

Leaf stomatal responses to vapour pressure deficit under current and CO₂-enriched atmosphere explained by the economics of gas exchange

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ABSTRACT

Using the economics of gas exchange, early studies derived an expression of stomatal conductance (g) assuming that water cost per unit carbon is constant as the daily loss of water in transpiration (f_c) is minimized for a given gain in photosynthesis (f_p). Other studies reached identical results, yet assumed different forms for the underlying functions and defined the daily cost parameter as carbon cost per unit water. We demonstrated that the solution can be recovered when optimization is formulated at time scales commensurate with the response time of g to environmental stimuli. The optimization theory produced three emergent gas exchange responses that are consistent with observed behaviour: (1) the sensitivity of g to vapour pressure deficit (D) is similar to that obtained from a previous synthesis of more than 40 species showing g to scale as $1 - m \log(D)$, where $m \in [0.5, 0.6]$, (2) the theory is consistent with the onset of an apparent 'feed-forward' mechanism in g , and (3) the emergent non-linear relationship between the ratio of intercellular to atmospheric [CO₂] (c_i/c_a) and D agrees with the results available on this response. We extended the theory to diagnosing experimental results on the sensitivity of g to D under varying c_a .

Key-words: gas exchange; optimal stomatal control; photosynthesis; stomatal conductance; transpiration.

INTRODUCTION

Jan Baptist van Helmont is credited with coining the word 'gas' in the 17th century and noting that 'gas sylvestre' (carbon dioxide) is given off by burning charcoal. He also investigated water uptake by a willow tree in 1648, in effect performing one of the earliest recorded experiments on stomatal conductance (g) to gas transfer. Centuries later, both of van Helmont's activities converged in a modern-day story: Atmospheric CO₂ is rising largely because of the combustion of fossil fuel, and the ability of terrestrial plants to uptake CO₂ is currently a leading mitigation strategy to offset this rise. Because the role of stomata in regulating the

exchange of CO₂ for water is central to many plant and ecosystem processes, services and products, variations in g and in their responses to environmental variables have been subjected to intense research for decades. And yet, despite numerous experiments and several modelling approaches, the precise mechanisms responsible for stomatal responses to certain environmental stimuli remain vague (see e.g. review by Buckley 2005).

Several empirical and semi-empirical models describing stomatal responses to environmental stimuli exist (e.g. Jarvis 1976; Collatz *et al.* 1991; Leuning 1995). These models, advanced primarily after the publication of the seminal work by Jarvis (1976), are based on an electrical circuit analogy – stomata are viewed as a resistor (or a conductor) with a maximum species-specific value of g attained when stomatal pores are fully open. The maximum g is reduced by non-linear functions that account for the effects of external environmental factors via increases in the concentration of CO₂ in the leaf's air space, or the capacity of the soil–plant hydraulics to supply water to the leaf relative to the potential rate of vapour loss rate from fully open stomata. These functions reflect decreasing light levels, increasing CO₂ concentration and vapour pressure deficit, departure from optimum leaf temperature, and also decreasing leaf water potential representing the hydration state of the stomatal system. Such a parsimonious representation of stomatal conductance, combined with the increased availability of portable equipment for measuring gas exchange, greatly contributed to quantifying differential species sensitivities to environmental stimuli and stresses.

The wealth of data on g led to certain generalities on stomatal responses to the environment. For example, Mott & Parkhurst (1991) demonstrated that stomatal closure is a response to leaf transpiration rate rather than to varying vapour pressure deficit (D). Nevertheless, a synthesis of stomatal responses to varying D , obtained from studies on over 40 species from grasses to deciduous and evergreen trees, revealed a general functional form that can be described as $g = g_{\text{ref}}(1 - m \log(D))$, where $m \approx 0.5$ – 0.6 and g_{ref} is g at $D = 1$ kPa (Oren *et al.* 1999). Further support for this value of m was provided in Mackay *et al.* (2003). It was also demonstrated that the value of $m \approx 0.6$ is consistent with a hydraulic model in which plants control transpiration

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rate to protect the transport system from excessive loss of hydraulic function (Sperry *et al.* 1998, 2002; Oren *et al.* 1999; Lai *et al.* 2002). Yet stomatal control cannot be only to regulate the rate of water loss. Indeed, it has long been suggested that, at the leaf scale, natural selection may have operated to provide increasingly efficient means of controlling the trade offs between carbon gain and the accompanying water vapour loss (e.g. Cowan 1977, 1982, 2002; Ball, Cowan & Farquhar 1988). If so, can such an optimization principle be used to constrain certain parameters in semi-empirical models, perhaps even replacing them by functional responses that naturally emerge from such optimization? Emergent functions are more general, unlike imposed functions that empirically describe data, limiting their application to the conditions represented by the experiment.

First presented by Cowan (1977) and Cowan & Farquhar (1977), and reformulated by Hari *et al.* (1986) and Berninger & Hari (1993), the cost (= daily water loss in transpiration) to benefit (= daily carbon gain in photosynthesis) analysis was framed as an 'economic' optimization. While the assumptions on the form of the underlying functions differ between Cowan & Farquhar (1977) and Hari *et al.* (1986), their optimal solutions are, in fact, identical. Moreover, while both studies implicitly assumed an integration time scale, their solution appeared independent of the time scale of flux integration. The stomatal control over gas exchange is described through a concept of invariant 'carbon cost of water' or 'water cost of carbon', without *a priori* specification of stomatal response to D or atmospheric CO_2 . The predicted expressions of stomatal responses to D or atmospheric CO_2 are 'emergent properties' of the optimization theory. We compare these emergent responses with data from studies from a wide range of conditions. We demonstrate that the optimization theory permits predictions of stomatal response to environmental stimuli, especially with respect to D in both current and CO_2 -enriched atmosphere. The analysis limits 'optimality' to bulk leaf gas-exchange; it may not be used to explain such inter-related questions as how guard cells operate to achieve optimality, or why leaves are oriented in a specific way within ecosystems.

THEORY

The basic equations for the leaf-level CO_2 and water vapour fluxes across stomata are given by:

$$f_c = g(c_a - c_i) \quad (1)$$

$$f_e = ag(e_i - e_a), \quad (2)$$

where f_c is the CO_2 flux, f_e is the water vapour flux, g is the stomatal conductance, c_a is ambient and c_i intercellular CO_2 concentration, $a = 1.6$ is the relative diffusivity of water with respect to carbon, and e_i is the intercellular and e_a the ambient water vapour concentration. Photosynthesis (p) is related to c_i via the Farquhar model (Farquhar, Caemmerer & Berry 1980a):

$$p = \alpha_1 \frac{c_i - \Gamma}{\alpha_2 + c_i}, \quad (3)$$

where α_1 and α_2 depend on whether the photosynthetic rate is light- or Rubisco-limited. For analytical tractability, assume that $\Gamma/c_i \ll 1$ and the expression $\alpha_1 c_i / (\alpha_2 + c_i) \approx \alpha_1 c_i / (a_2 + s c_a)$, where s relates c_i to c_a :

$$p \approx \alpha c_i \quad (4)$$

where $\alpha = \gamma_1 V_{c,\max}$ for temperature limited photosynthesis and $\alpha = \gamma_2 \text{PAR}$ for light-limited photosynthesis. Here, $V_{c,\max}$ stands for maximum carboxylation capacity, γ_1 and γ_2 are physiological parameters, and PAR is photosynthetically active radiation. Equation 4 demonstrates the correspondence between the assumed $p - c_i$ curve in Hari *et al.* (1986) and the parameters in the Farquhar model, although the precise value of α is irrelevant to the following optimization discussion. Assuming steady-state conditions,

$$f_c - p + r = 0 \quad (5)$$

where r is the leaf respiration rate. Combining Eqns 1, 2, 4 and 5 results in the following formulations:

$$c_i = \frac{g c_a + r}{g + \alpha} \quad (6)$$

$$p = \frac{\alpha(g c_a + r)}{g + \alpha}. \quad (7)$$

The two basic equations (Eqns 6 and 7) include three unknown state variables (c_i , g and p), generating a problem not closed mathematically. Standard approaches to 'close' this problem assume an empirical relationship between g , p and some environmental stimuli such as air relative humidity (RH) or D (Baldocchi & Meyers 1998; Lai *et al.* 2000). Two well-known formulations that fit a wide range of field data are given by the so-called 'Ball-Berry model' (Ball, Woodrow & Berry 1987; Collatz *et al.* 1991):

$$g_1 = \frac{m_1}{c_a} p \text{RH} + b_1, \quad (8)$$

and the 'Leuning model' (Leuning 1995):

$$g_2 = \frac{m_2}{c_a} p \left(1 + \frac{D}{D_o}\right)^{-1} + b_1, \quad (9)$$

where b_1 sets a minimum g , D_o is the sensitivity of g to vapour pressure deficit, and m_1 and m_2 are empirical parameters that vary among species. Another closure assumption, first proposed by Cowan (1977) and Cowan & Farquhar (1977), is a constant *marginal* water cost per unit carbon, $(\partial f_c / \partial g) / (\partial f_e / \partial g)$. This basic premise is retained in the work by Hari *et al.* (1986) and Berninger & Hari (1993). In their formulation, g is expressed as $g = g_o u$ where g_o is the maximum conductance and u is the degree of stomatal

opening ($0 < u \leq 1$). The carbon cost of a unit of transpired water, λ , is formulated as the inverse of $(\partial f_c/\partial g)/(\partial f_c/\partial g)$. Like in Cowan & Farquhar (1977), λ is assumed to be constant at time scale of 1 d, and the fluxes of CO₂ and water vapour are integrated over the same period.

Interestingly, in the following discussion, we show that a solution to an analogous optimization problem can be developed without time-integration (given the steady-state assumption in Eqn 5) and Lagrange multipliers. Results from such a solution are identical to those from Hari *et al.* (1986) and Cowan & Farquhar (1977), and actually establish some constraints on how constant the cost parameter needs to be for the solution to be accurate.

However, before presenting this optimum solution, we note that when $\alpha c_a \gg r$, Eqns 2 and 7 can be combined to arrive at an explicit relationship between f_c and f_e

given as $f_c \approx \frac{\alpha c_a f_e}{f_e + \alpha(e_i - e_a)}$. This expression has a negative

convexity for any positive f_e and $e_i - e_a$ because $\frac{\partial^2 f_c}{\partial f_e^2} = -\frac{(\alpha^2 c_a)(e_i - e_a)}{(f_e + \alpha(e_i - e_a))^3} < 0$.

Hence, despite the linearization in the $p - c_i$ curve adopted in Eqn 4, the f_c (dependent) versus the f_e (independent) expression proposed here maintains a negative convexity and thus our formulation admits an optimal solution as discussed in Cowan & Farquhar (1977). To find this optimum for the linearized $p - c_i$ curve, the maximization of the carbon gain function $f(u)$ with respect to stomatal aperture control (u) can be expressed as:

$$\begin{aligned} \max_u(f(u) = p - \lambda f_c) &\Rightarrow \frac{\partial f(u)}{\partial u} = \frac{\partial p}{\partial u} - \frac{\partial \lambda f_c}{\partial u} \quad (10) \\ &= \frac{\partial p}{\partial u} - \lambda \frac{\partial f_c}{\partial u} - f_c \frac{\partial \lambda}{\partial u} = 0; \\ &\text{if } |(1/\lambda)(\partial \lambda/\partial u)| \ll |(1/f_c)(\partial f_c/\partial u)| \Rightarrow \\ &\frac{\partial}{\partial u} \left(\frac{\alpha(u g_o c_a + r)}{u g_o + \alpha} - \lambda \alpha u g_o (e_i - e_a) \right) = 0. \end{aligned}$$

In comparison with Hari *et al.* (1986), it is clear that the optimization problem in Eqn 10 simplifies to a univariate maximization problem provided $\frac{\partial \lambda f_c}{\partial u} \approx \lambda \frac{\partial f_c}{\partial u}$.

This simplification was the basis of the definition of the Cowan & Farquhar (1977) marginal water cost per unit carbon, expressed as $(\partial f_c/\partial g)/(\partial f_c/\partial g)$ [or $\frac{\partial p}{\partial u} - \lambda \frac{\partial f_c}{\partial u} = 0 \Rightarrow \lambda = (\partial p/\partial u)/(\partial f_c/\partial u)$]. Maximization in Eqn 10 is achieved when

$$u = \frac{-\alpha a(e_i - e_a) g_o \lambda + (a(e_i - e_a) g_o^2 \lambda (\alpha c_a - r))^{1/2}}{a(e_i - e_a) g_o^2 \lambda}. \quad (11)$$

The condition $\partial f(u)/\partial u = 0$ in Eqn 10 alone does not rule out that the result in Eqn 11 is a local minimum rather than a maximum for $f(u)$. To ensure that $f(u)$ is maximum for the u given by Eqn 11, $f(u)$ must be concave (or negatively

convex). Upon twice differentiating $f(u)$ with respect to u , we obtain $\frac{\partial^2 f(u)}{\partial u^2} = -\frac{2\alpha g_o^2 (\alpha c_a - r)}{(\alpha + g_o u)^3}$, which is monotonically negative ($u > 0$) provided $\alpha c_a > r$. Hence, this negative convexity in $f(u)$ guarantees that u in Eqn 11 is a maximum and not a minimum. For $r/\alpha \ll c_a$

$$u \approx \frac{\alpha}{g_o} \left(-1 + \left(\frac{c_a}{a(e_i - e_a) \lambda} \right)^{1/2} \right). \quad (12)$$

Hence,

$$g = g_o u \approx \alpha \left(-1 + \left(\frac{c_a}{a(e_i - e_a) \lambda} \right)^{1/2} \right). \quad (13)$$

This expression states that g decreases with increasing $e_i - e_a$, and is sensitive to the slope of the $p - c_i$ curve. Because u is bounded between zero and unity, theoretical bounds on the cost parameter λ can be readily established and are given as:

$$\begin{aligned} \lambda_{\max} &= \frac{c_a}{a(e_s - e_a)}, \quad (\text{i.e. } u = 0) \quad (14) \\ \lambda_{\min} &= \frac{\lambda_{\max}}{\left(\frac{g_o}{\alpha} + 1 \right)^2}, \quad (\text{i.e. } u = 1). \end{aligned}$$

The variations in λ (as $\lambda_{\min}/\lambda_{\max}$) are entirely dictated by g_o/α – the maximum conductance and the basic physiological parameter of the linear $p - c_i$ curve. If $g_o/\alpha \sim 1$, then $\lambda_{\min}/\lambda_{\max} \sim 1/4$ (or fourfold variation). Using a similar maximization approach, we also derived the optimum conductance using the non-linear $p - c_i$ curve (Eqn 3). However, the resulting formulation does not reveal primitive scaling rules between environmental stimuli and stomatal conductance owing to the larger number of parameters.

Because of its ‘non-physical’ nature, λ cannot be independently inferred and the success of testing the optimization hypothesis at the leaf-level has been variable (Farquhar, Schultze & Küppers 1980b; Hall & Schulze 1980; Berninger, Mäkelä & Hari 1996; Guehl & Aussenac 1987; Fites & Teskey 1988; Berninger & Hari 1993; Hari *et al.* 1999; Thomas, Eamus & Bell 1999; Hari, Mäkelä & Pohja 2000; Aalto, Hari & Vesala 2002). Instead of testing the theory by searching experimental data for a constant λ , we focus on searching data for the emergent properties of the optimal solution, namely the sensitivity of g to D . This is somewhat more pertinent for two reasons: (1) optimality may still persist with some variations in λ provided these variations abide by the condition $|(1/\lambda)(\partial \lambda/\partial g)| \ll |(1/f_c)(\partial f_c/\partial g)|$ or simply $|(1/\lambda)(\partial \lambda/\partial g)| \ll |(\partial f_c/\partial g)|$, and (2) experimentally, it is difficult to estimate λ based on gas exchange data because uncertainties in measuring $\partial f_c/\partial g$ and $\partial f_c/\partial g$ may be large under certain combinations of environmental conditions.

Recall that no *a priori* specification of the stomatal response to D is imposed and that the shape of the

dependency of g on D emerges from the optimization. Hari *et al.* (2000) presented a convincing field test on the dependence of g on $D^{-1/2}$, suggesting that such a dependency is a 'validation' of the optimization hypothesis (assuming that atmospheric vapour pressure deficit, D well approximates leaf-to-air vapour pressure difference, $e_i - e_a$). However, the dependence of g on $D^{-1/2}$ clearly conflicts with the functional dependencies of g_1 or g_2 assumed by Ball *et al.* (1987) and Leuning (1995), respectively.

ANALYSES AND DISCUSSION

To assess whether the optimization principle can be used to constrain certain parameters in semi-empirical models of g , we firstly consider the sensitivity of g to D , and then evaluate how the sensitivity of g to D is impacted by changes in c_a .

Sensitivity of g and f_e to D

Consistency with observed response of g to D (Oren *et al.* 1999)

Assuming that D is a surrogate for $e_i - e_a$, g is expressed in Hari *et al.* (1986) as:

$$g = g_a u = \alpha \left(-1 + \left(\frac{c_a}{a\lambda} \right)^{1/2} D^{-1/2} \right). \quad (15)$$

The emerging conductance sensitivity is reflected in the dependence on $D^{-1/2}$, which may be expressed via a Taylor series expansion as:

$$D^{-1/2} = 1 - \frac{1}{2} \log(D) + \frac{(-1/2 \log(D))^2}{2!} + \frac{(-1/2 \log(D))^3}{3!} + \dots + \frac{(-1/2 \log(D))^n}{n!}, \quad (16)$$

where the leading term is of the form $1 - (1/2)\log(D)$. Figure 1 shows the variations of $D^{-1/2}$ and $1 + \sum_{n=1}^m \frac{(-1/2 \log(D))^n}{n!}$ for $n_1 = 1, 2, 3$ and for typical D varying from a low of 0.5 to an extreme of 6. The series converges rapidly, with $n_1 = 3$ indistinguishable from $D^{-1/2}$. Moreover, Fig. 1 shows that the Taylor series expansion $D^{-1/2} \approx 1 - 1/2 \log(D)$ is accurate for $D \in [0.5, 2]$ (i.e. to within 5% relative error), but for $D > 2$, higher order effects ($n_1 > 1$) become large.

From a broad survey of plant species representing many functional types, a functional form g in response to D was derived as $g = g_{\text{ref}}(1 - m \log(D))$, where g_{ref} is the so-called reference conductance determined for similar light and soil moisture conditions at $D = 1$ kPa (Oren *et al.* 1999). The synthesis showed that $m \approx 0.5 - 0.6$. Since then, other studies added many additional species showing similar response (Mackay *et al.* 2003). To compare this well-supported empirical finding with the optimization prediction, the empirical function can be expressed as $g = g_{\text{ref}}(1 - m \log(D))$. The

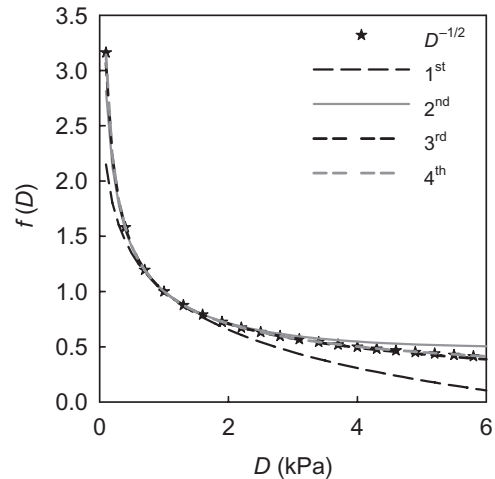


Figure 1. Variations of the square root of water vapour pressure deficit ($D^{-1/2}$) and its Taylor series expansion:

$$1 + \sum_{n=1}^m \frac{(-1/2 \log(D))^n}{n!} \text{ for } n_1 = 1, 2, 3 \text{ as a function of } D.$$

optimization result for g/g_{ref} is $g/g_{\text{ref}} = (-1 + \Phi/D^{1/2})/(-1 + \Phi)$, with $\Phi = \left(\frac{c_a}{a\lambda} \right)^{1/2}$. Upon replacing $D^{-1/2} \approx 1 - 1/2 \log(D)$,

$$\frac{g}{g_{\text{ref}}} = \frac{-1 + \Phi(1 - 1/2 \log(D))}{-1 + \Phi} = 1 - \frac{1}{2} \frac{\Phi}{\Phi - 1} \log(D).$$

For the case when $\Phi \gg 1$, $\frac{g}{g_{\text{ref}}} = 1 - \frac{1}{2} \log(D)$, close to the lower limit of the reported m values in Oren *et al.* (1999).

Even for large Φ , $\frac{\Phi}{\Phi - 1} > 1$ the optimization theory should yield an $m > 0.5$, also consistent with the empirical findings and the theory of water transport to leaves in Oren *et al.* (1999).

To further illustrate the similarity between the emergent behaviour from the optimization model and the general value of m [from $1 - m \log(D)$], we used the data of *Fagus crenata* Blume (Fig. 2; Iio *et al.* 2004) not included in Oren *et al.* (1999). The regression analysis on the data in Fig. 2 results in $m \approx 0.45$, similar to $D^{-1/2}$ scaling ($P > 0.05$). Thus, the optimization theory appears consistent with the well-documented general behaviour of g with respect to D .

Consistency with the sensitivity of f_e to D (Monteith 1995)

A joint reduction in g and f_e with increasing D can be seen as evidence of a feed-forward mechanism of stomatal response (Schulze *et al.* 1972). Such behaviour, under some conditions, can also be predicted based on optimal stomatal control (Buckley 2005). Here, we demonstrate that the emergent $g \sim D^{-1/2}$ from the optimization theory is qualitatively consistent with Monteith's (1995) view of the sensitivity of f_e to D and the apparent feed-forward mechanism.

The function $f_e = \alpha a \left(-D + \left(\frac{c_a}{a\lambda} \right)^{1/2} D^{1/2} \right)$ suggests that f_e is dominated by two opposing terms when D is increased.

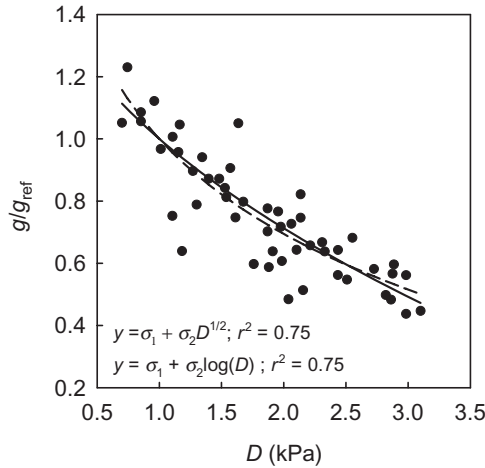


Figure 2. Comparison between measured (circles) and modelled g normalized by a reference g (g_{ref}), defined at $D = 1$ kPa, for *Fagus crenata* Blume (Iio et al. 2004). The lines represent predictions based on the optimization theory (solid line) and the functional relationship in Oren et al. (1999) (dashed line).

These terms are represented by the sum $-D + \left(\frac{c_a}{a\lambda}\right)^{1/2} D^{1/2}$ and imply that at low D , f_e increases rapidly with increasing D because the first term is small compared to the second term. However, at very high D , the first term may dominate and f_e begins to decline with increasing D , consistent with empirical findings (Monteith 1995; Pataki et al. 1998). This outcome is identical to a derivation from the $g - D$ response performed in Oren et al. (1999). The optimization model can be used to predict the value of D at which the onset of

such apparent feed-forward is likely to occur (critical D , D_{crit}). Because $\partial g/\partial D \sim -(1/2)D^{-3/2} < 0$ for all $D > 0$, the apparent feed-forward mechanism occurs only when $\frac{\partial f_e}{\partial D} \leq 0$. This D_{crit} can be readily computed as

$$\frac{\partial f_e}{\partial D} = \alpha a \left(-1 + \frac{1}{2} \left(\frac{c_a}{a\lambda} \right)^{1/2} D^{-1/2} \right) = 0; \text{ or } D_{crit} = \frac{1}{4} \frac{c_a}{a\lambda}, \quad (17)$$

and depends only on c_a and λ .

This critical limit can be assessed based on data from four-step measurements on three leaves of *Abutilon theophrasti*, two of which display an apparent feed-forward mechanism and one displaying a plateau [i.e. transpiration almost independent of D ; Bunce (1997)]. In this framework, a plateau indicates that D_{crit} is not yet exceeded. A regression model $g = \sigma_1 + \sigma_2 D^{-1/2}$ was fitted to the four-point conductance data, and then f_e was computed from the modelled g (along with D_{crit} determined from σ_1 and σ_2). The expected transpiration is similar to the data, as is the D at which the apparent feed-forward is observable (Fig. 3).

Finally, it should be noted that for a given λ , the optimization approach predicts that leaf transpiration becomes negligible when $f_e = 0 = -D + \left(\frac{c_a}{a\lambda}\right)^{1/2} D^{1/2}$, which results in

$D = 0$ (a trivial solution) and $D = \frac{c_a}{a\lambda} = 4D_{crit}$ (a non-trivial solution). The second solution suggests that transpiration becomes negligible when actual D exceeds $4D_{crit}$. Hence, leaves in dry climates, which routinely experience high D , must close stomata more often than leaves with similar λ in humid climates, which is a reasonable behaviour.

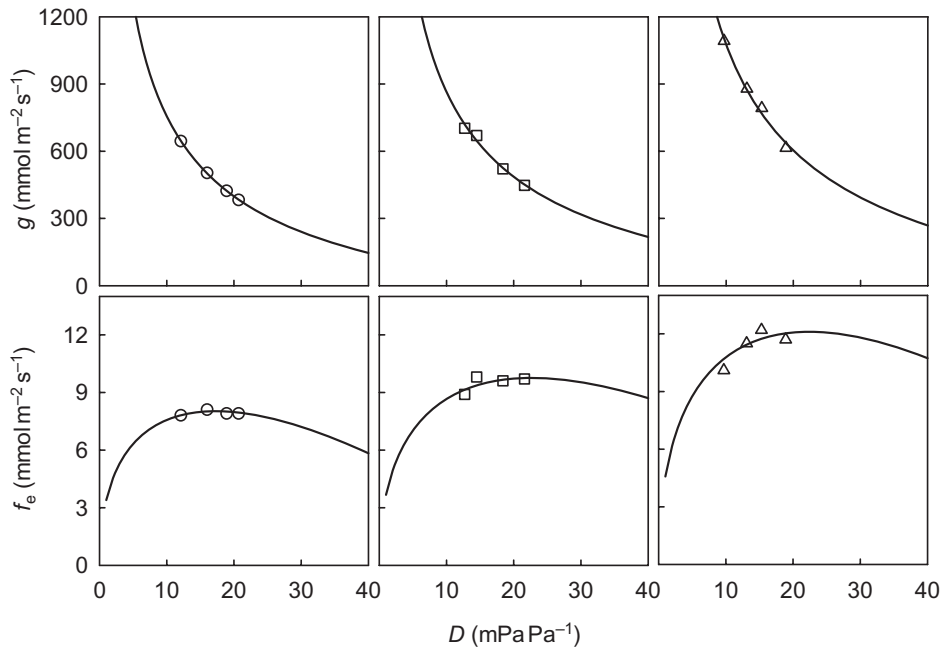


Figure 3. Comparison between predicted stomatal conductance (g) and transpiration rate (f_e) based on optimization theory, and data from *Abutilon theophrasti* (Bunce 1997) for the onset of a feed-forward mechanism in three leaves (represented by different symbols).

Dependence of c_i/c_a on D

An important yet unexplored consequence of this optimization model is that c_i/c_a varies in a predictable manner with D , and is given by

$$\frac{c_i}{c_a} = \frac{1}{1 + \frac{\alpha}{g}} \approx \frac{1}{1 + \frac{1}{\left(\frac{c_a}{a\lambda}\right)^{1/2} D^{-1/2} - 1}} = 1 - \left(\frac{a\lambda}{c_a}\right)^{1/2} D^{1/2}. \quad (18)$$

As reported in a large number of studies (see Katul, Ellsworth & Lai 2000), the hyperbolic dependence of c_i/c_a on g (i.e. first equality on the right-hand side) is well preserved by the optimization model (Fig. 4), suggesting that the linear $p - c_i$ approximation is perhaps appropriate for 'field' conditions and is consistent with the arguments in Leuning (1995) and Katul *et al.* (2000). As discussed in Katul *et al.* (2000), Leuning's semi-empirical conductance model leads to a linear decline of c_i/c_a with increasing D . In contrast, the optimization theory model predicts that as D decreases c_i/c_a increases asymptotically such that $c_i/c_a \rightarrow 1$ when $D \rightarrow 0$. Leuning (1995) used data on 9 of the 16 species from Turner, Schulze & Gollan (1984) to calibrate the stomatal response to D . Although the data can probably be represented equally well by a linear and a non-linear approximation, at low D , some degree of non-linearity in the dependence of c_i/c_a on D is apparent in the data of all species (see fig. 9 in Leuning 1995). Indeed, many field and laboratory studies have reported a non-linear decline of c_i/c_a with increasing D (Farquhar *et al.* 1980b; Lloyd & Farquhar 1994), or present data that appear to be a better fit with $D^{1/2}$ than D , as shown in Fig. 5 (Wong & Dunin 1987; Fites & Teskey 1988; Mortazavi *et al.* 2005; and several discussed in Katul *et al.* 2000).

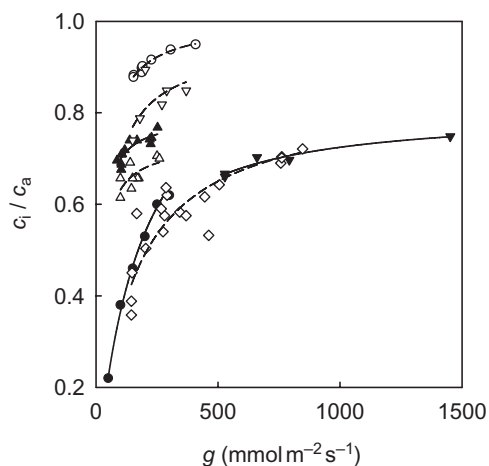


Figure 4. The hyperbolic dependence of the ratio of intercellular to atmospheric CO_2 concentration (c_i/c_a) on stomatal conductance (g) among a wide range of species and experiments [$0.46 \leq r^2 \leq 0.99$; data from fig. 2 in Katul *et al.* (2000)].

The conditions that lead to a near-linear dependence of c_i/c_a on D can also be delineated within the context of the optimization framework. By rewriting the gas-exchange equations as

$$f_c = f_e \frac{(c_a - c_i)}{a(e_i - e_a)},$$

a plausible condition can be derived by replacing the constant *marginal cost* $\lambda = (\partial f_c / \partial g) / (\partial f_e / \partial g)$ with a constant *flux-based water use efficiency* $\lambda_L = f_c / f_e$, to yield

$$\frac{f_c}{f_e} = \frac{c_a}{a(e_s - e_a)} \left(1 - \frac{c_i}{c_a}\right) = \lambda_L.$$

A constant λ_L (i.e. independent of D) can only be achieved if

$$\frac{c_i}{c_a} = 1 - \left(\frac{\lambda_L a}{c_a}\right) (e_s - e_a).$$

In other words, c_i/c_a may decline linearly with increasing D as suggested by Leuning (1995) if λ_L is a constant. By equating these two c_i/c_a formulations, it can be shown that λ_L can be related to λ using $\lambda_L = (\lambda c_a / a)^{1/2} D^{1/2}$. In typical field experiments, large variations in D are needed to discern the dependence of λ_L on D (assuming constant λ), perhaps explaining why data cannot conclusively reject a linear c_i/c_a decline with increasing D (e.g. Fig. 5).

Two studies criticized the optimality hypothesis by demonstrating that λ was not constant but varied with D (Fites & Teskey 1988; Thomas *et al.* 1999). As noted earlier, variations in λ alone do not disprove the optimality hypothesis and predictions of the response of g to D may still be reasonable, provided that $|(1/\lambda)(\partial \lambda / \partial u)| \ll |(1/f_c)(\partial f_c / \partial u)|$. Stated differently, as long as the relative variations in λ are much smaller than the relative variations in f_c , the scaling properties emerging from the optimization theory are robust. We analysed the data published in Fites & Teskey (1988; Fig. 6) and noted that (1) their g scales as $D^{-1/2}$ and is consistent with the optimality hypothesis, (2) regressing their reported f_c upon their f_e results in a near-constant λ_L (in disagreement with the optimality hypothesis), (3) regressing $\partial f_c / \partial g$ versus $\partial f_e / \partial g$ directly estimated from the data (digitized by us), suggests a constant λ (consistent with the optimality hypothesis), and (4) their c_i/c_a is not linearly related D , especially at high D (consistent with the optimality hypothesis but not the outcome in point 2). Notice that points (2) and (3) cannot be simultaneously satisfied given that $\lambda_L = (\lambda c_a / a)^{1/2} D^{1/2}$. In estimating $\partial f_c / \partial g$ and $\partial f_e / \partial g$, we used central differencing to approximate these gradients from the data published by Fites & Teskey (1988; their Figs 1 and 2). Estimating $\partial f_c / \partial g$ and $\partial f_e / \partial g$ from raw (and digitized) data increases the uncertainty when computing such derivatives because the random error is generally amplified by the differencing operator. We also confirmed that the residuals from the regression in step (3) are not significantly dependent on D . While similar analysis could not be repeated on the data in Thomas *et al.*

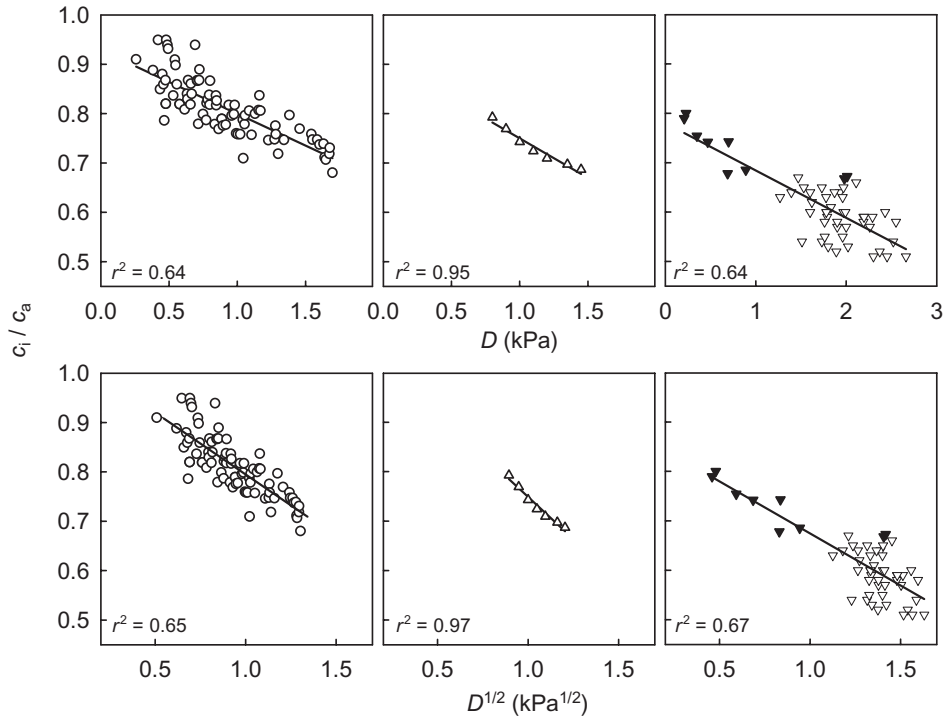


Figure 5. The ratio of intercellular to atmospheric CO₂ concentration (c_i/c_a) as a function of vapour pressure deficit (D , upper panels) and $D^{1/2}$ (lower panels). The gas-exchanged data sets are from a 12-year-old forest dominated by *Eucalyptus* ssp. (circles; Wong & Dunin 1987), a well-watered *Pinus taeda* seedlings (triangles up; Fites & Teskey 1988), and a 13-year-old *P. taeda* plantation at Duke Forest FACE facility (triangles down; Ellsworth 2000), where the measurements were collected 1996–1999 at multiple locations in the control plots at air temperatures between 20 and 30 °C. Filled triangles are obtained on ¹³C data reported in Mortazavi *et al.* (2005) for pine and hardwood foliage in the same stand.

(1999) because their fluxes and c_i/c_a were not published, $\partial\lambda/\lambda$ calculated based on five different methods resulted in estimates varying within 20%, possibly reflecting $|(1/\lambda)(\partial\lambda/\partial u)| \ll |(1/f_c)(\partial f_c/\partial u)|$. Thus, with a less stringent criterion for the constancy of λ , the results from both studies cannot be used to undermine the optimization theory.

Effects of high atmospheric CO₂ on the response of g to D

Because $g \sim \left(\frac{c_a}{a\lambda}\right)^{1/2} D^{1/2}$, the optimization approach can provide diagnostic results on how the $g - D$ response senses changes in c_a , a topic that has received much attention for over a decade (Ellsworth *et al.* 1995; Bunce 1998; Heath 1998; Medlyn, Barton & Broadmeadow 2001; Wullschleger *et al.* 2002; Herrick, Maherali & Thomas 2004).

To facilitate comparisons with a number of published studies, the effects of high c_a on g at a reference environmental state (i.e. the sensitivity of g to D in the neighbourhood of $D = 1$ kPa) are firstly considered. Beginning with $g = \alpha \left(-1 + \left(\frac{c_a}{aD\lambda}\right)^{1/2}\right)$, differentiating with respect to

D , setting $D = 1$ kPa, and re-arranging the terms, the sensitivity of g to D at $D = 1$ kPa can be expressed as

$$\left.\frac{dg}{dD}\right|_{D=1\text{kPa}} = -\frac{1}{2}(g - \alpha). \tag{19}$$

This outcome suggests that within the optimization framework, the slope of dg/dD versus g is constant ($= 1/2$) and not impacted by c_a ; however, the intercept α can vary appreciably with c_a . Recall that $\alpha \approx \frac{\alpha_1}{\alpha_2 + c_i}$, and an increase in c_a (and thus c_i) will result in a decrease in α even if the basic photosynthesis model parameters do not change with c_a (e.g. there is no reduction in $V_{c,max}$ because of down-regulation). In many published studies, data available for comparison with these optimization results are presented as linear relationships between g and D with no information on the $p - c_i$ relationship (Heath 1998; Medlyn *et al.* 2001; Wullschleger *et al.* 2002; Herrick *et al.* 2004). However, it may be possible to synthesize the results of such studies by evaluating dg/dD at $D = 1$ kPa as a ratio of the responses obtained under high and current c_a .

Beginning with $dg/dD = -\frac{1}{2}g(1 - \alpha/g)$ and noting that $g = \alpha[-1 + (c_a/(a\lambda))^{1/2}]$, the ratio of dg/dD (at $D = 1$ kPa) under high and current c_a is given by:

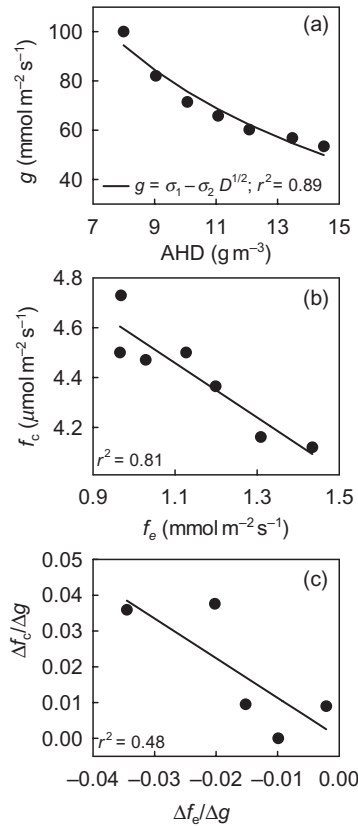


Figure 6. (a) Stomatal conductance (g) as a function of absolute humidity deficit (AHD), (b) the photosynthetic rate (f_c) as a function of transpiration rate (f_e), where the regression slope is $0.0011 \text{ mol CO}_2/\text{mol H}_2\text{O}$, and (c) the sensitivity of f_c to a change in g ($\Delta f_c/\Delta g$) as a function of sensitivity of f_e to a change in g ($\Delta f_e/\Delta g$) approximated using central differencing. The regression slope is $0.0018 \text{ mol CO}_2/\text{mol H}_2\text{O}$. Data from Fites & Teskey (1988).

$$y = \frac{[dg/dD]_{c_a+\delta c_a}}{[dg/dD]_{c_a}} \quad (20)$$

$$= \frac{[g]_{c_a+\delta c_a}}{[g]_{c_a}} \left(1 - \frac{1}{\left(\frac{c_a+\delta c_a}{a\lambda_e}\right)^{1/2} - 1} \right) \left(1 - \frac{1}{\left(\frac{c_a}{a\lambda_a}\right)^{1/2} - 1} \right)^{-1}; \text{ or}$$

$$y = \left(1 - \frac{1}{\left(\frac{c_a+\delta c_a}{a\lambda_e}\right)^{1/2} - 1} \right) \left(1 - \frac{1}{\left(\frac{c_a}{a\lambda_a}\right)^{1/2} - 1} \right)^{-1} x,$$

where δc_a is the atmospheric CO_2 increment, and λ_e and λ_a are the equivalent water costs for high and current c_a , respectively. Figure 7 shows that $y = [dg/dD]_{c_a+\delta c_a}/[dg/dD]_{c_a}$ (dependent variable) as a function of $x = [g]_{c_a+\delta c_a}/[g]_{c_a}$ (independent variable) from a number of studies (Heath 1998; Medlyn *et al.* 2001; Wullschlegel *et al.* 2002; Herrick *et al.* 2004). These studies

include both short-term CO_2 exposures and long-term experiments (e.g. Free Air CO_2 Enrichment facilities), where the CO_2 enrichment, $(\delta c_a + c_a)/c_a$, ranged from 1.5 to 2.0. Based on the optimization theory, the departure from unity in this data is captured by the terms $\left(\frac{c_a + \delta c_a}{a\lambda_e}\right)^{1/2}$ and $\left(\frac{c_a}{a\lambda_a}\right)^{1/2}$. In the case of $\lambda_e = \lambda_a$, and for $(\delta c_a + c_a)/c_a > 1$, the predicted y as a function of reasonable values of λ is close to unity though for large enough λ , y becomes negative. Accepting for the moment the linearity of the response of g to D , as reported by the authors, this analysis suggests that increased CO_2 should affect λ_e such that $\lambda_e/\lambda_a > 1 + \delta c_a/c_a$. Next, we analyse this 'excess cost' using data from two short-term exposure experiments (Bunce 1998; Heath 1998).

The conductance at high c_a relative to current c_a may be expressed as:

$$R'(D) = \frac{g_e}{g_a} = \left(\frac{\alpha_e}{\alpha_a} \right) \left(\frac{-1 + \left(\frac{c_a + \delta c_a}{a\lambda_e}\right)^{1/2} D^{-1/2}}{-1 + \left(\frac{c_a}{a\lambda_a}\right)^{1/2} D^{-1/2}} \right). \quad (21)$$

Hence, two effects must be simultaneously considered when assessing the effects of high c_a on the relationship between g and D : (1) the effect of c_a on α_e/α_a , which reflects only the degree to which the parameter of the linear $p - c_i$ curve shifts under high c_a (i.e. $\alpha \sim \frac{\alpha_1}{\alpha_2 + s c_a}$), and (2) the effect of the variation in D emerging from the theory outside the $p - c_i$

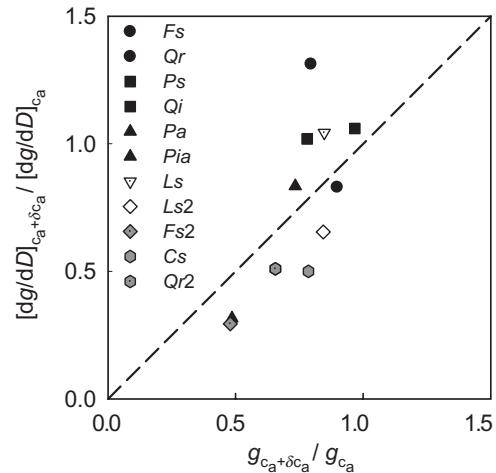


Figure 7. The ratio of the sensitivities of conductance to vapour pressure deficit (D) under current (c_a) and high CO_2 ($\delta c_a + c_a$) conditions as a function of the corresponding ratio of g (at $D = 1 \text{ kPa}$). Data were obtained from Medlyn *et al.* (2001; *Fagus sylvatica*, *Quercus robur*, *Pinus sylvestris*, *Quercus ilex*, *Philyrea angustifolia* and *Picea abies*), Herrick *et al.* (2004; *Liquidambar styraciflua*), Wullschlegel *et al.* (2002; *L. styraciflua2*) and Heath (1998; *Fagus sylvatica2*, *Castanea sativa*, *Quercus robur2*). Symbol fill from open to black indicates the enrichment level: $(\delta c_a + c_a)/c_a$: ~ 1.5 , ~ 1.7 and ~ 2.0 , respectively. Dashed line is 1:1 line.

physiology. Mathematically, if $D \rightarrow +\infty$, $R'(\infty) \rightarrow \alpha_e/\alpha_a$ and becomes independent of D ; stated differently, at high D , the $p - c_i$ physiology alone does not introduce a dependence on D – it simply modifies it by a fraction <1 . To facilitate a separate analysis of the effects of high c_a beyond the predictable multiplier factor emerging from the $p - c_i$ response, we define $R(D) = R'(D)/R(\infty)$. The problem considered next is how $R(D)$ changes with increasing D when $|\delta c_a| > 0$. To address this problem, three cases are considered:

Case (1): $\partial R(D)/\partial D > 0$

When $|\delta c_a| > 0$ and all other parameters, including $\partial \lambda/\partial c_a = 0$, are held constant, the optimization theory predicts that $R(D)$ must increase with increasing D . In fact, $R(D)$ must increase with increasing D as long as $\frac{\lambda_e}{\lambda_a} < \left(\frac{c_a + \delta c_a}{c_a}\right)$. The predicted increase for this case is consistent with data on three species (Heath 1998; Fig. 8).

Case (2): $\partial R(D)/\partial D = 0$

If $\lambda_e = \left(\frac{c_a + \delta c_a}{c_a}\right)\lambda_a$, then $R(D)$ is not affected by increasing D . We have not encountered a data set where this case emerges.

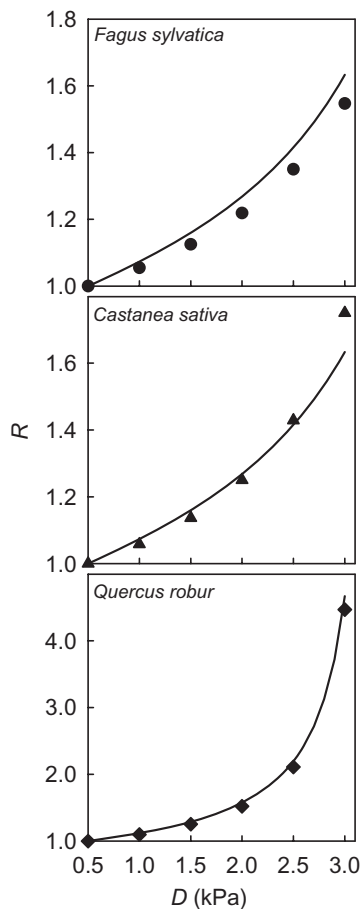


Figure 8. The ratio (R) between stomatal conductance under high atmospheric CO_2 conditions (current + 250 ppm) and current conditions as a function of water vapour pressure deficit (D). Data are for three species from Heath (1998).

Case (3): $\partial R(D)/\partial D < 0$

This case is possible only when $\lambda_e > \left(\frac{c_a + \delta c_a}{c_a}\right)\lambda_a$. Bunce

(1998) presented experimental evidence suggesting that $R(D)$ can decrease with increasing D opposite to the prediction in case (1). Can λ_e/λ_a increase sufficiently under c_a to result in the emergence of responses of the type of case (3)?

The information provided in Bunce (1998) does not permit us to address the question quantitatively. Thus we ask: Can such increases in λ_e/λ_a be observed under high c_a ? Leaf-level gas exchange data collected on *Pinus taeda* at the Duke Forest Free Air CO_2 Enrichment (FACE) facility were used to answer this question (data from trees experiencing current c_a are shown in Fig. 5). The value of $\left(\frac{a\lambda}{c_a}\right)^{1/2}$ for current and for elevated CO_2 plots ($c_a + 200 \mu\text{mol mol}^{-1}$) was first computed by regressing $1 - c_i/c_a$ versus $D^{1/2}$. No down-regulation in the $p - c_i$ curve was documented for the period used in this analysis (Ellsworth 2000; Rogers & Ellsworth 2002). For D (in kPa), these regression results suggest that $\left(\frac{a\lambda}{c_a}\right)^{1/2} = 0.096$ for

current and $\left(\frac{a\lambda}{c_a}\right)^{1/2} = 0.230$ for elevated c_a . The scatter is large (see Fig. 5), as expected when measurements are made on different fascicles in different seasons, and soil moisture conditions vary greatly among measurement campaigns. Nevertheless, the slopes of the regression were different between the c_a treatments ($P < 0.05$). Based on this rough assessment, $\lambda_e = \lambda_a(0.230/0.096)^2(580/380) = 8.72$, satisfying the inequality $\lambda_e > \left(\frac{c_a + \delta c_a}{c_a}\right)\lambda_a$, required for the

emergence of responses the like of case (3). Based on the FACE parameters, R was then modelled with Eqn 22 for a range of D and compared to data in Bunce (1998) – the modelled R agrees well with the data (Fig. 9).

The effects of elevated CO_2 on stomatal conductance response to D were evaluated based on a linear $p - c_i$ curve. However, it is well known that non-linearities in the $p - c_i$ curve become more pronounced under elevated atmospheric CO_2 . Thus, the results from the analysis above must be viewed with some caution. As we noted earlier, we derived the optimal stomatal conductance for the non-linear $p - c_i$ curve and intend to use it in future analyses to further evaluate these responses.

CONCLUSIONS

Analytical results from the original optimization theory were first derived by Cowan (1977) and Cowan & Farquhar (1977) assuming the daily water cost per unit carbon, $(\partial f_e/\partial g)/(\partial f_c/\partial g)$ is strictly a constant. Hari *et al.* (1986) and Berninger & Hari (1993) retained the conceptual framework of the ‘optimality hypothesis’ but assumed a linear response of p to c_i . We showed that the expected stomatal control (1) can be re-formulated as a univariate maximization problem not needing Lagrange multipliers or

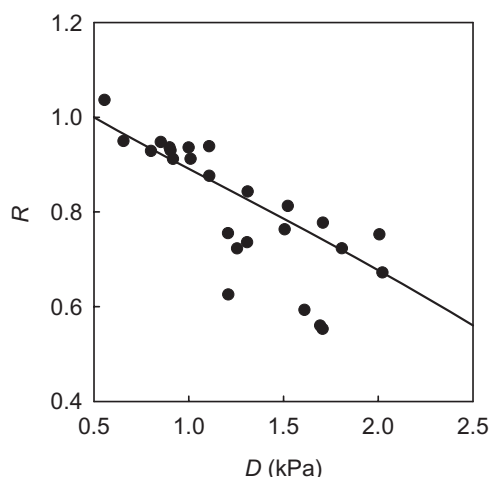


Figure 9. Measured and modelled ratio of stomatal conductance (R) under high atmospheric CO_2 conditions (700 ppm) to that under current conditions (350 ppm) as a function of water vapour pressure deficit (D). Data are from Bunce (1998) and the modelled R was predicted by the optimization theory using $\lambda_e/\lambda_a = 8.72$ (see text) obtained from the FACE experiment in a pine forest (Ellsworth 2000).

integration time scales, (2) is consistent with the onset of an apparent ‘feed-forward’ mechanism in g as discussed in Monteith (1995), (3) agrees with a synthesis survey suggesting that g scales as $1 - m \log(D)$ where $m \in [0.5, 0.6]$ (Oren *et al.* 1999), and (4) agrees with experiments reporting a non-linear variation in c_i/c_a with D . We have also shown that physical constraints on the degree of stomatal opening (i.e. $0 < u \leq 1$, $g \geq 0$) provide logical limits to λ that can be independently derived from the $p - c_i$ curve, maximum theoretical conductance, D and c_a .

How g responds to D (or in some models RH) is of central importance given that under future climate scenarios, warming is expected not to affect air relative humidity but to increase D exponentially (Kumagai *et al.* 2004). Using the optimization theory, we analysed the conflicting experimental results on the sensitivity of g to D under current and high CO_2 reported in Bunce (1998) and Heath (1998), among others. The approach provides a diagnostic tool and coherent predictions of changes in gas exchange (at least in the response of g to D and c_a).

In the optimization framework proposed here, the time scale at which the optimization is operating is commensurate with the time scales of opening and closure of stomatal aperture u , which is too short to be interpreted as being driven by whole-plant resource optimization when fixing a resource constraint (as is often done in the economics of gas exchange). It is conceivable that ‘whole-plant’ scale carbon gain may actually be achieved if stomatal aperture controls have evolved to be ‘efficient’ at the finest possible time scales (i.e. scales at which $\max_u(f(u) = p - \lambda f_e)$). This statement follows from a variant of Pontryagin’s maximum principle, which informally implies that beginning from known initial conditions (say a certain amount of carbon in the whole plant system), global optimality at the plant scale in

terms of maximizing its carbon gain (which is a linear sum acquired from all the leaves) is guaranteed if at each time step, the ‘local’ maximum is always selected at the stomatal level for the set of environmental conditions. In this context, the framework proposed here assumes that this local maximum amounts to maximizing the leaf photosynthesis while minimizing water loss rate.

It should be emphasized, however, that the apparent agreements with data cannot be viewed as an endorsement of the validity of the optimality hypothesis on stomatal behaviour. Nevertheless, such optimization formulations have joined semi-empirical models, such as the Leuning (1995) and the Collatz *et al.* (1991), to facilitate coupling leaf-level gas exchange to canopy scale and predicting photosynthesis, transpiration and tree growth under current and future climatic conditions (Mäkelä *et al.* 2006; Schymanski *et al.* 2007, 2008; Buckley 2008).

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