curves on the same 3 or 4 trees in each ring were measured and used to calculate the maximum apparent electron transport rate (Jₘₐₓ; μmol m⁻² s⁻¹) and apparent carboxylation capacity (Vₖₑₐ₅ₓ; μmol m⁻² s⁻¹). The Jₘₐₓ and Vₖₑₐ₅ₓ values were estimated with the “fitacis” function from the plantecophys R package.
The temperature dependencies of $J_{\text{max}}$ and $V_{c_{\text{max}}}$ were obtained from a different set of $A-C_i$ curves measured at four leaf temperatures ranging between 20 and 40 ºC during February 2016. We fitted peaked Arrhenius functions to the values of $J_{\text{max}}$ and $V_{c_{\text{max}}}$ obtained at each measurement temperature (Medlyn et al., 2002). The resulting $J_{\text{max}}$ and $V_{c_{\text{max}}}$ at 25ºC (i.e., $J_{\text{max,25}}$ and $V_{c_{\text{max,25}}}$) values were averaged for each ring on each measurement date. We also estimated one-point $V_{c_{\text{max}}}$ from the diurnal measurements using the “one-point method” (De Kauwe et al. 2016). As a result, each diurnal gas exchange measurement corresponded to a modelled $V_{c_{\text{max}}}$ based on $A-C_i$ curve data and the temperature response, and an in situ $V_{c_{\text{max}}}$ based on the “one-point method”.

A hydraulic vulnerability curve for *E. tereticornis* was constructed using benchtop dehydration (Sperry et al. 1988). Two-metre-long branches were excised from six mature canopy trees located outside the rings at EucFACE, using the canopy crane. Collections were made in the early morning (between first light and sunrise). Branches were placed in large plastic bags with moist towels to prevent dehydration and cut ends were recut under water and allowed to rehydrate. Branches were transported in water and were stored in a cool room 24 hours before measurements. Stem percent loss of conductivity was measured using hydraulic flow measurements on increasingly dehydrated branch segments using a flowmeter (Liqui-Flow L10, Bronkhorst High-Tech BV, Ruurlo, Gelderland, Netherlands) at low pressure (< 4 kPa). Four to six stem segments were measured per large branch at progressively lower water potentials (measured on covered leaves using a pressure chamber – PMS Instrument Company, Albany, OR, USA). To quantify the impact of cavitation for the Tuzet models, a Weibull function following Ogle et al. (2009) was fitted to produce a vulnerability curve using the ‘fitplc’ function in the *fitplc* R package (Duursma and Choat, 2017).

Canopy transpiration was estimated with sap flow measurements at both the EucFACE and the Castlereagh sites. At EucFACE, two custom-built two-probe heat-pulse sensors (Edwards Industries, Havelock North, New Zealand) were installed at two positions on each tree, on three or four trees per ring (Gimeno et al. 2018). The data from all six rings were upscaled to estimate stand averages using sap wood area, which was allometrically calculated with measured stem diameter. The volumetric soil water content ($\theta$) of the site was measured every ~20 days using neutron measurements at 25 cm intervals (NMM, 503DR Hydroprobe®, Instroteck, NC, USA) and averaged to the mean moisture of the top 150 cm of the soil (Figure 1; Gimeno et al. 2018). Sap flow at the Castlereagh site was obtained from...
Zeppel et al. (2008). The measurements used two-probe heat pulse sensors and sampled six trees with two sensors per tree from June to December 2006. The corresponding soil moisture measurements at Castlereagh were recorded with an array of frequency domain reflectometry sensors (Theta Probe, ML2-X; Delta-T devices, Cambridge, UK) for the top 70 cm.

**Leaf gas exchange models**

We used the Medlyn model as our baseline stomatal conductance model because it requires the fewest parameters (Medlyn et al., 2011):

\[ g_s = 1.6 \cdot (1 + \frac{g_{1,\text{MED}}}{\sqrt{D}}) \cdot \frac{A}{C_a} \]  

where \( g_s \) is the stomatal conductance to water vapour (mol m\(^{-2}\) s\(^{-1}\)); \( g_{1,\text{MED}} \) is the optimal stomatal behaviour parameter (kPa\(^{0.5}\)); see detailed explanation in Medlyn et al., (2011); \( A \) is the CO\(_2\) assimilation rate (μmol m\(^{-2}\) s\(^{-1}\)); \( C_a \) is the atmospheric CO\(_2\) concentration (μmol mol\(^{-1}\)). We modelled \( A \) with the plantecophys R Package (Duursma, 2015), which uses the Farquhar-von Caemmerer-Berry photosynthesis model (Farquhar et al., 1980).

An earlier \( g_s \) model was proposed by Leuning (1995), who assumed an inverse stomatal response to \( D \):

\[ g_s = 1.6 \cdot g_{1,\text{LEU}} \cdot \frac{A}{C_a} \cdot \frac{1}{1+D/D_0} \]  

where \( g_{1,\text{LEU}} \) is an empirical slope parameter determining the sensitivity of \( g_s \) to \( A \) and other environment variables (dimensionless); and \( D_0 \) reflects the sensitivity of \( g_s \) to \( D \) (kPa). Both the Medlyn and Leuning models can include a minimum stomatal conductance, \( g_0 \), as an intercept (Duursma et al., 2019). This study assumed \( g_0 = 0 \) since the estimated \( g_0 \) is negligible (Gimeno et al., 2016).

We also tested a modified version of the model proposed by Tuzet et al. (2003), following Duursma and Medlyn (2012):

\[ g_s = 1.6 \cdot g_{1,\text{TUZ}} \frac{A}{C_a} \cdot f_s(\psi_L) \]  

where \( g_{1,\text{TUZ}} \) is an empirical slope parameter and \( f_s \) is the sigmoidal function defined as:

\[ f_s(\psi_L) = \frac{1+\exp(s_f(\psi_f-\psi_L))}{1+\exp(s_f(\psi_f-\psi_L))} \]
where $\psi_L$ is leaf water potential (MPa); $\psi_f$ is an empirical reference water potential (MPa), and $s_f$ is a sensitivity parameter describing the steepness of the response of $g_s$ to $\psi_f$ (MPa$^{-1}$). The Tuzet model resembles the Medlyn and Leuning models but replaces the dependence on $D$ with a function of $\psi_L$.

The leaf water potential $\psi_L$ is obtained as follows. Assuming that the transpiration is a balance of demand and supply:

$$E = K \cdot (\psi_s - \psi_L) = g_s \cdot D/P_{atm} \quad (5)$$

where $K$ is the soil-to-leaf hydraulic conductance (mol m$^{-2}$ s$^{-1}$ MPa$^{-1}$); $\psi_s$ is the soil water potential (MPa) and $P_{atm}$ is the atmospheric air pressure (kPa). To solve for $\psi_L$ requires a value for $K$, which is assumed to decrease as plant water potential becomes more negative (Tyree and Sperry 1989):

$$K = K_{max} \cdot R_{PLC} \quad (6)$$

where $K_{max}$ is the maximum hydraulic conductance (mol m$^{-2}$ s$^{-1}$ MPa$^{-1}$). $R_{PLC}$ is the percentage loss of hydraulic conductance and takes the form of a Weibull function as fitted by Neufeld et al. (1992):

$$R_{PLC} = \frac{1}{1+\exp(a \cdot (\psi_L-\psi_{50}))} \quad (7)$$

where $a$ and $\psi_{50}$ are fitted parameters, representing the rate of decline of the curve and the leaf water potential at which plant hydraulic conductance is reduced to 50% respectively. This equation was fitted to the hydraulic vulnerability curves described above. Combining Equations 3 – 7 allows both $\psi_L$ and $g_s$ to be predicted.

We tested two alternative ways to represent non-stomatal limitations. In the first, $V_{cmax}$ was assumed to decline with leaf water potential (the $V$-PSI hypothesis):

$$V = V_{cmax} \frac{1+\exp(s_f \cdot \psi_{f})}{1+\exp(s_f \cdot (\psi_f - \psi_L))} \quad (8)$$

where $V$ is the $V_{cmax}$ modified by non-stomatal limitation and $s_f$ and $\psi_f$ are fitted parameters. $\psi_f$ is an empirical reference water potential (MPa), and $s_f$ is a sensitivity parameter describing the “steepness” of the response of $V_{cmax}$ to $\psi_f$ (MPa$^{-1}$). Note that this is the same form of sigmoidal function as used in the Tuzet model (Eqn. 3).

In the second representation of the non-stomatal limitation, we derived a direct empirical relationship between $V_{cmax}$ and $D$ (the $V$-$D$ hypothesis):
\[ V = \min(10, V_{\text{cmax}} \cdot (1 - c_D \cdot D)) \quad (9) \]

where \( c_D \) is a fitted parameter (kPa\(^{-1}\)). This relationship is different from that in Eqn. 8 because it assumes the apparent carboxylation capacity directly responds to \( D \). Although the mechanism for such a change is unclear, this simple empirical approach allows us to explore the possibility of direct downregulation of apparent \( V_{\text{cmax}} \) and \( J_{\text{max}} \). Similar simple empirical approaches have been used to explore non-stomatal limitation under low soil moisture content (e.g., Keenan et al., 2010, Verhoef and Egea, 2014; De Kauwe et al., 2015; Drake et al., 2017). We set a minimum \( V_{\text{cmax}} \) of 10 (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) to avoid negative values produced by the linear decline of \( V_{\text{cmax}} \) with \( D \). The same relationship is assumed for \( J_{\text{max}} \).

We assumed that the impact of reduced soil water availability could be represented in the Tuzet model by the reduction of soil moisture potential (\( \psi_s \)), which was estimated from the pre-dawn leaf water potential (\( \psi_{pd} \); MPa). For the Medlyn and Leuning models, we assumed an exponential dependence of the \( g_1 \) parameter on \( \psi_{pd} \) following Zhou et al. (2013):

\[ g_1 = g_{1,\text{MAX}} \cdot \exp(\beta \cdot \psi_{pd}) \quad (10) \]

where \( g_1 \) represents \( g_{1,\text{MED}} \) and \( g_{1,\text{LEU}} \); \( g_{1,\text{MAX}} \) is \( g_1 \) when \( \psi_{pd} = 0 \); \( \beta \) represents the sensitivity of \( g_1 \) to \( \psi_{pd} \). The impact of dry soil was implemented to account for the variation in the soil water availability among the campaigns.

**Parameterisation of leaf gas exchange models**

We used R (version 3.4.1 R Core Team) as the modelling and statistical tool. We used measured values of incident photosynthetically active radiation, leaf temperature, atmospheric \( \text{CO}_2 \) concentration, \( D \), \( \psi_{pd} \), \( J_{\text{max}} \), and \( V_{\text{cmax}} \) for the diurnal gas exchange data (at EucFACE only). We then parameterized the Medlyn and Leuning models at leaf scale using the differential evolution algorithm (\textit{DEoptim} package) to fit all the parameters (\( g_{1,\text{MAX}}, \beta, D_0 \), and \( c_D \)) in the coupled \( A-g_s \) model against the measured \( A \) and \( g_s \) data. We used a similar approach to determine the unknown parameter values in the Tuzet models. As a result, all the models tested at the leaf-scale were fitted to measurements of \( A \) and \( g_s \).

The fidelity of the leaf-scale models was evaluated via: (i) the Bayesian Information Criteria (BIC), which considered the relative residuals of predictions (both \( A \) and \( g_s \)) as well as the number of parameters in the models; (ii) the coefficient of determination (\( R^2 \)) of both \( A \) and
We ranked the models with these measures and selected the one with the highest overall ranking.

**Stand scale model**

We implemented the Medlyn model (Eqn. 1) with $V$-$D$ relationship (Eqn. 9) into a process-based stand-scale model MAESPA (Duursma and Medlyn 2012). For the purposes of this study, the plant hydraulics sub-model of MAESPA was not used; instead soil water content was prescribed rather than being simulated. The stand simulation included all six rings in EucFACE and covered the period between 1 January 2013 to 31 December 2013 on a half hourly basis. MAESPA considers the radiative transfer to an array of grid points within each tree crown and calculates gas exchange at each grid point based on light interception at each timestep. Understory plants were not included here because they do not contribute to tree transpiration. The model was parameterised with data on size and position of each tree as well as the smoothed and gap-filled leaf area index (Duursma et al., 2016; Figure S1).

Meteorological (Figure S1) and soil water content data (Figure 1) observed in each ring were input to the model. The original met data were aggregated to half-hourly averages and gap-filled with nearest available values (less than 1% of the total). Canopy physiology was parameterized with measurements of the light response of photosynthesis, dark respiration rate, and the temperature response of photosynthesis and respiration, all made at EucFACE and assumed not to vary across treatments. We assumed a minimum $g_s$ (Duursma et al., 2019) of 0.01 (mol H$_2$O m$^{-2}$ leaf s$^{-1}$) during daytime to avoid zero transpiration at extreme environmental conditions (e.g., high $D$). The transpiration of the canopy in the model is given by the Penman-Monteith equation, which considers net radiation, windspeed, relative humidity, and $g_s$.

The impact of low soil water content on stomatal conductance in MAESPA was modelled as a function of $g_1$ and volumetric soil water ($\theta$) content following Drake et al. (2017):

$$g_1 = g_{1, SAT} \cdot \left(\frac{\theta - \theta_{\text{min}}}{\theta_{\text{max}} - \theta_{\text{min}}}\right)^q$$

(11)

where $g_{1, SAT}$ is the value of $g_1$ (kPa$^{0.5}$) at saturating soil water content; $\theta_{\text{max}}$ and $\theta_{\text{min}}$ are empirically fitted parameters defining the upper and lower boundaries beyond which $g_1$ is not affected by $\theta$; and $q$ is the parameter describing the non-linearity of the function. We fitted Eqn. 11 to the data from Gimeno et al. (2016) to obtain the values of $\theta_{\text{max}}$, $\theta_{\text{min}}$, and $q$ (0.25,
0.11, and 0.38 respectively) with the non-linear least squares method (nls, R function). The fitted relationship between $g_{1,\text{MAX}}$ and $\theta$ used in the model is shown in Figure S2. $J_{\text{max}}$ in MAESPA is taken as a constant mean of 159 (μmol m$^{-2}$ s$^{-1}$) for all rings and time. $V_{c\text{max}}$ in MAESPA also remained constant over time but taken as 83 (μmol m$^{-2}$ s$^{-1}$) for elevated CO2 rings and 91 for ambient CO2 rings as per measurements (Ellsworth et al., 2017; Wujeska-Klause et al., 2019). The parameter values used in MAESPA are presented in Table S2.

Results

Leaf gas exchange models

The leaf gas exchange data from EucFACE showed a clear decline in both $A$ and $g_s$ with increasing $D$ (Figure 2). The baseline model (Medlyn with constant $V$) was unable to capture the response of $A$ (Figure 3a) or $g_s$ (Figure 3b) to $D$. As a result, this model ranked lowest amongst the models tested (BIC = -2452; Table 1). It over-predicted $A$ at high $D$ but under-predicted $g_s$ at low $D$. The Leuning model, despite its stronger sensitivity to $D$, shared the same problems as the Medlyn model (Table 1; Figure 3 c and d). In addition, we obtained unrealistic parameter values ($g_{1,\text{MAX}}$, $\beta$, and $D_0$) for the Leuning model (Table 1). Utilising the default parameter values for the Leuning model used in the CABLE land-surface model (for the evergreen broadleaf plant functional type), for example, led to severe under-prediction of $g_s$ (Figure S3). In other words, with commonly used parameter values, the Leuning model would have performed worse than all other models tested here (BIC = -2479).

The model incorporating hydraulic limitation (Tuzet K-PSI) showed a good agreement (BIC = -2387) with observations at both low and high $D$ (Figure 4 and Table 1). It achieved the second-best BIC value (Table 1). However, a comparison with the measured leaf water potential values shows that the Tuzet model performed well for the wrong reasons. The Tuzet K-PSI model predicted a decline of $\psi_L$ with increasing $D$ (Figure 5a); a large gradient between $\psi_s$ and $\psi_L$ (~4 MPa); and $\psi_L$ values below $\psi_{50}$ (~< -5 MPa). None of these predictions were supported by the observations (Figure 5 a and b). The observed $\psi_L$ did not change with $D$ (Figure 5a) and remained above the point of onset of embolism in all measurements (Figure 5b). The minimum observed $\psi_L$ value was -3.3 MPa, which was estimated to correspond to a PLC of 18%.

We examined the gas exchange data directly for evidence of non-stomatal limitation. Figure 6 shows the ratio of one-point $V_{c\text{max}}$ (estimated from gas exchange data using the “one-point”
method) to the predicted $V_{cmax}$ at the same temperature (estimated from $A$-$C_i$ curves performed at a range of temperatures). This ratio declined strongly with increasing $D$ as shown by data from EucFACE and Castlereagh sites. This decline in the one-point $V_{cmax}$ clearly demonstrates that non-stomatal limitation is a factor in the decline of $A$ at high $D$.

We then tested whether the non-stomatal limitation could be predicted as a function of leaf water potential (Tuzet V-PSI). Adding non-stomatal limitation to the Tuzet model comes at a cost of increased complexity, requiring six parameters to be fitted at the same time. This added complexity was not justified by the marginal improvements in $R^2$ resulting in the worst BIC value of all models tested (Table 1; Figure 7 a and b). Including the non-stomatal limitation in the Tuzet model did not lead to model improvement, which can be explained as follows. Firstly, we know that the plants did not reduce $\psi_L$ sufficiently to cause cavitation and a reduction in hydraulic conductance (Figure 5). Therefore, the non-stomatal limitation as a function of $\psi_L$ cannot predict a reduction in transpiration at high $D$. The observed decrease in $g_s$ at high $D$ leads to a less negative $\psi_L$ at high $D$, and a less negative $\psi_L$ implies a higher $V_{cmax}$. Higher $V_{cmax}$ at high $D$ contradicts both the assumption of non-stomatal limitation and the evidence shown in Figure 6.

Incorporating non-stomatal limitation into the Medlyn model (Medlyn V-D; Figure 7 c and d) improved the model predictions of both $A$ and $g_s$ (BIC = -2384). The Medlyn model, together with an empirical decline in $V_{cmax}$ with $D$, achieved better $R^2$ values for both $A$ and $g_s$ than the more complicated models, resulting in the best BIC value (Table 1).

It is not possible to determine from our measurements what mechanism causes this reduction in apparent $V_{cmax}$. Following Zhou et al. (2013), we investigated the possibility that the reduction is largely attributable to a reduction in mesophyll conductance by estimating how large the reduction in $g_m$ would need to be, to fully explain the observed reduction in one-point $V_{cmax}$. We assumed that all the discrepancy between the Medlyn model prediction and diurnal gas exchange data could be attributed to $g_m$. Then, for each diurnal measurement, a $g_m$ value was estimated as that which minimized the difference between the model predictions and the diurnal observations. A reduction in $g_m$ from 0.2 to 0.01 mmol m$^{-2}$ s$^{-1}$ would be implied if non-stomatal limitation were entirely due to a reduction of $g_m$ (Figure 8).
Stand scale model

Whole-tree transpiration estimated from sap flow measurements was used to evaluate the performance of the Medlyn V-D hypothesis at the whole-tree scale using the MAESPA model. The standard MAESPA using the Medlyn model overpredicted transpiration at EucFACE especially at high $D$ (example of Ring 2 in Figure 9a and b). The difference between the predicted and observed values increased strongly at high $D$ (compare green with red dots in Figure 9b). However, after incorporating the Medlyn V-D model, MAESPA closely followed the seasonal variation of the measurements (Figure 7c) and agreed with observations across the full range of $D$. Overall, incorporating the Medlyn V-D model increased the coefficient of determination from 0.78 to 0.87 and reduced the root mean squared error (0.027 to 0.025; L hr$^{-1}$). The improvements were even larger at high $D$ (>2.5 kPa) with a reduction of root mean squared error from 0.070 to 0.037. During the simulated year of 2013, incorporating non-stomatal limitation into MAESPA, resulted in a ~19% reductions in predicted annual transpiration (59.7 kg H$_2$O m$^{-2}$ yr$^{-1}$) and a ~14% reduction in gross primary production (222.4 g C m$^{-2}$ yr$^{-1}$). These findings indicate a large impact of non-stomatal limitation at high $D$.

We also explored whether the new model would improve predicted transpiration compared to observations at the Castlereagh site with similar species and climate conditions. Without canopy physiology or canopy structure data to parameterize the Castlereagh site, we took the approach of standardizing the observed sap flow and modelled $E$ by their respective maxima and comparing the relationships of $E$ with $D$ (Figure 10). Both sites show a peaked relationship of $E$ with $D$ with the turning point occurring between 1-3 kPa, which agrees with the prediction of MAESPA incorporating non-stomatal limitation (red line in Figure 10).

Discussion

We evaluated a suite of commonly used $g_s$ models and assumptions (hydraulic and non-stomatal limitation) used to represent the coupled $A$-$g_s$ response to $D$ at two native evergreen woodland sites in western Sydney. The observed decline of $A$ and $g_s$ at high $D$ could not be captured with current widely-used models of stomatal conductance, and models were not improved by incorporating hydraulic limitation and xylem cavitation. The model incorporating a non-stomatal limitation (i.e., a reduction of apparent photosynthetic capacity
with increasing $D$) gave the best agreement with the observations at a large range of $D$. This finding highlights the importance of accounting for non-stomatal limitation in TBMs.

_Standard models_

Standard leaf gas exchange models, embedded within TBMs, perform poorly when $D$ increases above 2.5 kPa, despite their wide use and important role (De Kauwe et al., 2015; Knauer et al., 2015). This finding is in line with previous studies showing the difficulties of modelling leaf gas exchange at high $D$ (e.g., Farquhar, 1978; Franks et al., 1997; Eamus et al., 2008). Our analysis re-emphasises the need to improve leaf gas modelling in ecosystems that experience high $D$. The concerned regions include drylands, which cover 41% of the Earth’s land surface (Reynolds et al., 2007) and potentially tropical, subtropical, and temperate ecosystems during dry seasons and heatwaves (Novick et al., 2016).

The comparison between the Leuning (1995) and Medlyn et al. (2011) models yields an important result, which is that improvements in the performance of the leaf gas exchange model at high $D$ are unlikely to be achieved by varying the stomatal sensitivity to $D$. The Medlyn model does not have a mechanism that allows $g_s$ or $A$ to decrease at high $D$ except via the temperature dependence of photosynthesis (Duursma et al., 2015; Kala et al., 2016). In contrast, the Leuning model does have a stronger regulation of $g_s$ at high $D$ but performs poorly at low $D$ (Figure 3 and S3), and requires an additional parameter to achieve this compared to the Medlyn model. Nonetheless, neither model is able to capture both $g_s$ and $A$ at high $D$.

_Models with hydraulic limitation_

The decline of $g_s$ at high $D$ in the models incorporating hydraulic limitation is achieved either by a small hydraulic conductance (resulting from a very negative $\psi_L$) or by a small pressure gradient (resulting from a $\psi_L$ close to $\psi_s$). The Tuzet model assumes the decline of $\psi_L$ drives the reduction of $g_s$ at high $D$. We found that this assumption led to an unrealistic decline in $\psi_L$ with increasing $D$, contradicting $\psi_L$ observations, which remained relatively consistent over the course of a day (Figure 5a). Moreover, the predicted $\psi_L$ fell below the estimated $\psi_{50}$ which is inconsistent with previous studies suggesting plant maintain $\psi_L$ above the point of onset of xylem embolism (Sperry et al., 2002; Choat et al., 2012; Li et al., 2018).

Incorporating non-stomatal limitation allowed a $\psi_L$ close to $\psi_s$ at high $D$. However, a less negative $\psi_L$ implied a higher $V_{max}$ at high $D$ which again contradicted the assumption of non-
stomatal limitation and the observations (Figure 6). As a result, the hydraulic limitation as implemented here, was an unable to capture the observed $D$ responses. Alternative models could potentially be more successful: Buckley (2013), for instance, proposed to model stomatal regulation via guard cell osmotic pressure in response to the water status of the surrounding epidermal cells. This approach is important because it can also incorporate increases in extra-xylary resistance that have been observed to occur in leaves (Yang and Tyree 1994; Scoffoni et al., 2017), roots (Cuneo et al., 2016), and the rhizosphere (North and Nobel, 1997). However, at this point the majority of models do not incorporate these resistances.

**Plausible mechanisms of non-stomatal limitation**

Studies on mesophyll conductance and photosynthetic capacity (e.g., Mediavilla et al., 2002; Nascimento and Marenco, 2013) have suggested the importance and mechanisms of non-stomatal limitation. The proposed mechanisms for non-stomatal limitation fall into two categories: (i) a biochemical-signalling-induced reduction in carboxylation capacity; or (ii) a reduction in mesophyll conductance, both of which have some empirical and theoretical support. Lawlor and Cornic (2002) and Lawlor and Tezara (2009) illustrated that carboxylation capacity is down-regulated at high water deficit due to reduction in adenosine triphosphate (ATP) synthesis. Huang et al. (2006) explored the cause of “midday depression” of $g_s$ and $A$ and suggested that the regulation of photosynthetic capacity is the likely explanation as plants aim to protect chloroplasts.

An alternative explanation for the decline of carboxylation capacity in the afternoon is sink limitation. It has been proposed that the accumulation of starch and sugar in the leaf over time causes an inhibition of photosynthesis (Paul and Foyer, 2001). We did not explore this effect because the data do not support this explanation at EucFACE (Wueska-Klause et al., 2019). We compared the diurnal time-course of photosynthesis for days with low and high $D$ (Figure S9). On days with low $D$, there is no reduction in afternoon photosynthesis even though morning photosynthesis was high, indicating that the accumulation of starch and sugar is not strong enough to cause a reduction in photosynthetic capacity.

It is also possible that non-stomatal limitation is due to a reduction of mesophyll conductance ($g_m$) with increasing $D$. Flexas et al. (2008) examined our current understanding of the response of $g_m$ to the environment (including $D$) and suggested that $g_s$ and $g_m$ could be co-regulated. Warren (2008) reported no $g_m$ response to $D$ in *Eucalyptus* seedlings. However,
that study only considered a small range of $D$ (1 kPa to 2 kPa) which is not sufficient to show the decline observed here. We investigated how large the reduction in $g_m$ would need to be to fully explain the observed reduction in apparent $V_{\text{max}}$ and found that a reduction in $g_m$ from 0.2 to 0.01 mmol m$^{-2}$ s$^{-1}$ would be implied if non-stomatal limitation were entirely due to a reduction of $g_m$ (Figure 8). These values and magnitude of change of $g_m$ are consistent with previous studies (Niinemets et al., 2009; von Caemmerer and Evans, 2015), suggesting that the apparent down-regulation could potentially be attributable to $g_m$. However, this result is not conclusive, because we are unable to quantify $g_m$ with the data available.

**Consequences for terrestrial biosphere models**

This study showed that the current gas exchange models in TBMs can perform poorly at high $D$. TBMs thus may be improved by incorporating non-stomatal limitation to predict $A$ and $g_s$ more accurately at high $D$. Previous studies have recommended using non-stomatal limitation to improve modelled response to decreasing soil moisture availability (e.g., Keenan et al., 2010; Egea et al., 2011; Zhou 2013; De Kauwe et al., 2015). Knauer et al. (2019) further demonstrated that incorporating non-stomatal limitation significantly changed the predicted CO$_2$ response in TBMs. Here we suggest that incorporating non-stomatal limitation at high $D$ may be necessary to capture the correct diurnal pattern of $g_s$ and $A$ as well as annual transpiration and gross primary production in ecosystems currently experiencing high $D$ (>2 kPa) and likely to under future warming.

However, we showed that under current hydraulic limitation assumptions, non-stomatal limitation cannot be successfully linked to $\psi_L$. We applied a simple empirical relationship to estimate non-stomatal limitation with $D$, but without a good understanding of the underpinning mechanism or its generality, it is unclear how widely this empirical dependence could be used. Further studies at high $D$ would be useful to quantify the impact of non-stomatal limitation more broadly, and to develop theoretical or mechanistic models (e.g., Gimeno et al., 2019). To inform mechanistic models of non-stomatal limitation, future studies need to collect extensive leaf gas exchange data across plant functional types under high $D$ (>2 kPa). In addition, mechanistic studies are needed to elucidate the key processes underlying non-stomatal regulation, including changes in photosynthetic capacity and $g_m$. The empirical relationship describing non-stomatal limitation that we present here could be replaced with theoretical or mechanistic alternatives as they emerge.
Data and Materials Availability

The code and parameters of the models are freely available via https://github.com/Jinyan-Yang/Yang_2019_VPD.

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Figure captions

Figure 1. (a) Soil water content (θ; dimensionless) averaged over the top 150 cm of each ring and (b) Leaf Area Index (LAI) at EucFACE in 2013. The LAI data were estimated by Duursma et al. (2016) from measurements of PAR transmittance and smoothed with a generalized additive model. Warm (red, orange and brown) and cold (blue, cyan and navy blue) colours depict elevated and ambient CO₂ rings.
Figure 2. The observed response of light-saturated photosynthesis (A) and stomatal conductance ($g_s$) to vapour pressure deficit (D) in the Licor chamber at EucFACE. Data are leaf gas exchange from four campaigns in 2013 in all six rings (obtained from Gimeno et al. 2016). The chamber D is similar to that of the outside air. Open circles: Ambient (A) rings; Closed circles: Elevated (E) rings.
Figure 3. Modelled photosynthesis (A) and stomatal conductance (gs) compared with observations. (a) and (b) Medlyn model (Eqn. 1). (c) and (d) Leuning model (Eqn. 2). Models were fitted to both A and gs data.
Figure 4. Modelled photosynthesis (A) and stomatal conductance (gs) incorporating hydraulic limitation (Tuzet K-PSI, Eqns. 3-7) compared with observations.
Figure 5. The Tuzet K-PSI model did not capture the observed leaf water potential ($\psi_L$). (a) Predicted and observed $\psi_L$ (circles and crosses, respectively) from the Tuzet model. Observations were made mid-morning (lower $D$, shown in blue) or early afternoon (higher $D$, shown in orange). (b) Estimated PLC curve based on dehydration measurements. Note in (a) that observed $\psi_L$ stays above the water potential corresponding to ~20% PLC ($> -3$ MPa), but the model predicts this value to fall to ~80% PLC ($< -5$ MPa).
Figure 6. Ratio of one-point $V_{cmax}$ (estimated from gas exchange data using the “one-point” method) to the predicted $V_{cmax}$ at the same temperature (estimated from $A-C_i$ curves performed at a range of temperatures), as a function of D. EucFACE data (orange) are from Gimeno et al. (2016); Castlereagh data (blue) are from Zeppel et al. (2008). Only the EucFACE data are used in parameterization; the Castlereagh data are used to show that the pattern is consistent across sites in the area.
Figure 7. Modelled photosynthesis (A) and stomatal conductance (gs) incorporating non-stomatal limitation (Eqn. 9) into Tuzet (Tuzet V-PSI) and Medlyn models (Medlyn V-D) compared with observations.
Figure 8. Estimated mesophyll conductance ($g_m; \text{mol m}^{-2} \text{s}^{-1}$) shows a decline with increasing vapour pressure deficit ($D; \text{kPa}$). The $g_m$ is estimated from diurnal leaf gas exchange measurements in EucFACE during 2013 under the assumption that the observed decline in $V_{cmax}$ is entirely due to decreasing $g_m$. The line marks the linear regression fit: $\ln(g_m) = -0.79 - 1.91 \cdot \ln(D)$ with a $R^2$ of 0.6. The fitting estimates a $g_m$ of 0.12 mol m$^{-2}$ s$^{-1}$ at $D = 2$ kPa; 0.03 mol m$^{-2}$ s$^{-1}$ at $D = 4$ kPa.
Figure 9. Modelled transpiration (E) compared to sap flow estimated by heat pulse sensors (measured E). Data shown are daytime for one stand (Ring 2) in 2013. Other stands are similar (Figures S4-S8). Panels (a) and (b) show measured and modelled E over time from original MAESPA. Panels (c) and (d) show the result from MAESPA with V-D hypothesis. The solid lines in Panels (a) and (c) show the daily average while the shading shows hourly variation (standard deviation).
Figure 10. Transpiration (E) across different sources/sites as a function of vapour pressure deficit (D). (a) is the sap flow data from Castlereagh (Zeppel et al., 2009). Bold line: generalised additive model (df = 5) fit to the data at saturated light (with PAR > 75% quantile). (b) and (c) are the estimated (sap flow) and modelled half-hourly daytime E for Ring 2 at EucFACE in 2013, respectively. Black and blue lines represent the same fitting to the modelled and sap flow data.
### Tables

**Table 1.** Summary of model parameter values and performance considered in this study. Note the differences in meanings and units in $g_s$ among models. Table shows both the coefficient of determination ($R^2$; higher is better) and inverse of Bayesian information criterion (BIC; lower is better) of both $A$ and $g_s$. Each criterion is ranked for the best two model combinations (best and second best marked as dark and light shade). Units for parameters are as follows: $g_{1,max}$ and $g_{1T}$, kPa$^{0.5}$; $\beta$, unitless; $D_0$, kPa; $\psi_f$ and $\psi_{fv}$, MPa; $s_f$ and $s_{fv}$, MPa$^{-1}$; $K_{max}$, mol m$^{-2}$ s$^{-1}$ MPa$^{-1}$; $c_{D0}$, kPa$^{-1}$.

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