OPINION

Relationship between plant hydraulic and biochemical properties derived from a steady-state coupled water and carbon transport model

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ABSTRACT

There is growing evidence that plant stomata have evolved physiological controls to satisfy the demand for CO₂ by photosynthesis while regulating water losses by leaves in a manner that does not cause cavitation in the soil–root–xylem hydraulic system. Whether the hydraulic and biochemical properties of plants evolve independently or whether they are linked at a time scale relevant to plant stand development remains uncertain. To address this question, a steady-state analytical model was developed in which supply of CO₂ via the stomata and biochemical demand for CO₂ are constrained by the balance between loss of water vapour from the leaf to the atmosphere and supply of water from the soil to the leaf. The model predicts the intercellular CO₂ concentration (Cᵢ) for which the maximum demand for CO₂ is in equilibrium with the maximum hydraulically permissible supply of water through the soil–root–xylem system. The model was then tested at two forest stands in which simultaneous hydraulic, ecophysiological, and long-term carbon isotope discrimination measurements were available. The model formulation reproduces analytically recent findings on the sensitivity of bulk stomatal conductance (gₛ) to vapour pressure deficit (D); namely, \( gₛ = gₛ^ref(1 - m \times \ln D) \), where \( m \) is a sensitivity parameter and \( gₛ^ref \) is a reference conductance defined at \( D = 1 \) kPa. An immediate outcome of the model is an explicit relationship between maximum carboxylation capacity (\( V_{max} \)) and soil–plant hydraulic properties. It is shown that this relationship is consistent with measurements reported for conifer and rain forest angiosperm species. The analytical model predicts a decline in \( V_{max} \) as the hydraulic capacity of the soil–root–xylem decreases with stand development or age.

Key-words: cavitation; hydraulic conductance; intercellular CO₂ concentration; maximum carboxylation capacity; photosynthesis.

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INTRODUCTION

More than two decades ago, Cowan & Farquhar (1977) argued that stomatal conductance varies so as to maximize net carbon gain while minimizing water loss to the atmosphere. Since their pioneering work, the literature on quantifying physiological controls on leaf carbon gain and hydrodynamics of water loss to the atmosphere has become quite extensive. Physiological control on leaf stomata can be quantified through a sequence of biochemical mechanisms, well described by combining the Farquhar, von Caemmerer & Berry (1980) model of photosynthesis and response of stomata to atmospheric humidity deficit (Leuning 1990, 1995; Collatz et al. 1991). Although these models are adequate for well-watered plants, it is clear that any complete description of stomatal conductance must include the interplay of biochemical processes in the leaves, loss of water through transpiration and the hydraulic limitations to water supply from the soil to roots and the leaf (Williams et al. 1996; Olioso, Carlson & Brisson 1996; Sperry et al. 1998; Oren et al. 1999; Tuzet, Perrier & Leuning 2002).

To quantify the relative importance of hydraulic and biochemical processes on annual canopy conductance, model calculations that account for the biochemical attributes of stomata can be compared to calculations that only consider plant hydraulics. Such comparisons were undertaken by Lai et al. (2002) in which bulk tree conductance derived from long-term sap flux measurements by Ewers et al. (2001a) were compared with mean annual conductance for two forest stands calculated by Lai et al. (2000) using a multilayer canopy model (CANVEG; Baldocchi & Meyers 1998). Lai et al. (2002) showed that the two approaches produced estimates of conductance close to values estimated theoretically on the basis of hydraulic limitations, calculated in Schäfer, Oren & Tenhunen (2000), and a stomatal response to water vapour pressure deficit prediction based on hydraulic theory with a broad empirical support (Oren et al. 1999). These predictions of stomatal conductance and behaviour is particularly striking for the CANVEG calculations because CANVEG does not consider the soil–root–xylem hydraulics (e.g. Lai et al. 2002) suggesting some equilibrium between the soil–plant hydraulic attributes and the...
biochemical parameters of the Farquhar et al. (1980) model at annual time scales.

Evidence for close relationships between stomatal conductance and plant hydraulic resistance have already been demonstrated by numerous measurements (Meinzer & Grantz 1990; Salinderra, Sperry & Comstock 1995; Fuchs & Livingston 1996; Lovisolo & Schubert 1998; Bond & Kavanagh 1999; Nardini & Salleo 2000; Comstock 2000; Sperry 2000; Schäfer et al. 2000; Hubbard et al. 2001). Equally important are the theoretical findings and field experiments demonstrating that leaf water potential cannot drop below a critical value (Tyree & Sperry 1988, 1989; experiments demonstrating that leaf water potential cannot 

It is also recognized that plant hydraulic and ecophysiological properties are not static but evolve with plant age and growth conditions (Yoder et al. 1991; Salinderra et al. 1995; Hubbard, Bond & Ryan 1999; Schäfer et al. 2000; Meinzer, Clearwater & Goldstein 2001). Given the connection between soil–root–xylem hydraulics, leaf stomatal conductance, and carbon gain, it may be argued that the key hydraulic and biochemical properties of plants must be related at some time scale relevant to stand development, although such a relationship has hitherto not been explored. Experimentally, one study has reported a strong correlation between leaf area-specific stem hydraulic conductivity and maximum photosynthetic capacity (Brodribb & Feild 2000), leading the authors to conclude that the maximum photosynthetic capacity of leaves and plant hydraulic conductivity do not operate independently.

In this study, we go further and suggest that photosynthetic parameters adjust so that the maximum biochemical demand for carbon uptake is in equilibrium with the maximum carbon gain permissible by the soil–root–xylem hydraulics on time scales relevant to stand development. We show that such an equilibrium hypothesis permits estimation of long-term, mean intercellular concentration (Ci), and hence, can be indirectly tested with carbon isotope discrimination measurements (e.g. Farquhar, Ehleringer & Hubick 1989; Ehleringer 1993; Ehleringer & Cerling 1995). An outcome of the equilibrium hypothesis is an analytic relationship between Vi,max and the maximum root-to-leaf hydraulic conductance.

**THEORY**

**Hydraulic limits on transpiration**

The transport of water from the soil reservoir to the leaf is given by

\[ J_w = \frac{\psi_s - \psi_l}{r_s + r_e} \]  

(1)

where \( J_w \) is the water flux from the soil to the leaf, \( \psi_s \) and \( \psi_l \) are the water potentials in the soil and leaf, respectively, and \( r_s \) and \( r_e \) are the hydraulic resistance values to the flow from the soil to the root and from the root to the leaf, respectively (Fig. 1). In unsaturated soils, \( r_e \) is primarily controlled by the hydraulic properties of the soil and is given by

\[ r_e = \frac{L_{at}}{K(\theta)} \]  

(2a)

where \( K(\theta) \) is the soil hydraulic conductivity function, \( \theta \) is the soil moisture content, and \( L_{at} \) is the effective distance travelled by a water molecule from the soil to the root surface. The hydraulic conductivity and soil water potential can both be estimated from \( \theta \) using the Clapp & Hornberger (1978) relationships, given by

\[ K(\theta) = K_{sat} \left( \frac{\theta}{\theta_{sat}} \right)^{2b+3} \]  

(2b)

\[ \psi_s(\theta) = \psi_{sat} \left( \frac{\theta}{\theta_{sat}} \right)^{-b} \]

where \( K_{sat} \) and \( \psi_{sat} \) are the soil hydraulic conductivity and soil water potential near field saturation (defined at \( \theta_{sat} \)) and \( b \) is an empirical parameter that varies with soil texture and pore-space structure. An order of magnitude estimate of \( L_{at} \) may be obtained from the root-zone depth (\( L_r \)) and root area index (\( R_{AI} \)) using a simplified cylinder model for root surface area.

\[ L_{at} = \pi L_r (R_{AI})^{1/2} \]  

(2c)

The hydraulic approach of Sperry et al. (1998) suggests that \( r_e \) is strongly dependent on \( \psi_i \) below a critical threshold value. The simplest analytical function which illustrate the key attributes of the variation of \( r_e \) with water potential is the ramp function given by

\[ \frac{1}{r_e} = \begin{cases} 0 & \text{if } \psi_i < \psi_{ti} \\ G_{r,max} \times \frac{\psi_e - \psi_{ti}}{\psi_{ti} - \psi_{di}} & \text{if } \psi_{ti} < \psi_e < \psi_{di} \\ G_{r,max} & \text{if } \psi_e > \psi_{di} \end{cases} \]

(3)

where \( G_{r,max} \) is the maximum root-to-leaf hydraulic conductance, \( \psi_{ti} \) is the threshold potential at which the root-to-leaf hydraulic conductivity begins to decline with decreasing potential, and \( \psi_{di} \) is the potential at which the root-to-
leaf hydraulic conductivity function becomes negligible. It should be pointed out that \( \psi_l \) and \( \psi_g \) represent whole-plant hydraulic parameters but are rarely measured at such a scale. Equations 1–3 describe the hydraulic capacity of the soil-root-xylem system to supply water to the leaf, \( J_w \).

**Atmospheric-demand limits on transpiration**

Using a big-leaf representation of the canopy (Fig. 1), water loss from the big leaf to the atmosphere (\( E \)) is given by

\[
E = 1.6g_s \times D_l
\]

where \( g_s \) is the bulk stomatal conductance to CO\(_2\), and \( D_l \) is the vapour pressure difference between the plant intercellular space and the atmosphere (assuming boundary layer conductance is much larger than stomatal conductance). Net photosynthesis (\( A_n \)) and \( g_s \) are related by

\[
g_s = \frac{A_n}{C_s - C_i}
\]

where \( C_s \) is the leaf surface CO\(_2\) concentration. Substituting Eqn 5 in Eqn 4, we obtain

\[
E = 1.6A_nD_l \times \frac{C_s - C_i}{C_s - C_i}
\]

**Steady-state water transport and hydraulic limitations on photosynthesis**

For a steady-state system (e.g. Fig. 1), the water supply from the soil-root system and atmospheric demand are in balance (i.e. \( J_w = E \)) leading to

\[
A_h = \frac{\psi_s - \psi_g}{r_s + r_e} \times \frac{C_s - C_i}{1.6D_s}
\]

The steady-state water balance results in a linear relationship between \( A_h \) and \( C_s \) in which the slope and intercept are dependent on soil water potential (\( \psi \)), leaf potential (\( \psi_g \)), and atmospheric driving force (\( D_l \)). It is possible to use Eqn 7 to assess the controls on the \( A_h \) curve for hydraulically limited plants.

As shown by Sperry (2000), plants typically operate at a value of \( \psi \), which is above or near the critical potential at which cavitation commences. Hence, at \( \psi_s = \psi_g \), the plant achieves the maximum permissible potential gradient that avoids significant loss of hydraulic conductivity in the root-xylem system. In a first-order analysis, and to retain tractability of the analytical derivation, we set \( \psi_s = \psi_g \),

\[ r_e = \frac{1}{G_{e,max}} \] (i.e. constant) so that Eqn 7 permits estimation of the maximum `hydraulically permissible' \( A_h \) without cavitation of the root or stem xylem. That is,

\[
A_h = \psi^* \times (C_s - C_i); \quad \text{where}
\]

\[
\gamma^*(D, \theta) = \frac{1}{1 + \frac{r_e}{K(\theta) + \frac{1}{G_{e,max}}}} \times \frac{\psi_s(\theta) - \psi_g}{1.6D}
\]

for \( D > 0 \). We have assumed \( D_s = D \) and \( C_i = C_s \) to obtain `first order' estimates of \( \gamma^* \) from long-term atmospheric drivers, where \( D \) is the atmospheric vapour pressure deficit and \( C_s \) is the atmospheric CO\(_2\) concentration. In short, for specified soil moisture (or \( \psi_g \)) and atmospheric forcing (\( D \)), the slope of the \( A_h \)–\( C_s \) curve (\( = \gamma^* \)) is the bulk stomatal conductance of the big leaf to CO\(_2\)) is controlled by the hydraulic properties of the soil-root-xylem system. We define the stomatal conductance per unit leaf area as \( \gamma^* = \gamma^*/L_{AI} \), where \( L_{AI} \) is the leaf area index. We also distinguish between \( \gamma^* \), the approximate conductance of the big leaf subject to all the hydraulic approximations in the soil-plant-atmosphere system, and \( g_s \), which is the exact conductance.

**Biochemical limitations on photosynthesis**

Equation 8 represents the maximum \( A_h \), resulting from the maximum hydraulically permissible supply of water at a given soil potential and for specified soil-root-xylem hydraulic properties. The biochemical demand for CO\(_2\) uptake also leads to an \( A_h \)–\( C_s \) curve described by the Farquhar et al. (1980) photosynthesis-biochemical model of \( C_3 \) plants and whose canonical form is given by

\[
A_h = \frac{\alpha_1(C_s - \Gamma^*)}{C_s + \alpha_2} - R_s,
\]

where \( \alpha_1 = \alpha_0 Q_{eq} e_m \) and \( \alpha_2 = 2\Gamma^* \) for light-limited photosynthesis, or \( \alpha_1 = V_{max} \) and \( \alpha_2 = k_c \left( 1 + \frac{\alpha_1}{k_o} \right) \) for photosynthesis limited by Rubisco activity, \( \alpha_0 \) is the leaf absorptivity for photosynthetically active radiation \( Q_{eq} \), \( e_m \) is maximum quantum efficiency, \( \Gamma^* \) is the compensation point for CO\(_2\) in the absence of dark respiration, \( V_{max} \) is the maximum carboxylation capacity of Rubisco, \( k_c \) and \( k_o \) are the Michaelis constants for CO\(_2\) fixation and O\(_2\) inhibition with respect to CO\(_2\), and \( o_i \) is the oxygen concentration. The biochemical parameters vary with temperature (\( T \)) as described in Campbell & Norman (1998) and Leuning (1995, 1997, 2002).

**Steady-state photosynthesis model**

We consider the `steady-state' \( C_i \) resulting from both hydraulic and biochemical limits on the \( A_h \)–\( C_s \) curves. Again, in a first-order analysis, we neglect \( R_s \) relative to \( A_h \) and match Eqn 8 to Eqn 9 which yields a quadratic equation in \( C_i \):

\[
k_1 C_i^2 + k_2 C_i + k_3 = 0
\]

\[ k_1 = -\gamma \]

\[ k_2 = \gamma(C_s - \alpha_2) - \alpha_1 \]

\[ k_3 = \alpha_1 \gamma C_s + \alpha_0 \Gamma^* \]

whose solution is given by

\[
C_i = \frac{-k_1 \pm \sqrt{k_1^2 - 4k_2k_3}}{2k_1}
\]

The \( C_i \) in Eqn 10 is the result of a balance between biochemical (enzyme kinetics) and hydraulically controlled
photosynthesis. The corresponding leaf $A_n$ and $g_s$ can be computed from Eqns 9 and 5. The solution in Eqn 10 has two roots, one where $C_i > C_a$, corresponding to a negative $E$, and the other where $C_i < C_a$, corresponding to a positive $E$. The second of these two roots must be chosen.

We restate that Eqn 10 is only approximate and subject to numerous simplifications, listed below:

1. The model is implicitly a ‘big-leaf’ and treats the entire plant as a single photosynthetic object. As such, its validity is proportional to the validity of the assumptions that underlie the big-leaf simplification. Similar scaling assumptions apply to soil–root resistances in which the roots are treated as cylinders perfectly connected to the soil water. Furthermore, the computed $L_{sr}$ is only an order of magnitude estimate and is likely to vary appreciably with root diameter and root length density (Campbell 1991).

2. $\psi_e$ is constant and near its permissible limit at all times of the day and over the entire duration of stand development.

3. Boundary layer resistance is assumed negligible compared to the stomatal resistance.

4. Dark respiration is assumed negligible relative to gross photosynthesis.

5. CO₂-water vapour diffusive interference (i.e. the ‘ternary effects’) is ignored.

Despite these numerous simplifications, which lead to $g_s = \gamma^*$, this equation captures analytically the major factors controlling long-term $C_i$, including basic attributes of plants ($G_{\text{gmax}}, \psi_{tl}, L_{Al}, V_c, \Gamma^*$), soil type ($\psi_{sat}, K_{sat}, b, \theta$), soil water status ($\theta$), the humidity deficit (i.e. $D_s$) at the leaf surface which we assume to be well approximated by the atmospheric vapour pressure deficit $D$, and CO₂ concentration. For example, we show in Fig. 2 how $C_i/C_a$ varies with soil water status ($\theta$) and atmospheric humidity deficit ($D_s$) for two contrasting soil types (sand and clay) and for two

Figure 2. Variation of $C_i/C_a$ with soil moisture ($\theta$) and atmospheric forcing ($D$) for two soil types (sand and clay) and two species having different vulnerability curves (also shown). As illustration, the vulnerability curve (right panels) for species 1 trees has high $G_{\text{gmax}}$ but low $\psi_{tl}$ whereas that of species 2 has low $G_{\text{gmax}}$ and high $\psi_{tl}$ (see Table 1).
tree species with different xylem vulnerability curves (species 1 – high $G_{\text{max}}$ and small negative $\psi_v$ and species 2 – low $G_{\text{max}}$ and more negative $\psi_v$). The numerical values of the parameters used in this hypothetical example are summarized in Table 1.

Intercellular CO$_2$ concentrations in Fig. 2, modelled based on the arbitrary set of parameter values shown in Table 1, clearly depend on soil type, atmospheric humidity deficit and leaf physiochemical demand. The model shows that $C_i/C_a$ for species 2 is expected to be less than for species 1 at high values of $\theta$ and low $D$ and that for species 1, which is more susceptible to cavitation than species 2, $C_i/C_a$ decreases rapidly with $\theta$ at any value of $D$. Note that the low $C_i/C_a$ shown in Fig. 2 reflects the asymptotic limits for the range in soil water availability and atmospheric demand for water vapour, and not aimed to demonstrate the ratio under realistic climate conditions. We emphasize that for short-term duration (– hours or even days), it is unlikely that the biochemical demand for CO$_2$ is in exact balance with the hydraulic limitations on its supply. Furthermore, it is unlikely that $\psi_v$ is constant and near its permissible limit at all times of the day and over the entire duration of stand development. However, it is plausible that the hydraulic and ecophysiological properties adjust in concert over the course of the stand development (~ year) so that the stand achieves some equilibrium between the maximum biochemical demand for carbon assimilation and hydraulic limitations imposed on its supply.

We selected $C_i$ as the ‘state variable’ in the evaluation of the proposed equilibrium for three reasons.

1 Long-term mean values of $C_i$ are now available based on carbon isotopes discrimination techniques (e.g. Farquhar et al. 1989; Ehleringer 1993);

2 The long-term $C_i/C_a$ is a dimensionless number constrained between 0:5 and 0:9 for several $C_i$ species (e.g. Wong, Cowan & Farquhar 1979; Norman 1982; Leuning 1995; Katul, Ellsworth & Lai 2000)

3 The value of $C_i$ can be readily interpreted as the operating point between the demand for CO$_2$ by photosynthesis and the maximum conductance permissible by soil–plant hydraulics at a given $C_i$, $D$ and $\theta$. Figure 3 illustrates such an interpretation with the demand curve for CO$_2$ computed from Eqn 9 and the stomatal conductance computed from Eqn 8. The fixed point on the abscissa is the external CO$_2$ concentration, $C_a$, and the straight lines geometrically represent $-\gamma$. The operating point of the leaves ($A_{\text{max}}$, $C_i$) is given by the intersection of the biochemical demand curve and the supply lines. This figure demonstrates that $C_i$ and its sensitivity to $D$ can vary with soil type even if all other parameters, including photosynthetic capacity and soil moisture, are held constant. Thus at $\theta=0.3$ and at any given humidity deficit, $g_{\text{co}}$, $A_{\text{max}}$ and $C_i$ are predicted to be higher for plants growing in clay soils than in sand. The difference in this hypothetical example arises because $\psi_v(\theta)$ and $K(\theta)$ (and hence $r_m$) differ for sand and clay at the same soil water content.

### RESULTS

#### Model testing

The steady-state model of photosynthesis and plant hydraulics was tested based on data from two forest stands for which we have measurements of the necessary hydraulic and ecophysiological properties and long-term values of $C_i/C_a$ from carbon isotope discrimination methods. With $C_i/C_a$ predicted, the model can be extended to predict the long-
In Table 2, and the variation of daytime ecophysiological parameters for each site are summarized. Details of the hydraulic and plant hydraulic parameters of the Duke Forest site, shown in Table 2, are used. For soil hydraulic properties, parameter values from Clapp & Hornberger (1978) are used.

Duke Forest and SETRES study sites

The two study sites are Pinus taeda L. tree plantations situated in North Carolina, USA. The first is a 15-year-old-plantation (in 1998) on a clay loam soil at the Duke Forest near Durham (35°58’ N, 79°8’ W) and is the same stand used for a free air CO$_2$ enrichment (FACE) project (Ellsworth 1999, 2000) and an AmeriFlux site (Katul et al. 1999). The second is a sandy soil site with a 14-year-old-plantation at the South-east Tree Research and Education Site (SETRES) in the sandhills of south-central North Carolina (34°48’N, 79°12’W; Albaugh et al. 1998; King et al. 1999; Hacke et al. 2000). Annual precipitation at both sites is, on average, about 1200 mm. Details of the hydraulic and ecophysiological parameters for each site are summarized in Table 2, and the variation of daytime $D$ (defined from local sunrise to local sunset) is shown in Fig. 4. We note that for these two stands, approximating $D$ by $D$ is shown to be reasonable by Ewers & Oren (2000).

Using Eqn 10 we estimate $C_i/C_a$ for both sites and for a wide range of $\theta$ and two values of $D$ (Fig. 4). The mean values of $C_i/C_a$ estimated from carbon isotope analysis of leaves for each site are also plotted as a function of mean soil moisture content in Fig. 4. Details of the carbon isotope analysis for SETRES and Duke Forest are presented in Lai et al. (2002), Katul et al. (2000), and Ellsworth (1999). Briefly, the carbon isotope ratio was determined on sun-type needles collected from the upper crown of eight trees during the growing season. The monthly daytime $D$ ranges from a minimum of 0·4 kPa (winter) to 1·5 kPa (summer) for both forests. The mean annual daytime $D$ value is about 0·8 kPa (Schäfer et al. 2002). The corresponding mean $\theta$ is about 0·08 for SETRES (Ewers et al. 2001a, b) and about 0·20 for the Duke Forest (Schäfer et al. 2002). The model predicts that $C_i/C_a$ remains relatively constant at high moisture content but drops rapidly as the soil dries, with the moisture content at which the decrease commences being dependent on soil type. The $C_i/C_a$ patterns modelled are similar to the patterns in reference canopy conductance found at the two sites (Oren et al. 1998; Hacke et al. 2000; Ewers et al. 2001a, b). Mean values of $C_i/C_a$ estimated using carbon isotopes also showed good agreement with model calculations when $D = 0·8$ kPa.

Another interesting point in Fig. 4 is the relationship between the value of $C_i/C_a$ and the soil moisture content at which bulk canopy conductance declines. From leaf porometry measurements in summer-time at both sites, we use the minimum recorded $C_i/C_a$ ($\sim 0·5$) to estimate this soil moisture. The resulting estimates for SETRES and Duke Forest are $\theta = 0·055$ and $\theta = 0·19$, respectively (again using $D = 0·8$ kPa). From sapflux measurements, Oren et al. (1998) reported a threshold $\theta = 0·20$ at which bulk canopy conductance declines.
conductance of the Duke Forest *P. taeda* trees are primarily controlled by θ. Similarly, Ewers *et al.* (2001b) reported a threshold of θ = 0.049 at which bulk canopy conductance measured using sap fluxes in SETRES rapidly declines with θ. Both soil moisture threshold limits are consistent with the analytical model calculations.

**Modelled conductance variation with D**

We assessed the consistency of the equilibrium model with the sensitivity of stomatal conductance to D found by Oren *et al.* (1999), given by \( g_s = g_{st}(1 - m \times \ln D) \), where \( g_{st} \) is a reference conductance defined at \( D = 1 \) kPa and \( m \) is a sensitivity parameter (Oren *et al.* 1999). Such a relationship can be derived if it is assumed that the response of \( g_s \) to \( D \) is due to stomatal regulation of plant water potential above the value in which catastrophic cavitation may be initiated (Oren *et al.* 1999; Tuzet *et al.* 2002). Based on this approach, higher stomatal conductance at a reference \( D \) leads to a proportional increased sensitivity of stomatal conductance to \( D \) to preserve the hydraulic integrity of the flow path.

Thus, when the conductance is expressed as \( g_s = g_{st}(1 - m \times \ln D) \), a near-constant value of \( m \in [0.53-0.60] \) emerges. The value of \( m \) computed in Oren *et al.* (1999) compares well with values obtained from whole-tree and leaf conductance measurements made on a wide range of non-woody and woody species, of different xylem types, in ecosystems representing the range from tropical to boreal (Black & Squire 1979; Oren *et al.* 1999, 2001; Ewers *et al.* 2000, 2001a, b; Schäfer *et al.* 2000; Oren & Pataki 2001).

These findings (including \( m \)) can be reproduced analytically by noting that Eqn 8 can be expressed as

\[
g_s = f(V_{\text{max}}, \theta, L_{\text{max}}, \psi_s, \ldots)\]

so that at \( D = 1 \) kPa \( g_s = g_{st} = f(\ast) \), where \( f(\ast) \) is a function given by Eqn 8 for \( D = 1 \) kPa. At first glance, the two formulations appear inconsistent as the equilibrium model predicts a \( g_s \) proportional to \( D^{-1} \) while the \( g_s \) model tested in Oren *et al.* (1999) predicts \( g_s \) proportional to \( 1 - m \times \ln(D) \). This apparent discrepancy can be rectified if we note that \( 1/D = 1 - 0.5 \ln(D) \) for \( D \) varying between 1 and 5 kPa. It is for this reason that the value of \( m \) in the Oren *et al.* (1999) model must be a near constant close to 0.5 and appears sensitive to the \( D \) range used, as well as the other factors in Eqn 8.

**DISCUSSION**

Thus far, we have shown that the steady-state photosynthesis and hydraulic conductance model produces realistic estimates of long-term \( C_s \) consistent with carbon isotope discrimination measurements at two sites. To achieve our stated goal, an analytic relationship between the leaf ecophysiological and soil-plant hydraulic properties must be established.

We express \( V_{\text{max}} \) as a function of \( \gamma^a, L_{\text{AI}}, \) and long-term \( C/C_s (= \xi) \) by combining Eqns 8 and 9 to give

\[
V_{\text{max}} = C_a \times \frac{\gamma^a}{L_{\text{AI}}} \times \frac{(1 - \xi^*) \times (\xi^* + \alpha_2/C_s)}{\xi^*}
\]  

(11a)

where \( \Gamma^a/C_s \) is neglected (when compared to unity, it is less than 10%). Also, \( \alpha_2/C_s \) is approximately constant \(-510/ \)
For a wide range of species, long-term $\xi_c$ is also restricted to a limited range (between 0.50 and 0.9 as in Leuning 1995; Katul et al. 2000). Hence, we find that an explicit relationship between ecophysiological and hydraulic attributes emerges, given by

$$V_{\text{max}} = \frac{K(\theta)G_{\text{re,max}}}{L\alpha} + \frac{1}{L\alpha} \times \frac{1}{6D} \times (\psi_\ell(\theta) - \psi_\ell)$$

In the above derivation, we have assumed that $\alpha_1 = V_{\text{max}}$. This derivation could be repeated with $\alpha_1 = \alpha_1 Q_c^e m$ and $\alpha_2 = 2I^e$ rather than $\alpha_1 = V_{\text{max}}$ and $\alpha_2 = k^e (1 + \frac{I_m}{I_e})$ if electron transport limits photosynthesis. From Eqn 11b, when $K(\theta) >> L\alpha G_{\text{re,max}}$, a linear relationship between $V_{\text{max}}$ and $G_{\text{re,max}}$ emerges assuming all other parameters are held constant. Such a linear relationship between photosynthetic capacity and plant hydraulic conductivity was observed by Brodribb & Feild (2000; their Fig. 2) using a combination of chlorophyll fluorescence and hydraulic analysis on seven conifers and 16 angiosperm rainforest species in New Caledonia and Tasmania.

In Fig. 5, we show the predicted variation of $V_{\text{max}}$ with $G_{\text{re,max}}$ for $D = 1$ kPa, $\psi_\ell = -0.5$ MPa (determined by us assuming the leaf pressure in Fig. 3 of Brodribb and Feild is near $\psi_\ell$), and an assumed $L\alpha = 3$, $C_a = 380$ p.p.m., and $\xi_c = 0.7$, and for a wide range of soil moisture conditions. In these calculations, the soil type was assumed to be sandy clay loam (for illustration) whose hydraulic properties are given by Clapp & Hornberger (1978). For well-watered conditions ($\theta > 0.3$), we show that $V_{\text{max}}$ increases linearly with $G_{\text{re,max}}$ with a slope not sensitive to $\theta$, compatible with the observations by Brodribb & Feild (2000; annual precipitation in New Caledonia and Tasmania exceeds 1800 mm). However, it is not possible to compare directly the results of our model with those of Brodribb & Feild (2000) because they reported the mean quantum yield of photosystem II electron transport ($\varphi_{\text{PSII}}$) and provided no information about soil type, $L\alpha$, and $\xi_c$. However, we do note that their $\varphi_{\text{PSII}}$ varied by a factor of 7 and our computed $V_{\text{max}}$ varied by a factor of 8 for the same range in $G_{\text{re,max}}$. The model in
Eqn 11b goes further to suggest that when \( \theta \) decreases, \( K(\theta) \) is no longer large when compared with \( G_{r,\text{max}} \) resulting in a non-linear relationship between \( V_{\text{max}} \) and \( G_{r,\text{max}} \) (Fig. 5). There is likely to be a curvilinear relationship between \( V_{\text{max}} \) and \( G_{r,\text{max}} \) in drier climates with the degree of non-linearity strongly dependent on soil type and soil moisture content.

Another consequence of the equilibrium model with an approximately constant \( \xi \) is that the ratio of \( V_{\text{max}} \) between two different species or for the same species at different developmental age is primarily driven by

\[
\frac{V_{\text{max}}(1)}{V_{\text{max}}(2)} = \frac{L_{\text{Al}}(1)}{L_{\text{Al}}(2)} \times \frac{\psi(1)^{\xi}}{\psi(2)^{\xi}}
\]  
(12)

So, it is possible to express Eqn 12 in terms of quantities that may be easier to model or estimate such as \( L_{\text{Al}} \) and \( g_{\text{s,\text{max}}} \):

\[
\frac{V_{\text{max}}(1)}{V_{\text{max}}(2)} = \frac{L_{\text{Al}}(1)}{L_{\text{Al}}(2)} \times \frac{g_{\text{s,\text{max}}}(1)}{g_{\text{s,\text{max}}}(2)}
\]  
(13)

We note that Eqn 13 also follows from Eqs 5 and 9 for Rubisco-limited photosynthesis at constant \( \xi \). The latter approximation appears to be valid across a wide range of species as demonstrated by Schultz et al. (1994), who reported a linear relationship between maximum bulk conductance and maximum photosynthetic capacity per unit ground area for tropical, temperate deciduous broad-leaved forests, temperate evergreen broad-leaved forests, tropical forest, and herbaceous tundra with an approximate slope consistent with \( \xi = 0.82 \).

To further illustrate the applicability of Eqn 13, we consider the fertilization experiment at SETRES-II described in Lai et al. (2002) in which \( V_{\text{max}} \) and \( L_{\text{Al}} \) were measured for a 6-year-old fertilized and control plots of \( P. \text{taeda} \) (see Table 3). The SETRES-II study site is adjacent to the SETRES experiment described in Ewers et al. (1998, 2001a,b). The stand, predominantly \( P. \text{taeda} \), was planted in 1993 at 1.5 m × 2.1 m spacing on an infertile, well-drained, sandy, siliceous, thermic Psammentic Hapludult soil (Wakulla series) with a water holding capacity of 12–14 cm in a 2 m profile. Foliar nutrient ratios are used to guide annual fertilizer applications aimed at maintaining a balanced and optimal supply of all nutrients in the fertilized plots, so as to stimulate rapid growth. The nitrogen treatment, approximately 11.2 g m⁻² per year as urea, supplemented as necessary with other nutrients is described in Albaugh et al. (1998). Using sapflux measurements, Ewers et al. (2001a,b) estimated canopy \( g_{e,\text{f}} \) for the fertilized and control plots from the nearby site (SETRES) with similar soil–root–plant hydraulic characteristics as the Lai et al. (2002) fertilization study. The measured canopy \( g_{e,\text{f}} \) increased 2:5-fold under an optimal fertilization regime. Using the measured leaf area index and \( g_{e,\text{f}} \) (the latter, as demonstrated earlier, includes all stomatal responses except to vapour pressure deficit) we estimate the enhancement.

**Figure 5.** The variation of \( V_{\text{max}} \) with \( \theta \) and \( G_{r,\text{max}} \) for the range of \( G_{r,\text{max}} \) reported in Brodribb & Feild (2000) using Eqn 11b, with \( \psi_0 = -0.5 \) MPa (from Brodribb & Feild 2000), \( \xi = 0.7, D = 1 \) kPa, and for a sandy-clay loam whose hydraulic properties are given in Clapp & Hornberger (1978). For wet conditions, Brodribb & Feild (2000) reported a linear dependence between mean \( \phi_{\text{out}} \) and specific xylem conductivity with a squared correlation coefficient (\( r^2 \)) of 0.74.

**Table 3.** Measured \( L_{\text{Al}} \) and \( V_{\text{max,25}} \) of \( P. \text{taeda} \) at SETRES-II (from Lai et al. 2002) after 6 years of nitrogen fertilization. The SETRES-II site is near the SETRES site whose ecophysiological and hydraulic parameters are described in Ewers et al. (2001a) and Hacke et al. (2000). The \( g_{e,\text{f}} \) are from Ewers et al. (2000)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Control</th>
<th>Fertilized</th>
</tr>
</thead>
<tbody>
<tr>
<td>( L_{\text{Al}} ) (m² m⁻²)</td>
<td>1.65</td>
<td>3.51</td>
</tr>
<tr>
<td>( V_{\text{max,25}} ) (µmol m⁻² s⁻¹)</td>
<td>85.4</td>
<td>100.2</td>
</tr>
<tr>
<td>( g_{e,\text{f}} ) (mmol m⁻² s⁻¹)</td>
<td>50</td>
<td>125</td>
</tr>
</tbody>
</table>
moment in $V_{\text{max}}$ to be: $\frac{V_{\text{max}}^{(t)}}{V_{\text{max}}^{(c)}} = \frac{1.65}{3.51} \times \frac{125}{50} = 1.18$ or about 18% enhancement, where $V_{\text{max}}^{(d)}$ and $V_{\text{max}}^{(c)}$ are the maximum carboxylation capacity for the fertilized and control stands, respectively. The gas-exchange measured $\frac{V_{\text{max}}^{(d)}}{V_{\text{max}}^{(c)}} = 1.00 \cdot 2 = 1.17$, which closely matches the enhancement calculated above.

An immediate consequence of this approach is that older forests will have lower $V_{\text{max}}$ when compared with younger forests because of the lower hydraulic conductances and $g_{\text{st}}$ of older and taller trees (e.g. Yoder et al. 1991; Salientra et al. 1995; Hubbard et al. 1999; Schäfer et al. 2000). Furthermore, older forests typically have reduced leaf nitrogen; hence, it is expected that they also have a smaller $V_{\text{max}}$ (Ellsworth 2000; Clearwater & Meinzer 2001; Lai et al. 2002). Both of these results (i.e. reduced $V_{\text{max}}$ and $g_{\text{st}}$ with age) are consistent with the numerous observations that photosynthetic rates also declines with age even after a stand achieves an $L_{\text{A}}$ that remains approximately constant during that decline period (Ryan & Yoder 1997a, Ryan, Binkley & Fownes 1997b).

CONCLUSIONS

Simple equations describing water supply by the soil and roots to leaves, water loss through transpiration, stomatal conductance and photosynthesis, have led to an expression between $V_{\text{max}}$, mean intercellular CO2 concentrations, leaf area index and the hydraulic conductance of the plant, $G_{\text{st}}$. The model predicts a strong, linear dependence of $V_{\text{max}}$ on $G_{\text{st}}$ which is independent of volumetric soil moisture contents, $\Theta > 0.3$, and a non-linear, decreasing dependence in drier soils.

Intercellular CO2 concentration, $C_{i}$, are shown to depend strongly on moisture content and atmospheric humidity deficit, plant hydraulic conductance and soil type. An equilibrium between maximum carbon demand by photosynthesis and maximum water supply by the soil leads to a unique long-term mean intercellular CO2 concentration. The $C_{i}$ at equilibrium can be thought of as a reference state to assess any shifts in hydraulic conductance of soil and plant and photosynthetic capacity. Where the long-term measured $C_{i}/C_{a}$ (e.g. as determined by the carbon isotope discrimination method) is consistent with this equilibrium value and does not vary in time, then the ecophysiological and hydraulic properties are invariant and in equilibrium. A consequence of equilibrium as defined in this study, is an analytical method that can be used to estimate shifts in ecophysiological properties such as $V_{\text{max}}$ based on shifts in hydraulic properties. Such understanding of the dynamics of $V_{\text{max}}$ on time scales relevant to stand development is necessary to quantifying future terrestrial carbon cycling.

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REFERENCES


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