

# Reconciling the optimal and empirical approaches to modelling stomatal conductance

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## Abstract

Models of vegetation function are widely used to predict the effects of climate change on carbon, water and nutrient cycles of terrestrial ecosystems, and their feedbacks to climate. Stomatal conductance, the process that governs plant water use and carbon uptake, is fundamental to such models. In this paper, we reconcile two long-standing theories of stomatal conductance. The empirical approach, which is most commonly used in vegetation models, is phenomenological, based on experimental observations of stomatal behaviour in response to environmental conditions. The optimal approach is based on the theoretical argument that stomata should act to minimize the amount of water used per unit carbon gained. We reconcile these two approaches by showing that the theory of optimal stomatal conductance can be used to derive a model of stomatal conductance that is closely analogous to the empirical models. Consequently, we obtain a unified stomatal model which has a similar form to existing empirical models, but which now provides a theoretical interpretation for model parameter values. The key model parameter,  $g_1$ , is predicted to increase with growth temperature and with the marginal water cost of carbon gain. The new model is fitted to a range of datasets ranging from tropical to boreal trees. The parameter  $g_1$  is shown to vary with growth temperature, as predicted, and also with plant functional type. The model is shown to correctly capture responses of stomatal conductance to changing atmospheric CO<sub>2</sub>, and thus can be used to test for stomatal acclimation to elevated CO<sub>2</sub>. The reconciliation of the optimal and empirical approaches to modelling stomatal conductance is important for global change biology because it provides a simple theoretical framework for analyzing, and simulating, the coupling between carbon and water cycles under environmental change.

**Keywords:** coupled conductance and photosynthesis models, marginal water cost of carbon, stomatal conductance, stomatal optimization

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## Introduction

Models of vegetation function have a major role to play in advancing our understanding of terrestrial ecosystem responses to global change. Land surface schemes are integral to climate models (e.g. Sellers *et al.*, 1997; Pitman, 2003), whereas dynamic vegetation models are our major tool for predicting climate impacts on biospheric carbon cycles (e.g. Scholze *et al.*, 2006; Sitch *et al.*, 2008), hydrological cycles (e.g. Gedney *et al.*, 2006; Piao *et al.*, 2007) and nutrient cycles (e.g. Ostle *et al.*, 2009).

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Fundamental to all these vegetation function models are descriptions of the key processes of plant carbon uptake (photosynthesis) and water use (transpiration).

Photosynthesis is widely represented using a mechanistic model in which rates of key processes are related to environmental drivers including the concentration of atmospheric CO<sub>2</sub>, light and temperature (Farquhar *et al.*, 1980). This mechanistic model has acted as a framework for much ecophysiological research, with the result that we now have a good understanding of how photosynthetic rates vary among species and ecosystems (e.g. Wullschlegel, 1993; Kattge *et al.*, 2009), and how photosynthesis acclimates to changes in temperature and atmospheric CO<sub>2</sub> (e.g. Medlyn *et al.*, 1999,

2002; Ellsworth *et al.*, 2004; Ainsworth & Rogers, 2007; Kattge & Knorr, 2007).

In contrast to the mechanistic model of photosynthesis, transpiration is generally modeled using an empirical representation of stomatal conductance. Experiments have shown that stomatal conductance ( $g_s$ ) is typically correlated with photosynthesis ( $A$ ) (Wong *et al.*, 1979), but that the ratio of  $g_s : A$  varies with atmospheric humidity (Ball *et al.*, 1987). These observations have been used to develop simple, empirical models of  $g_s$  (Ball *et al.*, 1987; Leuning, 1995). The use of these models is widespread because parameters are readily estimated from data and the models are simple enough to implement at global scales.

However, because these stomatal conductance models are empirical, their parameters have no meaning attached. Consequently, there is little understanding of how the parameters vary with species or acclimate to changes in climate, and many models simply assume that the parameters are constant for all  $C_3$  species (e.g. Sitch *et al.*, 2003; Krinner *et al.*, 2005; Law *et al.*, 2006). A successful theoretical model of stomatal behaviour is a high priority for vegetation modelers because it would provide a synthetic framework for research into acclimation and adaptation of carbon–water coupling in terrestrial ecosystems.

There is a long-standing theory of optimal stomatal behaviour (Cowan & Farquhar, 1977). This theory is based on the idea that stomata should act to maximize carbon gain (photosynthesis,  $A$ ) while minimizing water loss (transpiration,  $E$ ). That is, the optimal stomatal behaviour would be to minimize the integrated sum of

$$E - \lambda A, \quad (1)$$

where  $\lambda$  ( $\text{mol H}_2\text{O mol}^{-1} \text{C}$ ) is a parameter representing the marginal water cost of plant carbon gain. Model implementations of this theory have been attempted (e.g. Hari *et al.*, 1986; Lloyd, 1991; Arneth *et al.*, 2002; Katul *et al.*, 2009, among others), but several issues have restricted wider use of these implementations. A key problem has been parameterization –  $\lambda$  is perceived as difficult to estimate, and questions have been raised as to the timescale on which  $\lambda$  might remain constant (Cowan & Farquhar, 1977; Thomas *et al.*, 1999). A second major issue is that previous implementations do not correctly capture stomatal responses to atmospheric  $\text{CO}_2$  concentration. Thus, although there are occasional uses of the theory in the literature (e.g. Lloyd *et al.*, 2002; Kleidon, 2004; Mäkelä *et al.*, 2006; Schymanski *et al.*, 2007; van der Tol *et al.*, 2007; Mercado *et al.*, 2009), its use is far from widespread. For example, a recent compendium of stomatal models listed 35 alternative models, but did not include any derived from optimal

stomatal theory (Damour *et al.*, 2010). The general perception of this model is demonstrated by this statement from Pallardy (2008, p. 347): ‘This is an interesting hypothesis, but it remains to be adequately tested as a general plant response’.

In this paper, we reconcile the optimal and empirical models of stomatal conductance. We demonstrate that, under reasonable and generally applicable simplifying assumptions, the optimal stomatal conductance model is, in fact, functionally equivalent to the widely used empirical stomatal model. We derive a unified model that has the form of the empirical stomatal models but that is based on the optimal stomatal conductance theory. The benefit of this unified model is that it gives a biological interpretation for model parameters that previously were regarded as empirical constants. We demonstrate that the key model parameter varies significantly among species, and discuss hypotheses for this variation. This analysis provides a powerful quantitative framework for research into the long-term acclimation and adaptation of stomatal function under conditions of global environmental change.

## Background

### Empirical models

The model of Ball *et al.*, (1987) is based on the observation that stomatal conductance is strongly correlated with assimilation rate (Wong *et al.*, 1979). Based on a series of leaf gas exchange experiments, Ball *et al.* (1987) developed the following empirical expression for  $g_s$ :

$$g_s = g_0 + g_1 (A h_r / C_a), \quad (2)$$

where  $g_0$  and  $g_1$  are fitted parameters,  $A$  is net assimilation rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $h_r$  is relative humidity at the leaf surface (dimensionless) and  $C_a$  is atmospheric  $\text{CO}_2$  concentration at the leaf surface ( $\mu\text{mol mol}^{-1}$ ). This model has been criticized because it can be shown that stomata sense transpiration and/or peristomatal water fluxes, rather than relative humidity (Aphalo & Jarvis, 1991; Mott & Parkhurst, 1991; Eamus *et al.*, 2008). An alternative model incorporating an empirical dependence on leaf-to-air vapour pressure deficit ( $D$ , kPa), a proxy for transpiration, was developed by Leuning (1995). Leuning (1995) considered two alternative forms for the dependence on  $D$ , a linear and hyperbolic dependence, and found that a hyperbolic dependence provided a better fit to experimental data. The resulting model has the following form:

$$g_s = g_0 + g_1 \frac{A}{(C_a - \Gamma)(1 + D/D_0)}, \quad (3)$$

where  $\Gamma$  is the CO<sub>2</sub> compensation point of assimilation in the presence of dark respiration. This model has three empirically fitted parameters,  $g_0$ ,  $g_1$  and  $D_0$ .

These models [Eqns (2) and (3)] are widely used because they are straightforward to parameterize from leaf-scale data, are easy to implement at large scales, and nonetheless appear to capture the fundamentals of stomatal behaviour. However, there are several important criticisms that can be made of both models. As noted already, Eqn (2) is incorrect in its assumption of a dependence on  $h_r$ . A significant practical problem with Eqn (3) is that the parameters  $g_1$  and  $D_0$  are very strongly correlated. This correlation means that the parameters are difficult to estimate from data with confidence, and differences in the parameters among datasets cannot be clearly interpreted (e.g. Medlyn *et al.*, 2005). A model with formally identifiable parameters (i.e. one in which parameters are not correlated) is desirable.

The major criticism of both models, however, is that they are empirical in nature. They have been developed from experimental observations, rather than from any mechanistic understanding or theory of stomatal behaviour. This empirical basis is unsatisfactory because it means that we lack confidence in applying the model in novel situations (such as under increasing atmospheric CO<sub>2</sub> concentration). It also means that we have no theoretical basis for predicting or interpreting differences in parameter values among species and vegetation types. Lacking this basis, the parameters are simply assumed constant for all C<sub>3</sub> vegetation in many regional and global models (e.g. Krinner *et al.*, 2005), whereas in other models, parameter values are tuned to match large-scale observations (e.g. Cox, 2001; Oleson *et al.*, 2004).

#### Optimal stomatal conductance model

A theory of optimal stomatal behaviour was developed by Cowan & Farquhar (1977). This theory postulates that stomata should act to maximize carbon gain (photosynthesis,  $A$ ) while at the same time minimizing water lost ( $E$ , transpiration). That is, the optimal stomatal conductance is obtained when the following expression is minimized:

$$\int_{t_1}^{t_2} (E(t) - \lambda A(t)) dt, \quad (4)$$

where  $\lambda$  (mol H<sub>2</sub>O mol<sup>-1</sup> C) is a parameter describing the marginal water cost of carbon gain. Cowan & Farquhar (1977) showed, using calculus of variations, that minimizing this expression leads to the following optimization constraint:

$$\frac{\partial E}{\partial A} = \lambda. \quad (5)$$

Hari *et al.* (1986) combined this constraint with a very simple photosynthetic model in which  $A$  was assumed proportional to intercellular CO<sub>2</sub> concentration,  $C_i$ , and a function of incident light,  $f(I)$ , i.e.

$$A = C_i f(I). \quad (6)$$

They obtained the following expression for optimal stomatal conductance,  $g_s^*$ :

$$g_s^* = f(I) \left( \sqrt{\frac{C_a \lambda}{1.6D}} - 1 \right), \quad (7)$$

where  $D$  is vapour pressure deficit. We note that Hari *et al.* (1986) defined their parameter  $\lambda$  as the inverse of that used by Cowan & Farquhar (1977), whereas here we use Cowan's definition of the parameter and so have modified Hari *et al.*'s expression accordingly. Lloyd and Farquhar (1994) followed a similar derivation and obtained the following expression, which shows a close similarity to the empirical models:

$$g_s^* = A \left( \sqrt{\frac{1.6\lambda}{(C_a - \Gamma)D}} \right). \quad (8)$$

Both Eqns (7) and (8) have been tested with leaf scale stomatal conductance data (Lloyd *et al.*, 1995; Hari *et al.*, 1999; Mäkelä *et al.*, 2004; Kolari *et al.*, 2007), and have been implemented in canopy gas exchange models (Lloyd *et al.*, 1995, 2002; Mäkelä *et al.*, 2006; Mercado *et al.*, 2009). Katul *et al.*, (2009) explored the properties of this model and found that it was consistent with observed responses of  $g_s$ ,  $E$ , and the ratio  $C_i:C_a$  to  $D$ . However, this model does not correctly capture the response of  $g_s$  to changes in atmospheric CO<sub>2</sub>. This problem arises because of the simplifying assumption that  $A$  is proportional to  $C_i$  [Eqn (6)].

Arneth *et al.* (2002) combined the relationship with the more realistic model of photosynthesis developed by Farquhar *et al.* (1980). This model assumes that the photosynthetic rate is limited by either RuBP regeneration, in which case

$$A = \frac{J}{4} \frac{C_i - \Gamma^*}{C_i + 2\Gamma^*} - R_d \quad (9)$$

where  $J$  is the rate of electron transport,  $\Gamma^*$  is the CO<sub>2</sub> compensation point in the absence of dark respiration and  $R_d$  is the dark respiration rate; or it is limited by the rate of carboxylation, in which case

$$A = V_{cmax} \frac{C_i - \Gamma^*}{C_i + K_m} - R_d, \quad (10)$$

where  $V_{cmax}$  is the maximum rate of Rubisco activity and  $K_m$  is the Michaelis–Menten coefficient for Rubisco kinetics. Note that mesophyll conductance (Niinemets *et al.*, 2009) is implicit in this formulation of the model

and is not considered explicitly here. Arneeth *et al.* (2002) showed that, when photosynthesis is represented in this way, the optimal  $C_i$  depends on  $\lambda$  according to two quadratic equations corresponding to the two different limitations (see Appendix S1). In this paper, we focus only on the first limitation to photosynthesis [Eqn (9)]; the reasons for this choice are fully explained in the 'Discussion'.

### Theory

We coupled the optimal stomatal control model with Eqn (9), using the quadratic equation obtained by Arneeth *et al.* (2002) as a starting point. As described in the Appendix S1, we then derived the following approximation for the optimal stomatal conductance:

$$g_s^* \approx g_0 + \left(1 + \frac{g_1}{\sqrt{D}}\right) \frac{A}{C_a}. \quad (11)$$

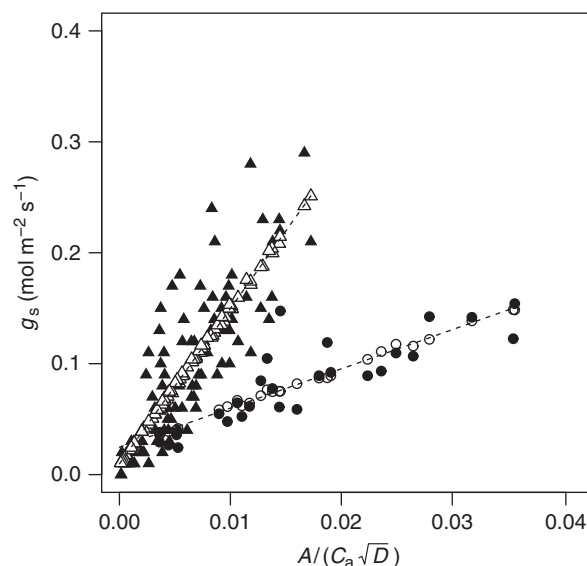
The analytical expression in Eqn (11) is closely analogous to the empirical models described by Eqns (2) and (3). In Eqn (11), the term  $g_1/\sqrt{D}$  is always  $> 1$ , and tends to dominate the term  $(1 + g_1/\sqrt{D})$ . As a result, Eqn (11) predicts a close linear relationship between  $g_s$  and the combination of terms  $A/(C_a\sqrt{D})$ , similar to the linear relationships given by the empirical models Eqns (2) and (3). This relationship is demonstrated for two example datasets in Fig. 1. In this figure, measured  $g_s$  and predicted  $g_s$  from Eqn (11) are plotted against  $A/(C_a\sqrt{D})$ , and it can be seen that predicted values closely follow a linear fit to measured data. This type of plot can therefore be used as a simple way of visualizing the fit of Eqn (11). The slope of this plot varies principally with  $g_1$ , although it also depends slightly on the range of  $D$  in the measurements. Differences in slope among plots of this kind therefore can be used to help visualize differences in  $g_1$  among datasets.

We term Eqn (11) the unified stomatal model, because it has the same form as the empirical models but is derived from the optimal model, thus combining both approaches into the one model.

The parameter  $g_1$  can be directly obtained by fitting to data in the same way as is usually done with the empirical models. However, we now have a theoretical interpretation for the parameter  $g_1$ : as shown in the Appendix S1,  $g_1$  is proportional to the combination of terms  $\sqrt{\Gamma^* \lambda}$ :

$$g_1 \propto \sqrt{\Gamma^* \lambda}. \quad (12)$$

That is, the parameter  $g_1$  should increase with the marginal water cost of carbon  $\lambda$ , and with the  $\text{CO}_2$  compensation point  $\Gamma^*$ .

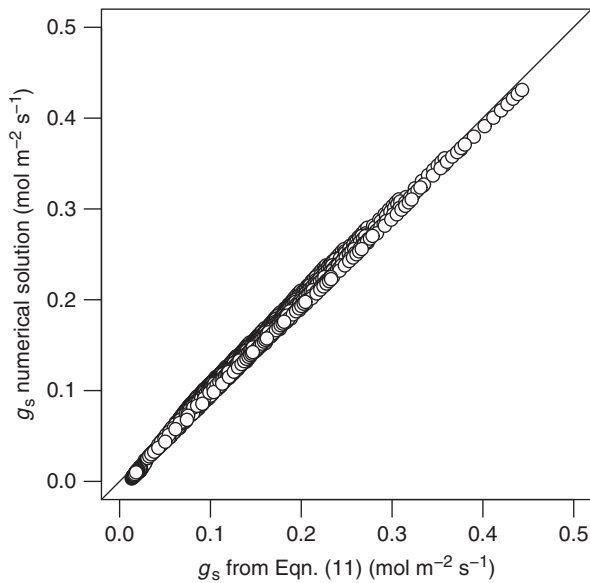


**Fig. 1** Measured and predicted values of stomatal conductance plotted as a function of  $A/(C_a\sqrt{D})$ . Sitka B (diamonds) and Red Gum (triangles) datasets are used as examples. Filled symbols show measured data. Open symbols show predicted values from a fit of Eqn (11) to the data. The line shows a simple linear regression to the measured data. The figure demonstrates that predicted values from Eqn (11) closely follow the linear regression of  $g_s$  against  $A/(C_a\sqrt{D})$ .

We compared the exact solution of the coupled stomatal–photosynthesis model with the simplified model given by Eqn (11), and found it is an excellent approximation to the optimal stomatal conductance over a realistic range of values of incident light,  $D$ ,  $C_a$  and  $\lambda$  (Fig. 2). The mean absolute deviation between the simplified model and the numerical solution was  $0.0044 \text{ mol m}^{-2} \text{ s}^{-1}$ .

The  $\text{CO}_2$  compensation point,  $\Gamma^*$ , and its temperature dependence, are generally assumed to be the same for all  $\text{C}_3$  species. It increases with temperature (Bernacchi *et al.*, 2001), suggesting that  $g_1$  should increase with growth temperature. For a given growth temperature,  $g_1$  is determined by the marginal water cost of carbon,  $\lambda$ . To date, it has been unclear how  $\lambda$  varies among species and growth conditions, partly because of the difficulty of quantifying  $\lambda$  using existing methods. The model proposed here offers a new and simple means of quantifying  $\lambda$ , by fitting Eqn (11) to stomatal conductance measurements and using the fitted parameter  $g_1$  as a proxy for  $\lambda$ .

Two key assumptions were needed to derive Eqn (11). First, the atmospheric  $\text{CO}_2$  concentration,  $C_a$ , is assumed to be much larger than the  $\text{CO}_2$  compensation point. The expression breaks down for  $\text{CO}_2$  concentrations below approximately  $120 \mu\text{mol mol}^{-1}$ . As the



**Fig. 2** Test of the accuracy of the approximate model. The figure compares the approximate solution Eqn (11) with the exact numerical solution to the optimal stomatal model coupled with the Farquhar *et al.* (1980) model of photosynthesis. To generate this figure, following environmental drivers were varied factorially: PAR (50–1550  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), relative humidity (30–80%),  $C_a$  (320–700 ppm). For several different values of  $\lambda$ , Eqn (11) was fitted to output from the numerical model and the corresponding parameters  $g_1$  and  $g_0$  obtained. These parameters were then used to estimate the optimal  $g_s$  from the environmental drivers, using Eqn (11).

Earth's atmospheric  $\text{CO}_2$  concentration has never fallen to this level (Ehleringer *et al.*, 2007), this assumption does not limit the applicability of the approximation. Second, we assume that stomata behave in such a way that they optimize for RuBP regeneration-limited photosynthesis [Eqn (9)], rather than for Rubisco-limited photosynthesis [Eqn (10)]. This assumption is discussed below.

### Model testing

We obtained eight datasets of diurnal courses of stomatal conductance measured on field-grown trees from a range of different forest types and climates. We fitted Eqns (2), (3) and (11) to these datasets using SIGMAPLOT (v. 11.0, Systat Software Inc.). Table 1 gives the details of the datasets used and Table 2 shows the statistics of the model fits. The unified model Eqn (11) gave the best fits for half of the eight datasets, when AIC statistics are compared (Table 2). The Ball *et al.* (1987) model [Eqn (2)] was the best fit for two of the smaller datasets, but gave a relatively poor fit for other datasets, particularly the Duke pine dataset, where  $R^2$  was just 17%. The Leuning

**Table 1** Details of example datasets used for model testing

Dataset	Species	Location	Latitude/ Longitude	Temperature ( $^{\circ}\text{C}$ )	VPD (kPa)	References
Sitka A	<i>Picea sitchensis</i>	Aberfeldy, Scotland	56 $^{\circ}$ 37'N, 3 $^{\circ}$ 48'W	13.5	0.5	Wingate <i>et al.</i> (2007), Medlyn <i>et al.</i> (2005)
Sitka B	<i>Picea sitchensis</i>	Glencorse, Scotland	55 $^{\circ}$ 31'N, 3 $^{\circ}$ 12'W	24.8	1.6	Barton & Jarvis (1999), Medlyn <i>et al.</i> (2001)
Fagus	<i>Fagus sylvatica</i>	Grib Skov, Denmark	55 $^{\circ}$ 59'N, 12 $^{\circ}$ 16'E	27.2	2.2	Freeman (1998), Medlyn <i>et al.</i> (2001)
Duke Pine	<i>Pinus taeda</i>	North Carolina, USA	35 $^{\circ}$ 59'N, 79 $^{\circ}$ 06'W	28.1	1.7	Ellsworth (1999), Ellsworth <i>et al.</i> (2004), Crous <i>et al.</i> (2008)
Macchia	<i>Phillyrea angustifolia</i> ; <i>Pistacia lentiscus</i>	Montalto di Castro, Italy	42 $^{\circ}$ 22'N, 11 $^{\circ}$ 32'E	32.7	2.9	Scarascia-Mugnozza <i>et al.</i> (1996) Medlyn <i>et al.</i> (2001)
Alpine Ash	<i>Eucalyptus delegatensis</i>	Snowy Mts, NSW, Australia	35 $^{\circ}$ 39'S, 148 $^{\circ}$ 56'E	20.6	1.2	Medlyn <i>et al.</i> (2007)
Savanna	Six tropical savanna species	Darwin, NT, Australia	12 $^{\circ}$ 29'S, 130 $^{\circ}$ 59'E	33.0	2.6	Thomas & Eamus (2002)
Parramatta Red Gum	<i>Eucalyptus parramattensis</i>	Western Sydney, NSW, Australia	33 $^{\circ}$ 39'S, 150 $^{\circ}$ 46'E	32.1	5.1	Zeppel <i>et al.</i> (2008)

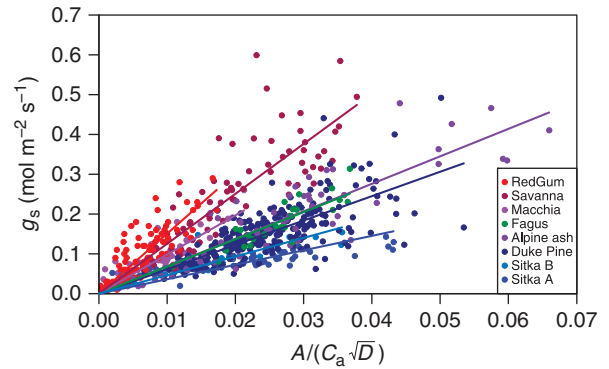
Temperature and vapour pressure deficit (VPD) refer to the average leaf temperature and VPD at which measurements were taken, and do not necessarily reflect growth temperature or VPD. At each site, data from different species were pooled where stomatal behaviour was not distinguishable between species.

**Table 2** Statistics of fits of the three alternative models to example datasets

Dataset	n	Eqn (2) (Ball <i>et al.</i> 1987)			R <sup>2</sup>	Eqn (3) (Leuning, 1995)			D <sub>0</sub>	Eqn (11) (this paper)		
		g <sub>0</sub>	g <sub>1</sub>	g <sub>0</sub>		g <sub>1</sub>	g <sub>0</sub>	g <sub>1</sub>		R <sup>2</sup>	g <sub>0</sub>	g <sub>1</sub>
Sitka A	77	0.039 (0.004)	4.55 (0.38)	0.038 (0.003)	0.651	7.35 (0.92)	0.35 (0.08)	0.724	0.033 (0.003)	1.66 (0.14)	0.759	
Sitka B	27	0.027 (0.008)	5.17 (0.67)	0.024 (0.01)	0.704	5.36 (2.24)	1.89 (2.22)*	0.729	0.022 (0.008)	2.57 (0.43)	0.732	
Duke Pine	136	0.057 (0.019)	7.14 (1.36)	0.007 (0.02)*	0.170	10.96 (2.67)	1.15 (0.58)	0.522	-0.007 (0.013)*	5.08 (0.49)	0.527	
Alpine Ash	60	0.016 (0.016)*	11.98 (1.0)	0.001 (0.01)*	0.716	14.43 (2.37)	0.95 (0.33)	0.801	-0.004 (0.014)*	6.06 (0.46)	0.797	
Macchia	47	<b>0.038 (0.008)*</b>	<b>9.09 (0.92)</b>	0.03 (0.01)	<b>0.684</b>	14.7 (10.1)*	1.22 (1.25)*	0.631	0.028 (0.01)	5.95 (0.89)	0.613	
Fagus	24	-0.002 (0.015)*	<b>11.24 (0.88)</b>	-0.06 (0.04)*	<b>0.881</b>	8.17 (1.94)	7.28 (10.0)*	0.782	-0.044 (0.025)*	6.99 (0.93)	0.778	
Savanna	77	0.048 (0.015)	13.62 (0.89)	<b>0.023 (0.02)*</b>	0.756	<b>141.3 (524)*</b>	<b>0.125 (0.5)*</b>	<b>0.77</b>	-0.004 (0.02)*	11.23 (0.97)	0.685	
Red Gum	96	0.016 (0.007)	15.27 (1.03)	<b>0.014 (0.007)</b>	0.702	<b>68.7 (103)*</b>	<b>0.43 (0.72)*</b>	<b>0.739</b>	0.009 (0.007)*	12.13 (0.96)	0.690	

Parameter standard errors are shown in brackets. Units are: g<sub>0</sub>, mol m<sup>-2</sup> s<sup>-1</sup>; g<sub>1</sub>, dimensionless; D<sub>0</sub>, kPa. Values of R<sup>2</sup> for each model fit are shown. Because Eqn (3) has one additional parameter, the Akaike Information Criterion (AIC) was also calculated to allow an unbiased comparison of the goodness-of-fit of the models (Hilborn & Mangel, 1997). The model having the lowest AIC for each data set is shown in bold.

\*Parameters that are not significantly different from zero.



**Fig. 3** Visualization of the unified stomatal model Eqn (11) fitted to eight datasets from contrasting forest ecosystems. Details of the ecosystems are given in Table 1. Blue shades show data from conifers, green shows data from deciduous angiosperms, and red/purple shades show data from broadleaf evergreen forests. For this figure, the model and linear regressions were fitted fixing the intercept to zero. Linear regression slopes are as follows: Sitka A, 4.2; Sitka B, 4.7; Duke Pine, 6.1; Fagus, 6.8; Alpine Ash, 7.1; Macchia, 9.8; Savanna, 12.5; Red Gum, 15.1. Estimated values for g<sub>1</sub> are: Sitka A, 3.0; Sitka B, 3.6; Duke Pine, 4.8; Fagus, 5.4; Alpine Ash, 5.9; Macchia, 8.2; Savanna, 11.1; Red Gum, 13.1.

(1995) model [Eqn (3)] gave the best fit for two datasets, but the parameter values were not identifiable (i.e. not significantly different from zero) for five of the eight datasets. Overall, the unified model performed best, giving high R<sup>2</sup> values for all datasets, and identifiable parameter values.

We visualize fits of the model to our eight datasets in Fig. 3. For this figure, relationships were fitted assuming the intercept g<sub>0</sub> to be zero; resulting values of g<sub>1</sub> are given in the figure caption. The key point demonstrated by Fig. 3 is that the slope of the relationship (and therefore g<sub>1</sub>) clearly differs among species, and varies in a consistent manner. As predicted from Eqn (12), g<sub>1</sub> increases with growth temperature, with values highest in tropical savanna species and lowest in Sitka spruce growing in Scotland. Also, although there is some confounding between growth temperature and plant functional type in the datasets presented in Fig. 3, we can nevertheless identify clear differences among plant functional types. Values for g<sub>1</sub> were lowest in gymnosperms and highest in angiosperms, and eucalyptus have a considerably higher g<sub>1</sub> than do pines growing at similar latitudes (Tables 1 and 2).

**Discussion**

Stomatal conductance plays a fundamental role in determining vegetation carbon and water balances. In this paper, we provide a new quantitative framework for

examining acclimation and adaptation of stomatal conductance to environmental change. The new framework was obtained by reconciling two long-standing approaches to modelling stomatal conductance. While it has been known for some time that there are mathematical similarities between the two models (e.g. Lloyd *et al.*, 1995; Katul *et al.*, 2009), we have taken this a step further and showed that the theory of optimal stomatal conductance leads to a model that is directly analogous to the widely used empirical models. The result is a unified model [Eqn (11)] which is simple to implement, has parameters that are identifiable from data, and are biologically meaningful. This unified model opens up a way forwards for developing a general theory for variation in stomatal behaviour across species, plant functional types and environments.

We show that the key model parameter  $g_1$  is proportional to both the CO<sub>2</sub> compensation point and the marginal water cost of carbon gain [Eqn (12)]. The CO<sub>2</sub> compensation point depends on temperature according to a well-defined relationship that can be assumed constant for all C<sub>3</sub> species (Bernacchi *et al.*, 2001). We predict that, for a given species, the parameter  $g_1$  should increase with growth temperature; and that the rate of increase should follow the square root of the temperature-dependence of the CO<sub>2</sub> compensation point [Eqn (12)]. The increase in  $g_1$  with temperature is borne out by the contrast among the sample datasets shown in Fig. 3 (see also Table 1). It is also consistent with a survey of stomatal conductance and stable isotope data across species and environments by Lloyd and Farquhar (1994). The values of  $\lambda$  derived by these authors are analogous to our parameter  $g_1$  [compare their Eqn (11), with constant  $C_a$  and Eqn (13) below]. They found that these values were lower for cold/cool zone vegetation than for warm temperate vegetation, as predicted by our model.

The parameter  $g_1$  is also related to the marginal water cost of plant carbon gain,  $\lambda$  (mol H<sub>2</sub>O mol<sup>-1</sup> C). The value of  $\lambda$  can be thought of as representing the amount of water that a plant is prepared to spend to gain carbon: a high value of  $\lambda$  indicates "profligate" behaviour whereas a low value of  $\lambda$  indicates "conservative" behaviour. Cowan & Farquhar (1977) argued that the parameter  $\lambda$  was only likely to remain constant on short time scales, varying from day to day, and this perception has limited the use of the model in the past. However, the fact that functionally equivalent empirical models have been successfully applied using constant parameter values strongly suggests that the value of  $\lambda$  is stable on longer time scales, making it an informative parameter. Theoretical studies of  $\lambda$ , and experimental studies using the empirical models, indicate two major sources of variation in  $\lambda$ : differences among species,

related to whole-plant water-use strategy, and effects of low soil moisture availability.

Theoretical work suggests that  $\lambda$  is likely to be related to whole-plant carbon-water economy (Givnish, 1986). Our comparison among ecosystems (Fig. 3) provides clear evidence for differences in stomatal behaviour among plant functional types, indicating a link with whole-plant traits. The contrast that we found between angiosperms and gymnosperms, with angiosperms having higher values of  $\lambda$ , is strongly supported by the cross-species survey by Lloyd and Farquhar (1994). The  $g_1$  parameter of the empirical stomatal models also varies among species in a way that appears linked to plant water use strategy (e.g. Medlyn *et al.*, 2001). Furthermore, evidence is accumulating that photosynthetic capacity and maximal stomatal conductance are related to plant hydraulic architecture (e.g. Nardini & Salleo, 2000; Clearwater & Meinzer, 2001; Hubbard *et al.*, 2001; Katul *et al.*, 2003; Mencuccini, 2003; Bucci *et al.*, 2005; Taylor & Eamus, 2008). Thus, values of  $\lambda$  obtained under well-watered conditions are likely to be a useful quantitative way of characterizing whole-plant level water-use strategies.

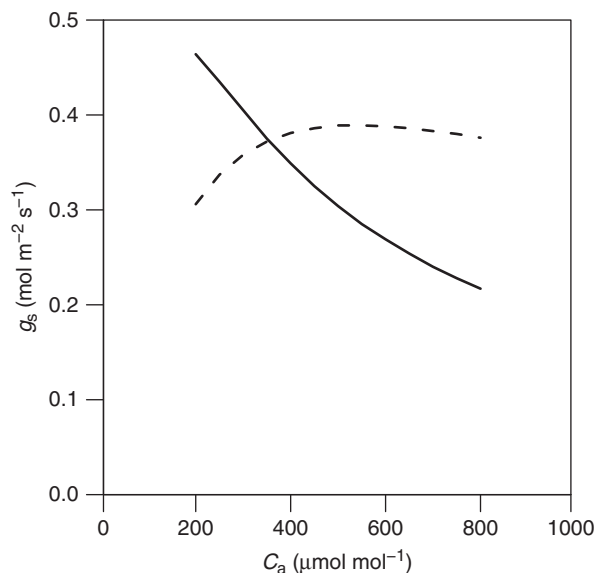
Under drought conditions, theoretical analysis of the optimal stomatal conductance indicates that the expected value of carbon assimilation is maximized if the value of  $\lambda$  declines as drought progresses, at a rate determined by the probability of rain on any given day (Mäkelä *et al.*, 1996). Some models that use the empirical approach incorporate an equivalent assumption, reducing the parameter  $g_1$  as a function of soil moisture content (e.g. Sala & Tenhunen, 1996; Kirschbaum, 1999). Some recent implementations decrease the  $g_1$  parameter as a function of leaf water potential rather than soil moisture content (e.g. Tuzet *et al.*, 2003). Such assumptions have been found to improve simulations of forest water use during drought (e.g. Sala & Tenhunen, 1996), and of leaf-level photosynthesis and transpiration over a growing season (Berninger *et al.*, 1996; Op de Beeck *et al.*, 2010). However, very few studies have directly examined how the relationship between photosynthesis and stomatal conductance is affected by drought. One study on *Pinus ponderosa* that directly examined this question found that the model intercept, rather than the slope, was related to soil moisture potential (Misson *et al.*, 2004). It can be questioned whether the optimization criterion assumed here Eqn (4) can still be said to be optimal if drought stress starts to threaten plant survival. It may be that the relationship given by Eqn (11) will break down as soil moisture potential is reduced. Nonetheless, Eqn (11) offers a quantitative framework within which it would be possible to critically examine how soil moisture stress affects stomatal behaviour.

By linking the optimal and empirical stomatal models, we have identified a new and simple way of estimating  $\lambda$  from measurements of stomatal conductance. We suggest that comparative studies of such values  $\lambda$  across species and soil moisture conditions are likely to bring new insights into adaptation of stomatal behaviour and plant water-use strategies.

#### Response to atmospheric CO<sub>2</sub> concentration

One of the major assumptions required by our derivation was that stomatal conductance acts as if it is optimizing for RuBP regeneration-limited photosynthesis Eqn (9), rather than Rubisco-limited photosynthesis [Eqn (10)]. Importantly, this is not the same as assuming that photosynthesis is always limited by RuBP regeneration; we only assume that stomata behave as if it were. We justify this assumption as follows. Stomatal responses to CO<sub>2</sub> can be observed in epidermal peels, indicating that the CO<sub>2</sub> sensing mechanism resides in the guard cells *per se*, not in the mesophyll (Travis & Mansfield, 1979; Assmann, 1999). However, although guard cells have a significant capacity for electron transport, they have a relatively low capacity for Rubisco C fixation (e.g. Outlaw *et al.* 1979; Shimazaki, 1989; Outlaw & De Vlieghere-He, 2001). Thus, while it is plausible that stomatal behaviour could be regulated by rates of electron transport, it seems implausible that stomatal behaviour would be regulated by rates of Rubisco activity, or the balance between the two processes. This conclusion is strongly supported by the observation that the correlation between photosynthesis and stomatal conductance breaks down in transgenic plants with impaired Rubisco activity (von Caemmerer *et al.* 2004). Reduced Rubisco activity reduces photosynthetic capacity in such plants, but does not appear to impact on stomatal conductance or its responsiveness to C<sub>a</sub>.

Importantly, when we make this assumption, the resulting model correctly captures the observed response to atmospheric CO<sub>2</sub> concentration (C<sub>a</sub>). The response to C<sub>a</sub> predicted by the optimal stomatal model differs considerably according to which limitation is considered, as shown in Fig. 4. If Rubisco-limited photosynthesis is considered, stomatal conductance is predicted to increase with increased C<sub>a</sub>, contrary to extensive experimental observations (see Morison, 1987 for a review). In contrast, if RuBP-regeneration-limited photosynthesis is considered, stomatal conductance is predicted to decline nonlinearly with C<sub>a</sub>, which agrees closely with observations (Morison, 1987). This assumption thus allows the model to be used to investigate responses to rising C<sub>a</sub>. For example, Katul *et al.* (2010) recently applied the optimal stomatal conductance model to datasets from a large-scale CO<sub>2</sub> enrich-



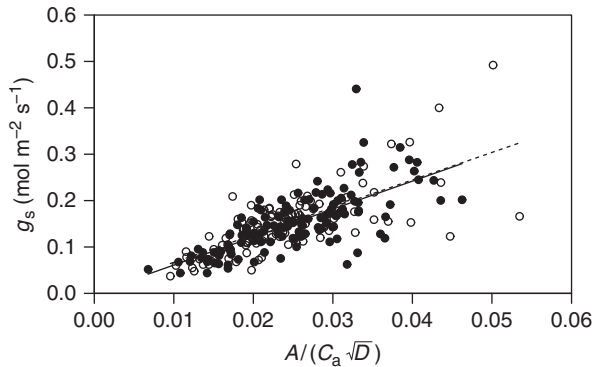
**Fig. 4** The response of stomatal conductance ( $g_s$ ) to atmospheric CO<sub>2</sub> concentration ( $C_a$ ) predicted by the full numerical solution to the optimal stomatal model. Solid line: coupled with RuBP-regeneration limited photosynthesis [Eqn (9)]; Dashed line: coupled with Rubisco-limited photosynthesis [Eqn (10)].

ment study, the Duke FACE experiment. They estimated  $\lambda$  from ambient and enriched CO<sub>2</sub> treatments, and concluded that this parameter differs between treatments. However, they assumed Rubisco-limited photosynthesis throughout their study, and their conclusion is thus driven by the use of a model with an incorrect short-term C<sub>a</sub> response. In contrast, we fitted our Eqn (11) to an expanded dataset with 10 years of data from the same FACE experiment, and found that there was no effect of CO<sub>2</sub> treatment on the value of  $g_1$  (Fig. 5). Therefore, because there is no change in the parameter value between treatments, we can conclude that there was no acclimation of stomatal conductance to CO<sub>2</sub> enrichment in this FACE experiment (cf. Medlyn *et al.* 2001).

#### Response to D

The response to vapour pressure deficit ( $D$ ) predicted by the optimal stomatal model was investigated by Katul *et al.* (2009). They showed that the predicted  $D$  response is consistent with observations and also quite consistent with the  $D$  response of the Leuning (1995) empirical model [Eqn (3)] over the normal operating range of  $D$ . We note that Leuning (1995) considered alternative forms for the  $D$  response, but specifically did not consider the form  $D^{-1/2}$ , despite observing that Lloyd (1991) had found this function to give the best fit to data from *Macadamia integrifolia*. The major difference be-





**Fig. 5** Visualization of the unified stomatal model [Eqn (11)] for data from ambient and elevated  $[\text{CO}_2]$  treatments in the Duke FACE experiment. Data are from spot measurements of pine needle gas exchange at ambient and elevated  $\text{CO}_2$  as described in detail in Ellsworth (2000) and Katul *et al.* (2000) for the first 3 years of the Duke FACE experiment, and from spot measurements extracted from complete photosynthetic  $\text{CO}_2$  response curves for unfertilized trees from Crous & Ellsworth (2004) and Crous *et al.* (2008) from the third through ninth years of  $\text{CO}_2$  exposure in FACE. Solid symbols and solid line: data from ambient  $[\text{CO}_2]$  treatment; open symbols and dashed line: data from elevated  $[\text{CO}_2]$  treatment. Values of  $g_1$  obtained by fitting Eqn (11) to these data were not significantly different: ambient  $[\text{CO}_2]$ : 4.83 (SE 0.146); elevated  $[\text{CO}_2]$ : 4.94 (SE 0.128).

tween the hyperbolic  $D$  response used in the Leuning model [Eqn (3)] and the square root dependence given by the optimal stomatal model [e.g. Eqn (11)] lies in the behaviour of  $g_s$  as  $D$  approaches zero. Stomatal conductance at low  $D$  is bounded in Eqn (3) but unbounded in Eqn (11). However, an unbounded  $g_s$  at low  $D$  should not be seen as a problem. There is evidence from eddy covariance studies to suggest that stomatal conductance is in fact unbounded as VPD approaches zero (Wang *et al.* 2009), supporting the  $D$  response emerging from the unified model. Also, although  $g_s$  may be unbounded, transpiration ( $E$ ) is not;  $E \approx g_s^* D$ , so that  $E$  goes to zero as  $D$  goes to zero. Thus, an unbounded value of  $g_s$  is acceptable, from viewpoints of both model correctness and model stability.

#### Connections to other concepts

A number of other related concepts appear widely in the literature. It is worth briefly mentioning here how the unified stomatal model connects to two of these concepts. Assuming that the intercept term  $g_0$  is zero, the ratio of intercellular to atmospheric  $\text{CO}_2$  concentration,  $C_i/C_a$ , is given by:

$$\frac{C_i}{C_a} = 1 - \frac{1.6\sqrt{D}}{g_1 + \sqrt{D}}. \quad (13)$$

Thus,  $C_i/C_a$  decreases with increasing  $D$ . For a given value of  $D$ , the  $C_i/C_a$  is independent of atmospheric  $\text{CO}_2$  concentration, consistent with experimental data (e.g. Wong *et al.* 1985), and depends only on  $g_1$ .

Secondly, the instantaneous transpiration use efficiency (ITE), which is the ratio of leaf photosynthesis to transpiration, is given by:

$$\frac{A}{E} = \frac{C_a}{g_1\sqrt{D} + D}. \quad (14)$$

That is, the ITE is predicted to decline with increasing  $D$ . At a given  $D$ , it is proportional to atmospheric  $\text{CO}_2$  concentration. Finally, species with a high  $g_1$  will have a low ITE.

#### Conclusion

Stomata determine the coupling between vegetation carbon and water cycles, so their behaviour under global environmental change is key to predicting vegetation function. Here, we provide a new quantitative framework for analyzing stomatal behaviour under environmental change. We combined Cowan & Farquhar (1977)'s theory of optimal stomatal behaviour with the Farquhar *et al.* (1980) model of photosynthesis, and derived a new model expression for stomatal conductance that has the same form as current empirical models. The unified model thus combines existing experimental evidence with an accepted theory for stomatal behaviour. This model has significant potential (i) to act as a framework for interpreting stomatal behaviour across species in response to a range of environmental conditions, including rising atmospheric  $[\text{CO}_2]$ ; and (ii) to improve simulations of vegetation carbon cycling and water use at large scales.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Derivation of analytical approximation to the optimal stomatal control model.

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