

# A canopy-scale test of the optimal water-use hypothesis

STANISLAUS J. SCHYMANSKI<sup>1\*</sup>, MICHAEL L. RODERICK<sup>2</sup>, MURUGESU SIVAPALAN<sup>3†</sup>, LINDSAY B. HUTLEY<sup>4</sup> & JASON BERINGER<sup>5</sup>

<sup>1</sup>*School of Environmental Systems Engineering, The University of Western Australia, Perth, Australia,* <sup>2</sup>*Environmental Biology Group, Research School of Biological Sciences, The Australian National University, Canberra, Australia,* <sup>3</sup>*Centre for Water Research, The University of Western Australia, Perth, Australia,* <sup>4</sup>*School of Science and Primary Industries, Charles Darwin University, Darwin, Australia and* <sup>5</sup>*School of Geography and Environmental Science, Monash University, Clayton, Vic., Australia*

## ABSTRACT

**Common empirical models of stomatal conductivity often incorporate a sensitivity of stomata to the rate of leaf photosynthesis. Such a sensitivity has been predicted on theoretical terms by Cowan and Farquhar, who postulated that stomata should adjust dynamically to maximize photosynthesis for a given water loss.**

**In this study, we implemented the Cowan and Farquhar hypothesis of optimal stomatal conductivity into a canopy gas exchange model, and predicted the diurnal and daily variability of transpiration for a savanna site in the wet-dry tropics of northern Australia. The predicted transpiration dynamics were then compared with observations at the site using the eddy covariance technique. The observations were also used to evaluate two alternative approaches: constant conductivity and a tuned empirical model.**

**The model based on the optimal water-use hypothesis performed better than the one based on constant stomatal conductivity, and at least as well as the tuned empirical model. This suggests that the optimal water-use hypothesis is useful for modelling canopy gas exchange, and that it can reduce the need for model parameterization.**

*Key-words:*  $\partial E/\partial A$ ; adaptation; assimilation; optimization; photosynthesis; transpiration; vegetation optimality.

## INTRODUCTION

Evapo-transpiration is often seen as a physical process (e.g. evaporation as a result of the energy partitioning into latent and sensible heat flux) controlled by available energy, vapour pressure and turbulence. Vegetation is thereby treated as a wick that facilitates the flow of water from the soil to the atmosphere along a potential gradient. In vegetated areas, however, evapo-transpiration is usually

dominated by transpiration, which is a biological process controlled by stomatal regulation and vegetation dynamics. Biologists consider transpiration as a coupled process with photosynthesis, as leaf-scale water vapour and CO<sub>2</sub> exchange occurs along a common pathway within leaf tissues. Leaves are organs that have developed to maximize CO<sub>2</sub> uptake while minimizing water loss in a given environment. The biological control of transpiration hence depends on many factors other than energy, vapour pressure and turbulence. For example, stomatal conductivity per unit leaf area is coupled to photosynthesis via internal and external CO<sub>2</sub> concentration, and is also controlled by plant hormonal signals (Larcher 1995). Gas exchange can be optimized at a canopy scale via seasonal modification of canopy leaf area (Hutley, O'Grady & Eamus 2001), depending on the species composition and the phenologies of the species on a given site.

Current practice for modelling transpiration in ecology and hydrology relies on long-term observations of the system in question and the derivation of correlations between observed variables. This is also true to some extent for physically based process models, where parameter values are usually estimated based on prior observations. Unfortunately, such observations are only available at intensively studied field sites, and the correlations often turn out to be highly non-linear and complicated by hysteresis and auto-correlation effects (e.g. Jarvis 1976). Furthermore, establishment of correlations for a given set of conditions does not guarantee the validity of these correlations in other conditions, which is a particular problem in connection with environmental change.

However, it may be possible to get away from simple extrapolations of past observations if the problem is approached from a different perspective. Cowan & Farquhar (1977) assumed *a priori* that plants would optimize stomatal conductivity dynamically in order to maximize total photosynthesis for a given amount of transpiration. This optimality assumption allowed them to formulate how stomatal conductivity should vary in response to the rate of photosynthesis and atmospheric water vapour deficit, given a fixed amount of water available for transpiration. The distinct advantage of this approach compared with empirical approaches is that it does not require any calibration as

*Correspondence:* S. J. Schymanski. Fax: +49 3641 577274; e-mail: sschym@bgc-jena.mpg.de

\*Present address: The Max Planck Institute for Biogeochemistry, Jena, Germany.

†Present address: Departments of Geography and Civil and Environmental Engineering, University of Illinois at Urbana-Champaign, Urbana, IL, USA.

long as the photosynthetic properties of a leaf and the total amount of water available for transpiration are known. This is particularly useful at a canopy scale, as it allows linking plant physiological principles with processes relevant to hydrological and atmospheric sciences. For example, if the photosynthetic properties can be inferred from site investigations, and the monthly water use from the water balance of the site, the within-month dynamics of transpiration at canopy scale could be computed directly from the optimality hypothesis. Furthermore, we have shown in a previous study that the photosynthetic properties of a savanna canopy can be inferred using optimality principles (Schymanski *et al.*, 2007) if transpiration rates, foliage projective cover and atmospheric conditions are known, even without the need for information about nutrient supplies. Hence, the implementation of the Cowan–Farquhar theory at the canopy scale would constitute an important step towards a complete model of self-optimizing vegetation allowing the estimation of CO<sub>2</sub> and water fluxes as a function of the environment only. This would be an invaluable tool for the inclusion of vegetation in hydrological models.

The Cowan–Farquhar theory has been successfully used in a number of studies to model gas exchange at leaf level under field conditions (Berninger & Hari 1993; Berninger, Mäkelä & Hari 1996; Hari *et al.* 1999; Koskela, Hari & Pipatwattanakul 1999; Hari, Mäkelä & Pohja 2000; Aalto, Hari & Vesala 2002), but experiments under controlled conditions often led to questioning of the theory (e.g. Franks, Cowan & Farquhar 1997; Thomas, Eamus & Bell 1999b). At canopy scale, the Cowan–Farquhar theory has been used only very rarely to date (e.g. Styles *et al.* 2002; Wilson *et al.* 2003; Mercado *et al.* 2006), and more empirically based models of conductivity, such as for example the Ball–Berry model and its modification by Leuning (Ball, Woodrow & Berry 1987; Leuning 1990, 1995) are considered state-of-the-art. The latter will be referred to as the Ball–Berry–Leuning model in this paper. It is interesting to note that the motivation for formulating stomatal conductivity as a function of photosynthesis in the Ball–Berry–Leuning model actually came from observations supporting the Cowan–Farquhar theory (Wong, Cowan & Farquhar 1979), but the shape of this function was then parameterized empirically.

The present study tests the Cowan–Farquhar theory of stomatal conductivity at canopy scale by implementing it into a canopy gas exchange model and testing its predictive power using canopy-scale gas exchange measurements. The test is very simple: given the total amount of transpiration in a month, can the model predict the observed within-month variability of transpiration? The same challenge is then tackled using a model of constant stomatal conductivity and a Ball–Berry–Leuning style model, and the results of the different models are compared with each other and with observations. Another criterion for the usefulness of a model besides reproducing observations is how much we can learn from it about the processes for a given site. This will also be a central point of discussion with respect to the comparison of the different models.

## METHODS

Both water loss by transpiration ( $E_t$ ) and rate of photosynthesis ( $A_g$ ) are linked by canopy conductivity ( $G_s$ ), such that any increase in CO<sub>2</sub> uptake rate under given atmospheric conditions and foliage properties has the inevitable consequence of increased water loss through the stomata. The relationship between  $E_t$  and  $A_g$  is non-linear, as  $A_g$  reaches saturation at high values of  $G_s$ , while  $E_t$  always increases with  $G_s$  if other limitations to  $E_t$  are neglected. The shape of the function depends on the photosynthetic properties of the canopy, the light environment and the atmospheric demand for water. It changes dramatically during the day because of variations in light and atmospheric vapour pressure deficit (VPD), with the result that the timing of water use can make a difference to the total carbon uptake achieved for a limited amount of water available for transpiration. Cowan and Farquhar postulated that for any given amount of total water available for transpiration in a period of time, a leaf can achieve a maximum CO<sub>2</sub> uptake if it adjusts leaf scale conductivity ( $g_s$ ) in such a way that the derivative of  $E_t$  with respect to  $A_g$  ( $\partial E_t / \partial A_g = \lambda$ ) is maintained at a constant value throughout the period (Cowan 1977; Cowan & Farquhar 1977). This was originally derived at leaf level, but later extended to a whole plant by postulating that the optimality criterion would require all leaves to function at the same value of  $\lambda$  (Cowan 1982). The value of  $\lambda$  has to be adapted to the total amount of water available during the period. Furthermore, in the presence of other processes competing for water (e.g. drainage and soil evaporation), the value of  $\lambda$  should vary with varying soil water content (Cowan & Farquhar 1977; Cowan 1982).

To compute the relationship between  $E_t$  and  $A_g$ , we followed a canopy gas exchange model derived earlier based on a biochemical photosynthesis model, a canopy light absorption model and a number of simplifying assumptions (Schymanski *et al.*, 2007). This model has been used in the previous study to derive the optimal photosynthetic properties of a seasonally dynamic tall-grass savanna vegetation, given observed water use and climate data. Based on these previous results, four months with relatively stable canopy dynamics were chosen for the present study, and the optimal canopy properties computed for these months were prescribed in the present study. Together with atmospheric variables measured on the site, the model enabled us to calculate rates of  $E_t$  and  $A_g$  for any value of  $G_s$  at any time step within a given month.

The diurnal and daily variations of  $E_t$  and  $A_g$  were modelled using three different approaches: (1) the Cowan–Farquhar hypothesis prescribing a constant  $\lambda$ ; (2) prescribing constant  $G_s$ ; and (3) the Ball–Berry–Leuning model (Ball *et al.* 1987; Leuning 1990, 1995). The values of  $\lambda$  in the constant  $\lambda$  model and  $G_s$  in the constant  $G_s$  model were chosen such that the modelled monthly  $E_t$  matched the observed monthly  $E_t$ , while the three parameters of the Ball–Berry–Leuning model were calibrated to match the observed time series of  $E_t$  as closely as possible. Note

that assuming a constant  $\lambda$  for a whole month diverges from previous work by Cowan and the group of Mäkelä and Hari, dealing with how  $\lambda$  should change with environmental conditions (e.g. Cowan 1982; Mäkelä, Berninger & Hari 1996). However, this assumption allowed a comparison of the different models with minimal parameter fitting.

The performances of the three models were assessed by comparison of the predicted daily and diurnal variations of  $E_t$  and  $A_g$  with observations on the site. In the following section, the models and data are described in more detail.

### Canopy gas exchange model

The gas exchange model is discussed in more detail elsewhere (Schymanski 2007; Schymanski *et al.*, 2007) and will only be summarized here.

The process of photosynthesis was subdivided into two steps: light processing (generation of electron transport) and CO<sub>2</sub> uptake. The modelled electron transport rate per leaf area ( $J$ ) (mol m<sup>-2</sup> s<sup>-1</sup>) as a function of photosynthetically active irradiance ( $I_t$ , mol quanta m<sup>-2</sup> s<sup>-1</sup>) and biochemical electron transport capacity ( $J_{\max}$ ) (mol m<sup>-2</sup> s<sup>-1</sup>) is summarized in Eqn 1.

$$J = J_{\max} \left( 1 - e^{-\frac{0.3I_t}{J_{\max}}} \right) \quad (1)$$

The canopy was modelled as a series of layers with horizontal leaves that were randomly distributed in each layer, with a leaf area ( $L_A$ ) of 0.1 per layer (see Table 1 for the number of layers in each month). Each layer was further subdivided into a sunlit and shaded fraction, where the sunlit fraction receives direct and diffuse light, while the shaded fraction only receives diffuse light. The intensity of diffuse light in each layer ( $I_{d,i}$ , where  $i$  denotes the layer) was calculated using Eqn 2, while the intensity of direct light was assumed to be the same throughout the canopy. The sunlit leaf area in each layer was calculated using Eqn 3. Equations 2 and 3 are based on the assumption that each foliage layer is composed of randomly distributed horizontal leaves, and hence, diverges from the common approach assuming certain leaf angle distributions (e.g. Monsi & Saeki 1953). For the derivation of the equations, see appendix A.2.1.2 in (Schymanski 2007).

$$I_{d,i} = I_{d,1}(1 - L_A)^{i-1} \quad (2)$$

$$L_{A\text{sun},i} = L_A(1 - L_A)^{i-1} \quad (3)$$

The leaf area-based electron transport rates of the shaded and sunlit leaf area fractions in each layer of foliage were obtained by inserting the irradiances incident on them ( $I_{d,i}$  and  $I_{\text{sun},i}$ , respectively) into Eqn 1. The total electron transport rate in each layer per unit of vegetated ground area ( $J_i$ ) (mol m<sup>-2</sup> vegetated ground area s<sup>-1</sup>) was then calculated by multiplying the leaf area-based electron transport rates of the shaded and sunlit leaf area fractions with their respective leaf areas ( $L_{A\text{shade},i}$  and  $L_{A\text{sun},i}$ ):

**Table 1.** Photosynthetic canopy properties for the investigated periods, as obtained from a previous study (Schymanski *et al.*, 2007)

Month	$M_A, L_{AI}$	$J_{\max 25,i}$ (μmol m <sup>-2</sup> s <sup>-1</sup> , from top to bottom layer)
July 2004	0.3, 0.75	517.9, 467.4, 421.9, 380.6, 343.1, 308.9, 277.7, 249.0, 222.6, 198.1, 175.4, 154.2, 134.2, 115.4, 97.8, 81.3, 66.3, 53.3, 42.8, 34.6, 28.4, 23.7, 20.0, 17.1, 14.7
October 2004	0.3, 0.78	480.4, 429.4, 384.0, 343.6, 307.2, 274.4, 244.7, 217.8, 193.2, 170.8, 150.1, 131.1, 113.5, 97.4, 82.7, 69.6, 58.1, 48.4, 40.3, 33.8, 28.6, 24.3, 20.8, 18.0, 15.6, 13.6
January 2005	1.0, 2.5	435.8, 385.1, 340.3, 300.6, 265.2, 233.7, 205.6, 180.1, 157.2, 136.7, 118.0, 101.3, 86.3, 73.2, 62.0, 52.5, 44.5, 37.9, 32.4, 27.9, 24.1, 20.9, 18.2, 16.0, 14.0
February 2005	1.0, 2.4	497.0, 439.2, 388.1, 342.9, 303.0, 267.2, 235.1, 206.1, 179.9, 156.1, 134.3, 114.5, 96.7, 80.8, 67.0, 55.4, 46.0, 38.4, 32.3, 27.4, 23.4, 20.1, 17.4, 15.2

$M_A$  denotes the ground fraction covered by vegetation,  $L_{AI}$  is the leaf area index of the site and  $J_{\max 25,i}$  is the electron transport capacities per unit leaf area, starting with the top layer of foliage. The number of values in the right column corresponds to the number of layers of foliage, for example, for July 2004, the parameters imply a canopy with a leaf area index of 2.5 (i.e. 25 foliage layers of 0.1 leaf area index in each), covering 30% of the site, so that total site  $L_{AI} = 2.5 \times 0.3 = 0.75$ .

$$J_i = L_{A\text{shade},i} \left( 1 - e^{-\frac{0.3I_{d,i}}{J_{\max,i}}} \right) J_{\max,i} + L_{A\text{sun},i} \left( 1 - e^{-\frac{0.3I_{\text{sun},i}}{J_{\max,i}}} \right) J_{\max,i} \quad (4)$$

$I_{\text{sun},i}$  (mol quanta m<sup>-2</sup> s<sup>-1</sup>) was hereby taken as the sum of direct and diffuse irradiances in layer  $i$ .

To account for clumped vegetation interspersed with bare soil patches, the electron transport rate of the whole site per unit ground area ( $J_A$ ) (mol m<sup>-2</sup> ground area s<sup>-1</sup>) was obtained by adding up the electron transport rates of all layers of foliage and multiplying the sum by the ground fraction covered by vegetation ( $M_A$ ). This is given in Eqn 5, where  $N_i$  denotes the total number of layers and  $J_i$  (mol m<sup>-2</sup> vegetated ground area s<sup>-1</sup>) denotes the electron transport rate in each layer of foliage.

$$J_A = M_A \sum_{i=1}^{N_i} J_i \quad (5)$$

While the canopy light environment was described using a sun-shade approach, the gas exchange was calculated using a big leaf approach. Specifically, the equations and variables, originally defined for the leaf scale (Farquhar, von Caemmerer & Berry 1980; von Caemmerer 2000) were now formulated at the canopy scale. It was assumed that, to a good approximation, carboxylation is predominantly light

limited in a canopy, so that Eqn 6 was deemed adequate for modelling canopy photosynthesis (Farquhar & von Caemmerer 1982). A calculation of the likely error because of neglecting ribulose 1·5-bisphosphate carboxylase/oxygenase (Rubisco) limitation of carboxylation in the model is also given in Appendix 2.2 in Schymanski (2007).

In Eqn 6,  $A_c$  denotes the carboxylation rate (mol m<sup>-2</sup> ground area s<sup>-1</sup>),  $C_i$  denotes the mole fraction of CO<sub>2</sub> inside the big leaf (mol CO<sub>2</sub> mol<sup>-1</sup> air) and  $\Gamma_*$  denotes the CO<sub>2</sub> compensation point in the absence of mitochondrial respiration (mol CO<sub>2</sub> mol<sup>-1</sup> air). The rate of CO<sub>2</sub> exchange between the inside of the leaf and the atmosphere ( $A_g$ ) (mol CO<sub>2</sub> m<sup>-2</sup> ground area s<sup>-1</sup>) is formulated in Eqn 7, where  $G_s$  is the stomatal conductivity (mol m<sup>-2</sup> ground area s<sup>-1</sup>) while  $C_i$  and  $C_a$  (both in mol CO<sub>2</sub> mol<sup>-1</sup> air) are the mole fractions of CO<sub>2</sub> inside the leaf and in the atmosphere, respectively (Cowan & Farquhar 1977). Inside the leaf, leaf respiration ( $R_l$ ) (mol m<sup>-2</sup> ground area s<sup>-1</sup>) replenishes some of the CO<sub>2</sub> consumed by  $A_c$ , so that at steady state, only the difference between  $A_c$  and  $R_l$  has to be balanced by  $A_g$ . This is expressed in Eqn 8.

$$A_c = \frac{J_A(C_i - \Gamma_*)}{4C_i + 8\Gamma_*} \quad (6)$$

$$A_g = G_s(C_a - C_i) \quad (7)$$

$$A_g = A_c - R_l \quad (8)$$

Inserting Eqns 6 and 7 into Eqn 8 gives  $C_i$  as a function of  $G_s$ ,  $J_A$  and  $R_l$ , which can then be inserted back into Eqn 7 to obtain  $A_g$  as a function of  $G_s$ ,  $J_A$  and  $R_l$ , as shown in Eqn 9.

$$A_g = \frac{1}{8} \left( 4C_a G_s + 8\Gamma_* G_s + J_A - 4R_l \right) - \frac{1}{8} \sqrt{(-4C_a G_s + 8\Gamma_* G_s + J_A - 4R_l)^2 + 16G_s \Gamma_* (8C_a G_s + J_A + 8R_l)} \quad (9)$$

Leaf respiration ( $R_l$ ) was modelled as a linear function of photosynthetic capacity ( $A_{\max}$ ) using Eqn 10, where  $c_{Rl} = 0.07$  following Givnish (1988), who showed for a wide range of species that  $R_l$  is approximately 7% of  $A_{\max}$ .

$$R_l = c_{Rl} A_{\max} \quad (10)$$

$A_{\max}$  was modelled by substituting the total electron transport capacity of the canopy ( $J_{\max \text{ tot}}$ , given in Eqn 12) for  $J_A$  and  $C_a$  for  $C_i$  in Eqn 6. The result is shown in Eqn 11.

$$A_{\max} = \frac{J_{\max \text{ tot}}(C_a - \Gamma_*)}{4C_a + 8\Gamma_*} R_l \quad (11)$$

$$J_{\max \text{ tot}} = L_A M_A \sum_{i=1}^{N_l} J_{\max, i} = 0.1 M_A \sum_{i=1}^{N_l} J_{\max, i} \quad (12)$$

The temperature dependencies of  $\Gamma_*$  and  $J_{\max}$  were modelled empirically (Medlyn *et al.* 2002), where we assumed that leaf temperature is the same as air temperature,

irrespective of the position in the canopy. The temperature dependence of  $\Gamma_*$  was modelled using eqn 12 in Medlyn *et al.* (2002), and the temperature response of  $J_{\max}$  using eqn 18 in Medlyn *et al.* (2002) with their parameter values for *Eucalyptus pauciflora* after converting everything to SI units. The 'optimal temperature' of the  $J_{\max}$  response function was set at the mean monthly daytime temperature for the study site.

Transpiration ( $E_t$ ) was modelled as a diffusive process, similar to the CO<sub>2</sub> uptake through stomata. The different diffusivities of CO<sub>2</sub> and H<sub>2</sub>O vapour were taken into account by multiplying the stomatal conductivity for CO<sub>2</sub> ( $G_s$ ) by a constant factor  $a$ , which was set to 1.6, following Cowan & Farquhar (1977). This is shown in Eqn 13, where  $W_i$  and  $W_a$  are the mole fractions of water vapour inside and outside the leaf, respectively. Assuming that the air inside the leaf is at 100% relative humidity, we approximated the term  $(W_i - W_a)$  by dividing the measured atmospheric VPD by the air pressure, and called it  $D_v$ :

$$E_t = aG_s(W_i - W_a) \approx aG_s D_v \quad (13)$$

## Models of stomatal conductivity

The general gas exchange model described above was used to compute canopy-scale fluxes of CO<sub>2</sub> and water vapour using three different approaches to modelling canopy-scale stomatal conductivity, as explained below.

### Cowan–Farquhar hypothesis

The relationship between  $E_t$  and  $A_g$  was obtained by solving Eqn 9 for  $G_s$  and inserting into Eqn 13 using Mathematica (version 5.2) (Wolfram Research, Inc., Champaign, IL, USA):

$$E_t = \frac{aA_g D_v (4A_g - J_A + 4R_l)}{C_a(4A_g - J_A + 4R_l) + (8A_g + J_A + 8R_l)\Gamma_*} \quad (14)$$

The characteristics of this function are shown in Fig. 1. Both  $A_g$  and  $E_t$  depend on stomatal conductivity, but while  $A_g$  has an upper limit determined by  $J_A$ ,  $E_t$  increases indefinitely with increasing stomatal conductivity. The slope of the curve ( $\lambda$ ) at any value of  $A_g$  is thus determined by  $D_v$  and  $J_A$ , the latter of which is determined by irradiance and canopy properties.

The slope of the relationship between  $E_t$  and  $A_g$  ( $\lambda$ ) can be expressed either as a function of  $A_g$  or a function of  $E_t$  by solving

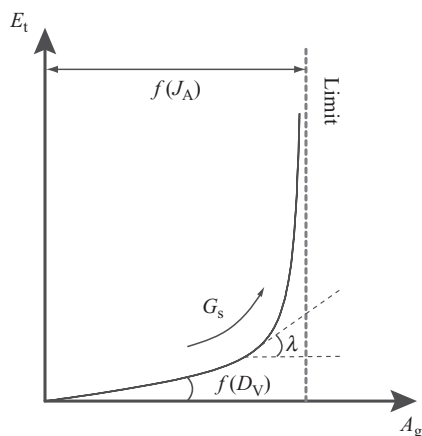
$$\lambda = \frac{\partial E_t}{\partial A_g} \quad (15)$$

or

$$\frac{1}{\lambda} = \frac{\partial A_g}{\partial E_t} \quad (16)$$

respectively.





**Figure 1.** Relationship between  $E_t$  and  $A_g$  for a fixed electron transport rate ( $J_A$ ) and atmospheric vapour deficit ( $D_v$ ), but variable stomatal conductivity ( $G_s$ ). The upper limit for  $A_g$  is determined by  $J_A$ , while the initial slope of the relationship is determined by  $D_v$ .

After solving Eqn 16 for  $E_t$  using the derivative of Eqn 14 with respect to  $A_g$ , we obtained  $E_t$  as a function of  $\lambda$ :

$$E_t = \frac{aD_v(Y - 4(J_A + 2R_l)\Gamma_*)}{4(C_a + 2\Gamma_*)^2} + \frac{\sqrt{3XZ}}{4(C_a + 2\Gamma_*)^2 X} \quad (17)$$

where

$$X = (\lambda C_a - aD_v + 2\lambda\Gamma_*) \quad (17a)$$

$$Y = C_a(J_A - 4R_l) \quad (17b)$$

$$Z = aD_v J_A \Gamma_* (\lambda C_a - 2aD_v + 2\lambda\Gamma_*)^2 (Y - (J_A + 8R_l)\Gamma_*) \quad (17c)$$

In Eqn 17, all parameters are either general model parameters ( $a$ ,  $\Gamma_*$ ), site-specific climatic variables ( $D_v$ ,  $C_a$ ) or variables computed using the canopy properties given in Table 1 ( $J_A$ ,  $R_l$ ), except for the value of  $\lambda$ , which was determined based on the observed monthly total  $E_t$ . The value of  $\lambda$  was assumed to be constant each month. To estimate the appropriate value for each month, we calculated the total monthly  $E_t$  using different assumed values of  $\lambda$ , and selected the  $\lambda$  that reproduced the total monthly  $E_t$  estimated from site measurements. The resulting instantaneous rates of modelled  $E_t$  and  $A_g$  were then plotted against measured values in each month.

### Constant conductivity

As an alternative to the Cowan–Farquhar model, the value of  $G_s$  was assumed to be constant during a month, and was adjusted to match the monthly modelled  $E_t$  with the monthly value estimated from site measurements. The resulting instantaneous rates of modelled  $E_t$  and  $A_g$  were then plotted against measured values in each month.

### Calibrated Ball–Berry–Leuning model

To test the potential of the gas exchange and photosynthesis model to reproduce the observed results, given the simplifications of the model and the uncertainty in the observations, we also applied a fitted model of stomatal conductivity with three degrees of freedom to the data. For this purpose, the Ball–Berry–Leuning (Leuning 1995) model of stomatal conductivity was chosen and reformulated in our notation as:

$$G_s = \frac{a_1 A_g}{\left(\frac{D_v}{D_0} + 1\right)(C_a - \Gamma_*)} + G_0 \quad (18)$$

where  $a_1$  (dimensionless),  $D_0$  (mol H<sub>2</sub>O mol<sup>-1</sup> air) and  $G_0$  (mol m<sup>-2</sup> s<sup>-1</sup>) are fitted constants, while all other symbols are the same as described earlier.

As  $A_g$  itself depends on  $G_s$ , we inserted Eqn 9 into Eqn 18 and solved for  $G_s$  analytically using the software Mathematica. This gave  $G_s$  as a function of atmospheric variables, photosynthetic properties and the three unknown constants  $a_1$ ,  $D_0$  and  $G_0$ .

The constants were fitted to minimize the sum of squares between half-hourly modelled and observed  $E_t$  for each month, after removing obvious outliers in the observations. The fit was performed using the ‘FindMinimum’ function in Mathematica, with 6, 0.0167 mol H<sub>2</sub>O mol<sup>-1</sup> air and 0.01 mol m<sup>-2</sup> s<sup>-1</sup> as starting values for  $a_1$ ,  $D_0$  and  $G_0$ , respectively.

### Study site

For the test of the different models, seasonally dynamic tall-grass savanna vegetation of the wet–dry tropics of north Australia was chosen. The study site was the Howard Springs eddy covariance site, which is located in the Northern Territory (Australia), 35 km south-east of Darwin, near Howard Springs in the Howard River catchment (12°29′39.30″ S, 131°09′8.58″ E). The climate is subhumid, with approximately 1750 mm mean annual rainfall and 2300 mm mean annual class A pan evaporation. Around 95% of the annual precipitation falls during the wet season (December to March), when atmospheric water demand is low (daytime relative humidity >60%), while the dry season (May to September) is characterized by virtually no rainfall and high atmospheric water demand (daytime relative humidity 10–40%). Air temperatures ranged between roughly 25 and 35 °C in the wet season and between 15 and 30 °C in the dry season. The vegetation has been classified as Eucalypt open forest (Specht 1981), and is characterized by a C<sub>3</sub> open-forest canopy (tree cover of less than 50%) that consists of evergreen and deciduous tree species above a dense, short-lived C<sub>4</sub> grass layer, where the latter completes its life cycle during the 5 month wet season and then senesces (Beringer *et al.* 2007). In terms of canopy gas exchange, the vegetation changes intra-annually from a tree–grass codominated one in the wet season to a tree-dominated one in the dry season.

A more detailed description of the study site is given in Schymanski *et al.* (2007).

### Measurements

The measurement techniques used at the site are described elsewhere in detail (Beringer *et al.* 2003, 2007; Hutley *et al.* 2005) and will only be summarized here. Gas exchange from this savanna ecosystem was measured using the eddy covariance method (Baldocchi, Hicks & Meyers 1988). Flux instrumentation was mounted at the top of a 23 m tall tower over the 15 m tall canopy, in flat terrain (slopes  $<1^\circ$ ) with a near-homogeneous fetch of more than 1 km in all directions. The eddy covariance technique was used to calculate vertical fluxes of latent heat and  $\text{CO}_2$  from three-dimensional wind velocities and turbulent fluctuations of  $\text{CO}_2$  and water vapour in the air (Hutley *et al.* 2005). Incoming short-wave radiation, air pressure and air temperature were also measured at the top of the tower. Soil moisture was measured using time domain reflectometry (TDR) probes (CS615 probes; Campbell Scientific, Logan, UT, USA) at 10 cm depth, and soil temperature was obtained from an averaging soil thermocouple with sensors at 2 and 6 cm depth. All flux variables were sampled at 10 Hz and averaged over 30 min. Flux measurements have been made at this site since 2001, and are ongoing. To create a continuous data set, small gaps (less than 2 h) were filled using linear interpolation, while larger gaps were filled using a neural network model, fitted to the whole data set (Beringer *et al.* 2007). Periods with gap-filled data were flagged for later recognition. As the gap filling procedure is a major contributor of uncertainty in the results (Oren *et al.* 2006) and nocturnal-derived estimates of ecosystem respiration can be systematically underestimated by the eddy covariance method (Hutley *et al.* 2005), we chose a period in the data set with only a low proportion of gap-filled values (July 2004 to June 2005) and we only summed over daytime fluxes for the computation of daily data. Daytime was hereby defined as the time intervals with a mean photosynthetically active photon flux ( $I_a$ ) greater than  $100 \mu\text{mol s}^{-1} \text{m}^{-2}$ .

Measured short-wave irradiance in the wavelengths  $0.2\text{--}4.0 \mu\text{m}$  ( $K_{\text{short}}$ , in  $\text{W m}^{-2}$ ) was converted to photosynthetically active irradiance ( $I_{\text{aw}}$ , in  $\text{W m}^{-2}$ ) in the wavelengths  $0.4\text{--}0.7 \mu\text{m}$  using a constant conversion coefficient of 0.45 ( $I_{\text{aw}} = 0.45 K_{\text{short}}$ ), which was derived from an online database (Pinker & Laszlo 1997). To convert from energy flux density ( $\text{W m}^{-2}$ ) to molar units ( $\text{mol quanta s}^{-1} \text{m}^{-2}$ ), we used a conversion coefficient of  $4.57 \times 10^{-6} \text{ mol J}^{-1}$  (Thimijan & Heins 1983). The ratio between diffuse and direct sunlight was estimated from the relationship between global irradiance and top-of-the-atmosphere irradiance (Spitters, Toussaint & Goudriaan 1986; Roderick 1999; Schymanski 2007).

To obtain an observational estimate of the transpiration part of the measured latent heat flux, soil evaporation had to be subtracted from the ecosystem total flux, which is especially significant in the wet season when soil moisture is high. Soil evaporation was typically between  $0.1$  and  $0.5 \text{ mm d}^{-1}$  in

the dry season and up to  $0.65 \text{ mm d}^{-1}$  in the wet season, i.e. around 10% of total evapo-transpiration (Hutley, unpublished data). The diurnal and day-to-day variation of soil evaporation ( $E_s$ , in  $\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$ ) was estimated using a flux-gradient approach as described in Eqn 19, where  $W_s$  denotes the mole fraction of water in the laminar layer immediately above the soil, and  $W_a$  the mole fraction of water in the atmosphere, while  $G_{\text{soil}}$  is the conductivity of the soil to water vapour fluxes.  $W_s$  was calculated as the vapour pressure in the laminar layer immediately above the soil ( $p_{\text{vs}}$ ) divided by air pressure.  $p_{\text{vs}}$  was modelled as a function of the atmospheric vapour pressure, the saturation vapour pressure at the measured soil temperature, measured volumetric soil moisture and volumetric soil moisture at field capacity on the site (Lee & Pielke 1992).

$$E_s = G_{\text{soil}}(W_s - W_a) \quad (19)$$

The value for soil moisture at field capacity for the site was set to 0.156, equivalent to the soil moisture of a sandy loam at a matrix pressure head of  $-0.01 \text{ MPa}$  (Kelley 2002).

The parameter  $G_{\text{soil}}$  in Eqn 19 was set to the value  $0.03 \text{ mol m}^{-2} \text{s}^{-1}$ , which resulted in a time series of soil evaporation equivalent to around  $0.1\text{--}0.2 \text{ mm d}^{-1}$  in the dry, and  $0.4\text{--}1.0 \text{ mm d}^{-1}$  in the wet season, given the measured soil water content and meteorological conditions (Schymanski 2007). Transpiration ( $E_t$ ) was then calculated as the difference between the measured latent heat flux and the estimated soil evaporation.

The measured net  $\text{CO}_2$  uptake by the soil-vegetation system ( $F_{\text{nc}}$ ) ( $\text{mol m}^{-2} \text{s}^{-1}$ ) was partitioned conceptually into net  $\text{CO}_2$  uptake by foliage ( $A_g$ ),  $\text{CO}_2$  release by soil respiration ( $R_s$ ) and  $\text{CO}_2$  release by sapwood respiration ( $R_w$ ). Soil respiration rates were estimated using a model formulated for an African savanna (Hanan *et al.* 1998), after setting the 'critical temperature' to the maximum soil temperature recorded in our data set ( $44.95^\circ\text{C}$ ), and the intrinsic soil respiration rate at  $20^\circ\text{C}$  to  $1.86 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The estimated soil respiration rates corresponded well with point measurements at our study site (Chen, Eamus & Hutley 2002; Schymanski 2007). Total above-ground woody tissue respiration ( $R_w$ ) has been estimated based on measurements at the study site to be around  $297 \text{ g C m}^{-2} \text{year}^{-1}$  (Cernusak *et al.* 2006), which is equivalent to  $0.78 \mu\text{mol m}^{-2} \text{s}^{-1}$  averaged over the whole year. To estimate the diurnal variation in  $R_w$ , we followed eqn 2 in Cernusak *et al.* (2006), and their formulation of stem temperature ( $T_w$ ,  $^\circ\text{C}$ ) as a linear function of air temperature ( $T_w = 1.11 T_a - 1.36$ ), while the stem  $\text{CO}_2$  flux at the reference temperature was fitted to match the observed total above-ground woody tissue respiration of  $297 \text{ g C m}^{-2} \text{year}^{-1}$ .

### Model parameters

Based on a previous study (Schymanski *et al.*, 2007), we chose four months with relatively stable canopy properties, two in the dry season (July and October 2004) and two in

the wet season (January and February 2005). July and October were the only dry-season months in the previous study when the fluxes were not clearly affected by a moderately hot fire that occurred in August 2004 (see Beringer *et al.* 2007). The canopy properties ( $M_A$ ,  $N_i$  and  $J_{\max 25,i}$  in each layer) were taken from the previous study, where, given estimated  $M_A$ , the other properties were calculated using another optimality hypothesis, the maximization of the net carbon profit of the canopy, and where they were shown to lead to realistic results in terms of canopy  $\text{CO}_2$  uptake. The values are given in Table 1.

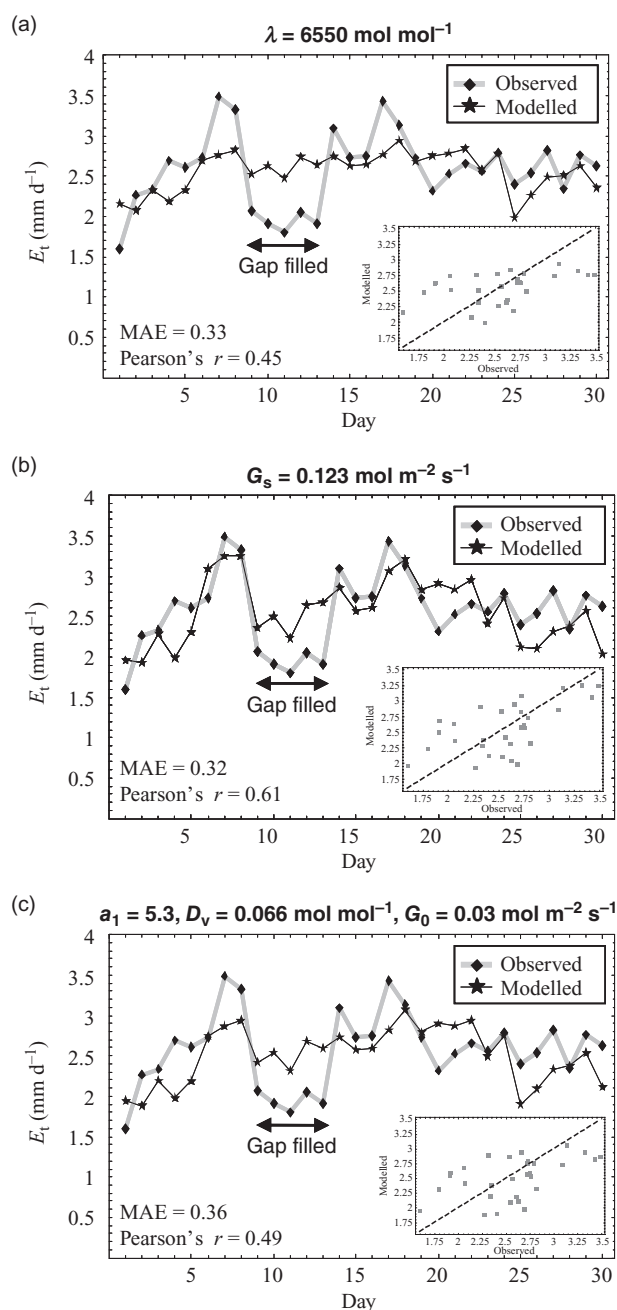
The present model could also be applied to transitional periods (e.g. dry-to-wet seasons), if the dynamics of the canopy properties are known. For the purpose of testing the optimality hypothesis, however, we attempted to avoid the uncertainty associated with modelling canopy dynamics.

## RESULTS

The following results only consider daytime fluxes, as outlined in Materials and methods. Thus, 'monthly total' and 'daily total' really refer to 'monthly daytime total' and 'daily daytime total', respectively.

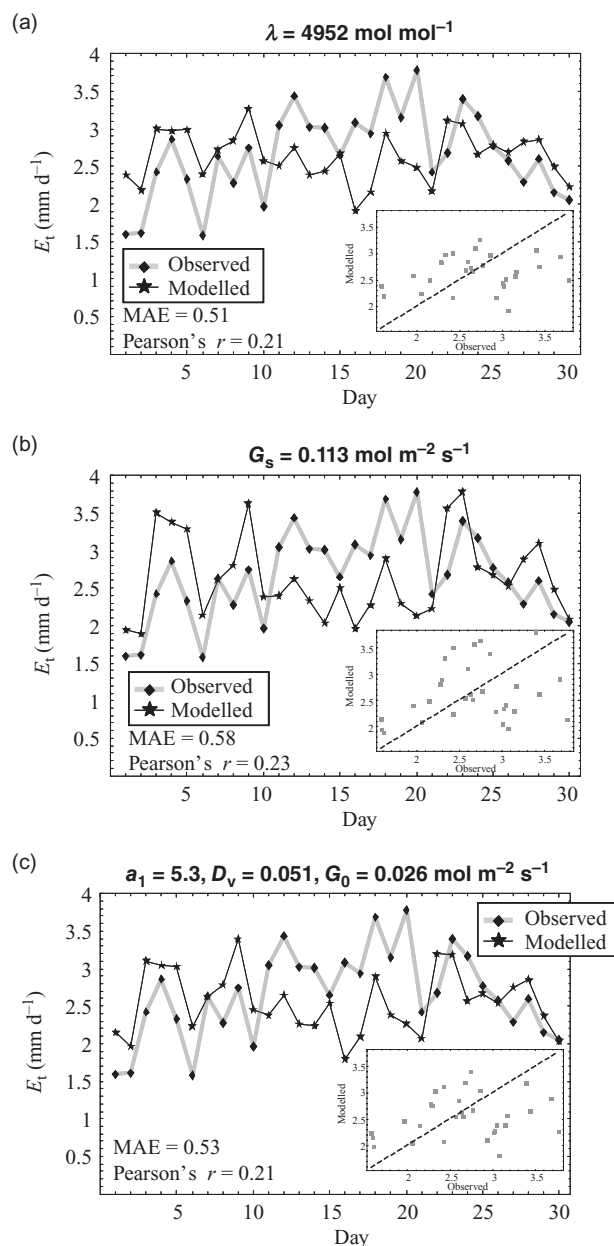
To match the modelled total  $E_t$  for July 2004 with the observed total,  $\lambda$  was set to  $\lambda = 6550 \text{ mol mol}^{-1}$  and held constant throughout the month. The resulting daily dynamics, however, did not match the observed data very well (Fig. 2a). In fact, the daily dynamics of  $E_t$  were reproduced better by assuming a constant  $G_s$  of  $0.123 \text{ mol m}^{-2} \text{ s}^{-1}$  (Fig. 2b), while the calibrated model of stomatal conductivity (Fig. 2c) led to a very similar daily dynamics as the one based on a constant  $\lambda$ . Of note was the divergence between modelled and observed data for a gap-filled period (8–13 July) where a neural network model was used to replace missing observations and daily  $E_t$  was decreased relative to observational data before and after this period. For gap-filled periods, we are thus comparing the results of four different models: the neural network, constant  $\lambda$ , constant  $G_s$  and the Ball–Berry–Leuning model. Nevertheless, the data from the remaining days allow a meaningful comparison between observations and models. Recall that July and October were the only dry-season months in the data set analysed by Schymanski *et al.* (2007), where the fluxes were not obviously affected by a moderately hot fire that occurred in August 2004 (see Beringer *et al.* 2007).

In October 2004, modelled monthly  $E_t$  matched the observed total if  $\lambda$  was held constant at  $\lambda = 4952 \text{ mol mol}^{-1}$ , or  $G_s$  was held constant at  $G_s = 0.113 \text{ mol s}^{-1} \text{ m}^{-2}$ . For this month, prescribing a constant value for  $\lambda$  led to a slightly better match of modelled daily  $E_t$  with observed daily  $E_t$ , than if the value of  $G_s$  was held constant (mean absolute error of  $0.51 \text{ mm d}^{-1}$ , compared with  $0.58 \text{ mm d}^{-1}$  achieved by the constant  $G_s$  model, which showed a large overestimation of the fluxes at days 3–5 and 9 in Fig. 3). Again, the calibrated Ball–Berry–Leuning model did not reproduce the observed daily  $E_t$  better than the optimality-based Cowan–Farquhar model. All models under-predicted daily  $E_t$



**Figure 2.** Comparison of observed (thick, grey lines) and modelled (thin, black lines) daily transpiration rates ( $E_t$ ) during daylight hours in July 2004. Daylight hours are defined as time intervals with mean  $I_a > 100 \mu\text{mol s}^{-1} \text{ m}^{-2}$ . (a) Model based on constant  $\lambda$ ; (b) model based on constant  $G_s$ ; and (c) calibrated model. The arrows highlight a period between 9 and 13 July when data were not available because of equipment failure, and the 'observed' values were estimated using a neural network model. The insets show 1:1 plots of the observed and modelled daily values. MAE, mean absolute error in  $\text{mm d}^{-1}$ .

between the 10th and 21st of October and over-predicted daily  $E_t$  before the 10th of October (Fig. 3). To test whether two different values of  $\lambda$  before and after the 10th of October would lead to a better reproduction of the observed fluxes,  $\lambda$



**Figure 3.** Comparison of observed (thick, grey lines) and modelled (thin, black lines) daily transpiration rates ( $E_t$ ) during daylight hours in October 2004. Daylight hours are defined as time intervals with mean  $I_a > 100 \mu\text{mol s}^{-1} \text{m}^{-2}$ . (a) Model based on constant  $\lambda$ ; (b) model based on constant  $G_s$ ; and (c) calibrated model. The insets show 1:1 plots of the observed and modelled daily values. MAE, mean absolute error in  $\text{mm d}^{-1}$ .

was arbitrarily set to a value of  $3000 \text{ mol mol}^{-1}$  before this date, and to  $7000 \text{ mol mol}^{-1}$  after this date. The results are shown in Fig. 4, and reveal that the abrupt change of  $\lambda$  coincides with the first rainfall after a long dry period and led to a significantly improved reproduction of the observed daily  $E_t$ . Only after the 20th of October did the modelled and observed daily values start to deviate again.

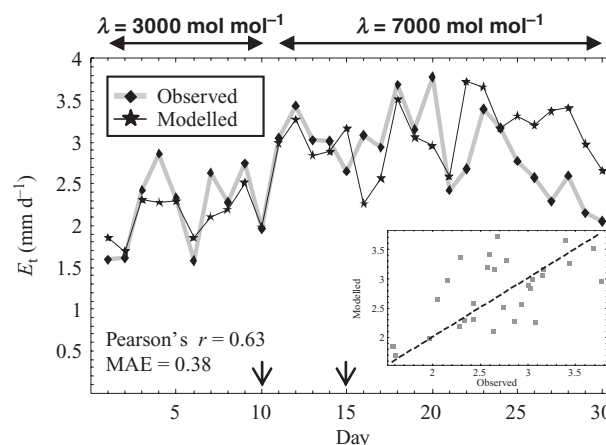
The modelled monthly total  $E_t$  for January 2005 matched the observed total if  $\lambda$  was held constant at  $\lambda =$

$1681 \text{ mol mol}^{-1}$ . At the same time, the modelled daily  $E_t$  followed the observed pattern very closely (Fig. 5a). When stomatal conductivity was held constant, a value of  $G_s = 0.242 \text{ mol m}^{-2} \text{ s}^{-1}$  led to the same monthly total  $E_t$  as the observed. The correspondence between the modelled and observed daily  $E_t$  was comparable with the Cowan–Farquhar model, but constant  $G_s$  led to a large spike in  $E_t$  on 7 January, which was not in accordance with observations (Fig. 5b).

The results for February follow the same pattern, with a slightly worse reproduction of the daily fluxes by the constant  $G_s$  model compared with the other two models (Fig. 6). Consistently with the other months, the calibrated Ball–Berry–Leuning model did not lead to a better reproduction of the observations, compared with the Cowan–Farquhar model.

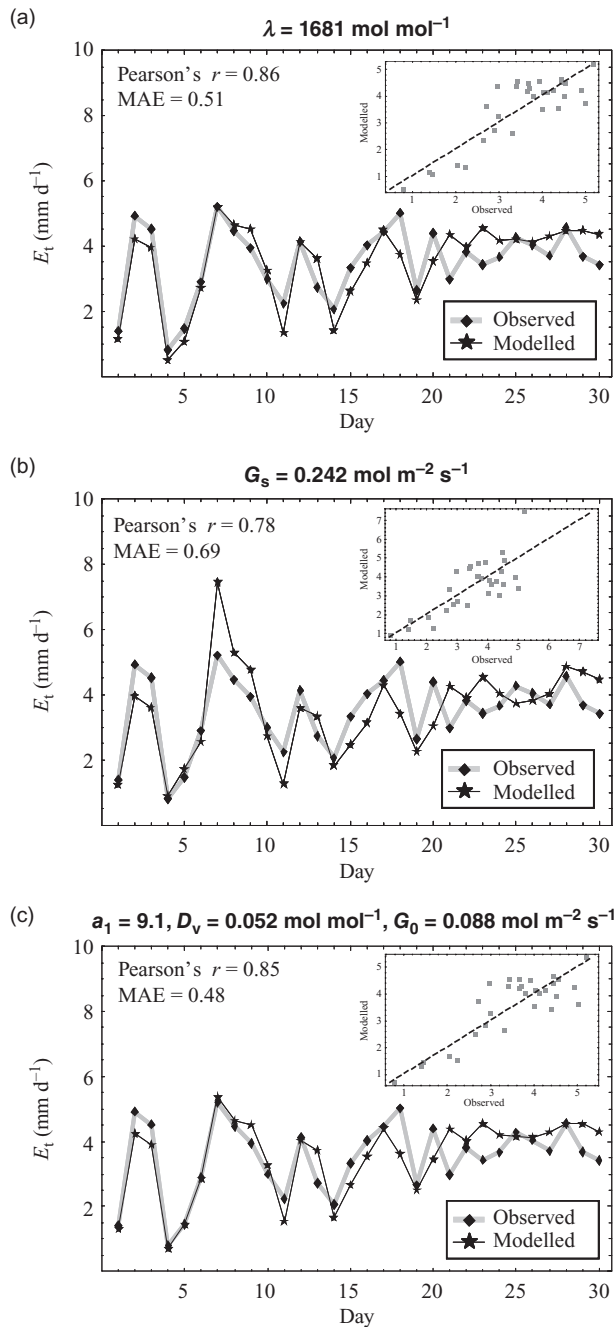
In all four months, ensemble means of observed diurnal  $E_t$  rates were better reproduced by both the optimality-based Cowan–Farquhar model and the calibrated Ball–Berry–Leuning model than the model based on constant  $G_s$ , the latter of which resulted in a skew towards the afternoon (Fig. 7). The diurnal variations predicted by the calibrated model were not substantially different from the ones predicted by the optimality-based model, and both fitted the observed diurnal variations remarkably well in all four months (Fig. 7).

The values for  $\lambda$  obtained for each month were generally higher during the dry season than during the wet season. In contrast, the values for  $G_s$  were lower during the dry-season months compared with the wet-season months. Within the same season, a higher  $G_s$  corresponded with a higher value of  $\lambda$  in both cases. Of the Ball–Berry–Leuning model



**Figure 4.** Evidence of an abrupt change in  $\lambda$  after a rainfall event in October 2004. The match between observed (thick, grey line) and modelled (thin, black line) daily daytime  $E_t$  was significantly improved if  $\lambda$  was set to different values before and after the first occurrence of a rainfall event (cf. Fig. 3a). The two days with more than 20 mm of precipitation are indicated by vertical arrows, and the periods over which  $\lambda$  was held constant are indicated by horizontal arrows. The inset shows a 1:1 plot of the observed and modelled daily values. MAE, mean absolute error in  $\text{mm d}^{-1}$ .



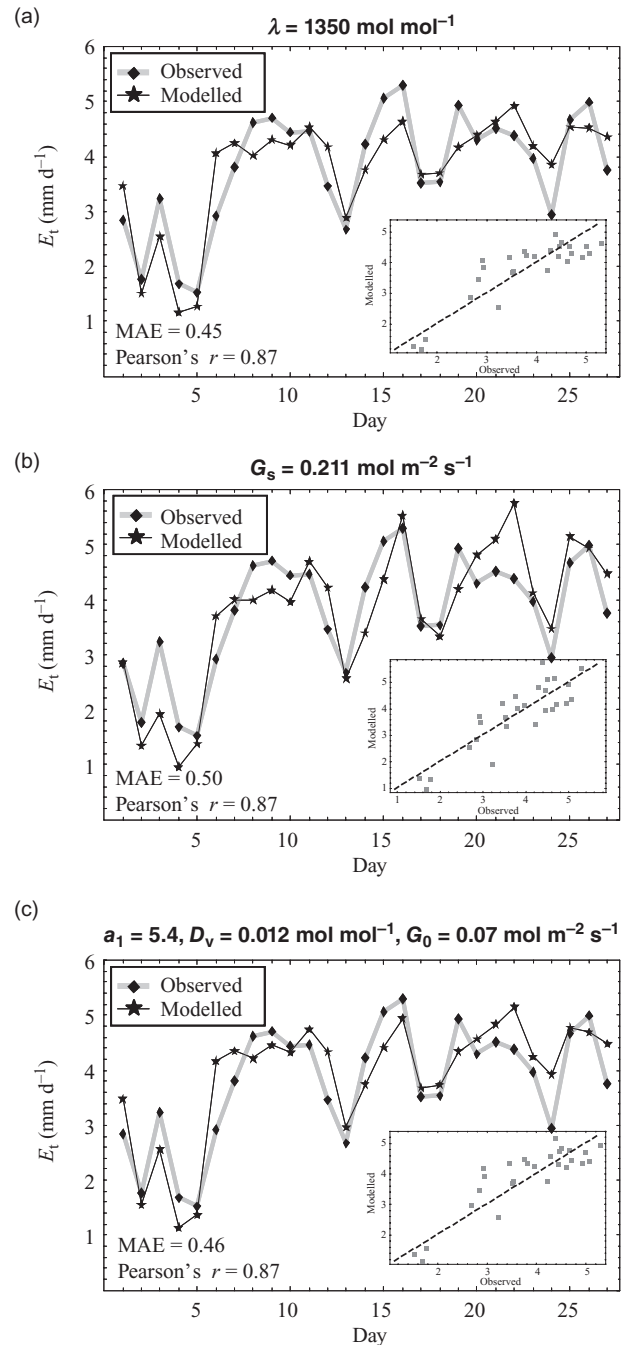


**Figure 5.** Comparison of observed (thick, grey lines) and modelled (thin, black lines) daily transpiration rates ( $E_t$ ) during daylight hours in January 2005. Daylight hours are defined as time intervals with mean  $I_a > 100 \mu\text{mol s}^{-1} \text{m}^{-2}$ . (a) Model based on constant  $\lambda$ ; (b) model based on constant  $G_s$ ; and (c) calibrated model. The insets show 1:1 plots of the observed and modelled daily values. MAE, mean absolute error in  $\text{mm d}^{-1}$ .

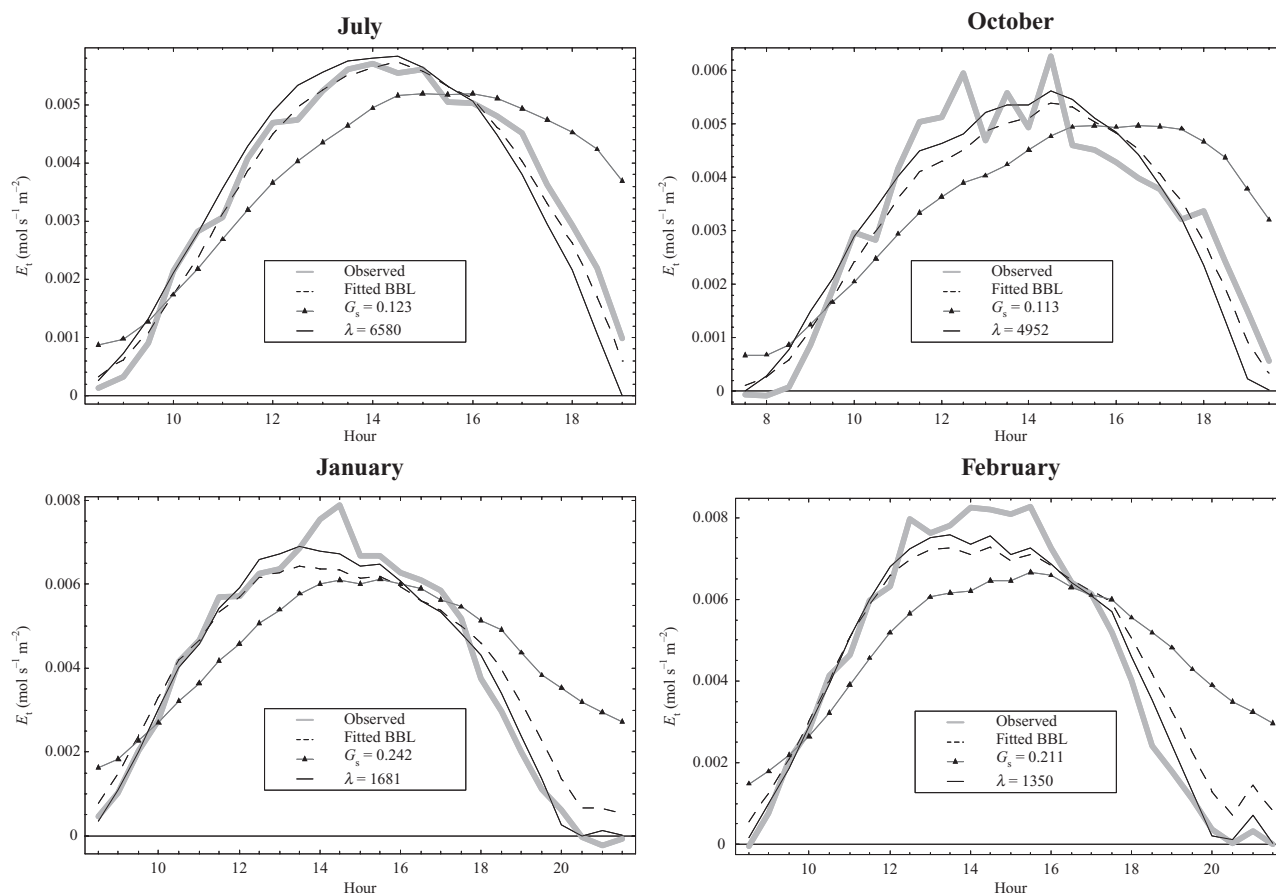
parameters, only  $G_0$  showed a seasonality in the four months compared, with lower values in the dry and higher values in the two wet-season months (Table 2).

The simulated daily and diurnal rates of  $\text{CO}_2$  uptake were affected much less by the choice of a particular stomatal conductivity model than were the simulated rates of  $E_t$ . In

fact, no clear differences between the curves produced by either of the models were visible, and hence, the results were not shown here, but can be viewed elsewhere (Schymanski 2007).



**Figure 6.** Comparison of observed (thick, grey lines) and modelled (thin, black lines) daily transpiration rates ( $E_t$ ) during daylight hours in February 2005. Daylight hours are defined as time intervals with mean  $I_a > 100 \mu\text{mol s}^{-1} \text{m}^{-2}$ . (a) Model based on constant  $\lambda$ ; (b) model based on constant  $G_s$ ; and (c) calibrated model. The insets show 1:1 plots of the observed and modelled daily values. MAE, mean absolute error in  $\text{mm d}^{-1}$ .



**Figure 7.** Ensemble means of diurnal transpiration rates ( $E_t$ ) during daylight hours. Grey lines, observed values; solid black lines without markers,  $E_t$  modelled assuming constant  $\lambda$  (values given in  $\text{mol mol}^{-1}$ ); solid black lines with markers,  $E_t$  modelled assuming constant  $G_s$  (values given in  $\text{mol m}^{-2} \text{s}^{-1}$ ); dashed lines, calibrated Ball–Berry–Leuning model. Means were computed for all days of the respective month. Error bars are left out for clarity.

## DISCUSSION

The present study supports Cowan and Farquhar's theory of optimal stomatal conductivity (Cowan & Farquhar 1977), which suggests that diurnal variations in stomatal conductivity can be predicted by prescribing a single constant ( $\lambda$ ), if the functional dependency of photosynthesis and transpiration

on stomatal and canopy conductivity is known. In contrast, experiments under controlled conditions led to questioning of the theory (e.g. Franks *et al.* 1997; Thomas *et al.* 1999b). However, this is not surprising, considering that:

The optimisation hypothesis, relating as it does to the ideal adaptation of stomatal behaviour to a putative

**Table 2.** Parameter values obtained by calibration of the different models for each month

Month	WUE ( $\text{mol mol}^{-1}$ )	C–F $\lambda$ ( $\text{mol mol}^{-1}$ )	Constant $G_s$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )	B–B–L		
				$a_1$	$D_v$ ( $\text{mol mol}^{-1}$ )	$G_0$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )
July 2004	0.0024	6550	0.123	5.3	0.066	0.030
October 2004	0.0023	4952	0.113	5.3	0.051	0.026
January 2005	0.0034	1681	0.242	9.1	0.052	0.088
February 2005	0.0031	1350	0.211	5.4	0.012	0.070

All variables are computed per unit ground area.

C–F, model based on the Cowan–Farquhar hypothesis; constant  $G_s$ , constant conductivity model; B–B–L, Ball–Berry–Leuning model; WUE, water-use efficiency for each month, as derived from the eddy flux measurements (total monthly daytime  $A_g$  in  $\text{mol CO}_2$ , divided by total monthly daytime  $E_t$  in  $\text{mol H}_2\text{O}$ ).

selection pressure, can only be tested in the circumstances in which we think adaptation has occurred.

(Cowan 2002)

Some authors have found that the observed dynamics of transpiration were similar to the dynamics that would be achieved using constant  $\lambda$ , while  $\lambda$  was not constant when derived directly from the measurements (Williams 1983; Thomas, Eamus & Bell 1999a; Thomas *et al.* 1999b). Some of these observations have been related to conditions under which  $\lambda$  is very sensitive to environmental conditions, while  $E_t$  and  $A_g$  are not, for example under low light, low VPD or low wind conditions (Williams 1983). Thomas *et al.* (1999a,b), on the other hand, found that some Australian monsoon rain forest tree species exhibit small but systematic deviations from optimality of leaf-scale gas exchange, as  $\lambda$  increased when VPD was artificially increased. However, the effect of diurnal variations of VPD on stomatal conductivity under natural conditions is likely to be small compared with the effect of changing irradiance in the course of a day. This might explain why stomatal conductivity is often seen to be close to optimal during a day despite a non-constant  $\lambda$  with respect to varying VPD. Cowan (1982) already noted that most investigations concentrate on the influence of changing ambient humidity or temperature on  $\lambda$ , while it would be interesting to investigate the effect of varying irradiance.

Cowan (1982, 2002) also pointed out that the benefit of an optimal variation of stomatal conductivity is often very small compared with constant stomatal conductivity. This implies that the selective pressure for a stomatal apparatus that is able to respond rapidly to changes in environmental conditions is low, and the benefits of such an apparatus may not outweigh the energetic costs. This might explain why stomata have a relatively slow response to environmental conditions, in the order of minutes rather than seconds, and why  $\lambda$  is often not kept strictly constant during a day.

Nevertheless, the results of this study indicate that the Cowan–Farquhar hypothesis is useful for predicting the diurnal and daily dynamics of canopy-scale gas exchange under wide ranging, but natural environmental conditions. Transpiration rates modelled using a constant value of  $\lambda$  reproduced observed transpiration rates better than a model based on constant conductivity ( $G_s$ ) and performed as well as the fitted Ball–Berry–Leuning model. Previous results also show that the assumption about the temporal dynamics of  $G_s$  had a much smaller effect on the modelled rates of  $\text{CO}_2$  uptake than on the modelled transpiration rates (Schymanski 2007). This suggests that stomatal dynamics of the savanna vegetation of this site operated at a level where photosynthesis was strongly co-limited by factors other than  $G_s$ . Support for this hypothesis can be obtained from the modelled values of  $\lambda$ , which can be seen as a measure for how conservatively vegetation utilizes water. As illustrated in Fig. 1, a high value of  $\lambda$  means that a large decrease in canopy transpiration ( $E_t$ ) would only lead to a small decrease in canopy  $\text{CO}_2$  uptake ( $A_g$ ), while a low value of  $\lambda$  implies that a small increase in  $E_t$  would result in

a large increase in  $A_g$ . Thus, we would expect that so-called ‘water-stressed’ vegetation would operate at a lower value of  $\lambda$  than vegetation with ample water supply. In this context, it is interesting that the values of  $\lambda$  were more than twice as high in the dry season as in the wet season (July and October versus January and February in Table 2). This suggests that the plants used water less conservatively in the dry season than in the wet. In fact, if vegetation adopted a lower value of  $\lambda$  in October 2005, the monthly total  $E_t$  could be decreased by more than 20%, while the monthly total  $A_g$  would only decrease by 6% (data not shown). Describing the trees as ‘water stressed’ during the dry season does not seem reasonable from this perspective, and is not supported by pressure bomb measurements on tree leaves and transpiration measurements made at this site (see O’Grady, Eamus & Hutley 1999; Hutley *et al.* 2001). It appears that the adaptation of vegetation to the more restricted water supply during the dry season is primarily not achieved by means of stomatal closure, but by a reduction of vegetation cover ( $M_A$ ), while the remaining vegetation continues transpiring at a high rate (see Table 1 for the values of  $M_A$ ). This is supported by observations of seasonal patterns of tree canopy water use at this site by O’Grady *et al.* (1999), who found higher sap-flow rates in the dry season relative to the wet season, which were attributed to higher dry season VPD. In the present study, the reduction of  $M_A$  and associated change in leaf area index was greater than the reduction in stomatal conductivity per ground area, so that stomatal conductivity per leaf area was on average higher during the dry than during the wet season ( $G_s$  doubles from the dry to the wet season in Table 2, but  $L_{AI}$  triples in Table 1). This suggests that the seasonal variations of stand-averaged stomatal conductivity can show opposite effects, depending on whether stomatal conductivity is calculated per unit ground area or per unit leaf area, as transpiration is optimized by canopy adjustment as well as  $G_s$  (Hutley *et al.* 2001).

The site received 26.2 mm of rainfall in an afternoon storm lasting 1 h on 10 October 2004, followed by smaller rain events between 14 and 17 October. Observed transpiration rates were reproduced best by the Cowan–Farquhar model using  $\lambda = 3000 \text{ mol mol}^{-1}$  before the rainfalls, and  $\lambda = 7000 \text{ mol mol}^{-1}$  after the rainfalls (Fig. 4). This is consistent with the theory that the value of  $\lambda$  should depend on the amount of available soil water (Cowan 1982, 1986), and with the results of other authors that identified such a sensitivity of  $\lambda$  to soil moisture (Hall & Schulze 1980; Thomas *et al.* 1999b). It also emphasizes that knowledge about the quantitative dependence of  $\lambda$  on soil moisture in addition to the knowledge about canopy dynamics is needed to apply the Cowan–Farquhar theory at longer time-scales. Part of the observed increase in  $\lambda$  after rainfalls could also be caused by the evaporation of intercepted water, which has not been considered in the present model, and hence, could have led to an overestimation of transpiration from the measured fluxes. However, this effect is unlikely to last for more than a day after the rainfall, and hence, cannot explain the persistently increased  $\lambda$  shown in Fig. 4. Another

possible source of error with regards to the increased transpiration rates after the rainfalls is the calculation of soil evaporation. It could be that Eqn 19 underestimated the increase in soil evaporation after the rainfalls, which would lead to an overestimation of the transpiration rates. However, such an error is unlikely as the calculated soil evaporation rates reached values of up to 1 mm d<sup>-1</sup> after the rain falls, which is already higher than the typically observed soil evaporation rates of 0.1–0.65 mm d<sup>-1</sup> at the study site (Schymanski 2007).

As shown in a previous study, canopy dynamics can also be obtained using optimality assumptions (Schymanski *et al.* 2007) if water use is known. Thus, coupling the vegetation optimality model with the site water balance and implementation of the Cowan–Farquhar hypothesis could yield a model of self-optimizing vegetation, capable of including adaptation to the environment in hydrological models without the need for prescribing any site-specific vegetation parameters *a priori*.

### Advantages and limits of the optimality model

Leuning (1990) rejected the Cowan–Farquhar hypothesis for modelling stomatal conductivity based on the claim that there was ‘no *a priori* method of determining the appropriate value of  $\lambda$ , and hence, no way of predicting the diurnal course of stomatal conductance for a given set of environmental conditions’. This led him to refine the Ball–Berry model instead and formulate what is referred to as the Ball–Berry–Leuning model in this study. The results of the present study suggest that the Cowan–Farquhar hypothesis can in fact be very useful for modelling canopy-scale stomatal conductivity and that it can lead to similar results as the Ball–Berry–Leuning model. However, the application of the Cowan–Farquhar hypothesis has some advantages. Recall that the value of  $\lambda$  used here was determined by the observed total monthly  $E_t$ , while the diurnal and daily dynamics of  $E_t$  were predicted without further parameter fitting. Thus, the use of the Cowan–Farquhar hypothesis allowed predicting the observed diurnal and daily dynamics of transpiration given the monthly transpiration without parameter fitting. The Ball–Berry–Leuning model, in contrast, needed to be fitted to the time series of  $E_t$  itself, because it had too many degrees of freedom (three unknown parameters instead of one). The application of the Cowan–Farquhar hypothesis also gave us new insights into the adaptation of the local vegetation to the seasonality of the site. The comparison of the values of  $\lambda$  between seasons led to the conclusion that the vegetation on the site uses water less conservatively during the dry season than during the wet season. A high value of  $\lambda$  implies that  $E_t$  could be reduced more for a given reduction of  $A_g$  than if stomata operate at a lower value of  $\lambda$  (Fig. 1). Comparison of the values of  $\lambda$  obtained from the optimality model with the values of  $G_s$  from the model based on constant  $G_s$  reveals that within the same season, a higher  $\lambda$  coincided with higher  $G_s$ , while between seasons, a higher  $\lambda$  coincided with lower  $G_s$  (Table 2). Of the Ball–Berry–Leuning parameters,

only  $G_0$  showed a similar behaviour to  $\lambda$ , but this parameter cannot be interpreted in a similar way. This emphasizes that the information obtained from the value of  $\lambda$  can neither be obtained from the constant  $G_s$  nor the Ball–Berry–Leuning model. For example, looking at the constant  $G_s$  model results alone would lead us to think that vegetation suffers from water stress in the dry season and therefore transpires at a reduced  $G_s$  compared with the wet season. This would be difficult to reconcile with the observation that the canopy-scale water-use efficiency (WUE) is lower in the dry season compared with the wet season (Table 2), and that the average conductivity per leaf area is even increased during the dry season compared with the wet season. On the other hand, Eamus *et al.* (1999) measured seasonal patterns of leaf-scale gas exchange for savannah tree species at a similar site and observed higher instantaneous transpiration efficiency (instantaneous CO<sub>2</sub> assimilation rate divided by the instantaneous transpiration rate under saturating light conditions) during the dry season compared with the wet season. This illustrates that the averaged  $G_s$  and the Ball–Berry–Leuning model parameters depend on the scale of integration, and hence, cannot tell us much about the individual plants in the system when used in a big leaf model. The value of  $\lambda$ , in contrast, seems to reflect the water-use strategies of the plants in the system, with a lower value indicating more conservative water use. The C<sub>4</sub> grasses that dominate the fluxes during the wet season (Eamus, Hutley & O’Grady 2001) may generally function at a lower value of  $\lambda$  than the C<sub>3</sub> trees, which are largely responsible for the fluxes during the dry season. Within each of these two life-forms, the value of  $\lambda$  is likely to vary with the soil moisture. Thus, between seasons, we observe a decrease of  $\lambda$  with the change of dominating vegetation type as the soils wet up, while within a season,  $\lambda$  increases with increasing soil wetness.

The implicit assumption in our use of the Cowan–Farquhar hypothesis at a canopy scale is that all leaves of all plants operate at the same value of  $\lambda$ . On the other hand, it has been shown that the value of  $\lambda$  depends on the available soil water, but because different plants have different access to soil water (especially significant at this site, with trees and grasses utilizing differing soil horizons), it is unlikely that they would operate at the same value of  $\lambda$ . However, this heterogeneity argument would apply to all the three models presented here, and it can even apply at leaf scales, as patchy stomatal closure can lead to errors in the calculation of gas exchange parameters (van Kraalingen 1990).

The present model is based on the biochemistry of light-limited C<sub>3</sub> photosynthesis, and hence, may not represent the value of  $\lambda$  for C<sub>4</sub> species accurately. Despite this potential shortcoming, the model was able to reproduce the observed daily and diurnal dynamics of the fluxes as accurately in the C<sub>4</sub>-dominated as in the C<sub>3</sub>-dominated season, which suggests that the shapes of the  $E_t(A_g)$  curves might not be all that different for the different photosynthetic pathways.

The values of  $\lambda$  obtained in the present study are considerably higher than values reported from other studies. Williams (1983) reported values between 400 and 800 mol



$\text{mol}^{-1}$  in the middle of the day for an evergreen shrub at Jasper Ridge Biological Preserve; Lloyd *et al.* (1995) used a value of  $1950 \text{ mol mol}^{-1}$  for  $\lambda$  in a big leaf model of a Brazilian rain forest site, and Hall & Schulze (1980) observed values of  $\lambda$  in the range of roughly  $200\text{--}1000 \text{ mol mol}^{-1}$  for cowpeas after different treatments. Lloyd & Farquhar (1994) reviewed reported values of  $\lambda$ , which ranged from 250 in a tundra to  $1500 \text{ mol mol}^{-1}$  in a tropical seasonal forest. Note, however, that calculated values of  $\lambda$  can vary by more than double depending on the method of how it is derived from the observations (Thomas *et al.* 1999a). On the other hand, values of  $\lambda$  used in a canopy-scale model should reflect the values of  $\lambda$  at leaf scale, as  $\lambda = \partial E_t / \partial A_g$  and both  $E_t$  and  $A_g$  are divided by the same reference area. Hence, the use of the Cowan–Farquhar hypothesis leads to a model with only one unknown parameter ( $\lambda$ ), which has a direct physiological meaning and is, at least in theory, independent of the scale, as optimality requires that all leaves maintain the same value of  $\lambda$ .

Another assumption in the presented model was that limitations to gas exchange by a boundary layer resistance, and temperature differences between leaves and the ambient air are negligible. In the contrary case, evaporative cooling of the leaves could lead to a decrease of the vapour pressure gradient between the leaf and the atmosphere, while  $\text{CO}_2$  exchange would remain unaffected. This in turn could result in a partial reversal of the curvature of the  $E_t$  to  $A_g$  relationship in Fig. 1 because at low  $G_s$ ,  $A_g$  would increase faster than  $E_t$ . In such a case, maintaining constant  $\lambda$  would not constitute the optimal behaviour, as increasingly higher returns per unit of water used could be achieved by increasing  $G_s$ , and the optimal behaviour given limited water would be patchy stomatal closure (Buckley, Farquhar & Mott 1999). A similar reversal of the curvature was proposed by Cowan (1978) at the canopy scale if the canopy is decoupled from the atmosphere in such a way that increasing  $E_t$  would decrease the VPD in the canopy air, and hence, lead to a decrease in subsequent  $E_t$  at the same values of  $G_s$ . From this perspective, having a high boundary layer resistance would seem to constitute an advantage for the plants in terms of reducing water loss. However, the same boundary layer could limit photosynthesis if  $\text{CO}_2$  within the boundary layer becomes depleted. The diurnal fluctuations of  $\text{CO}_2$  above the canopy at the study site suggest that daytime photosynthesis indeed leads to depletion of  $\text{CO}_2$  (data not shown), so that it would appear to be beneficial for the plants to insure a strong coupling with the atmosphere by forming a rough canopy structure and small leaves. Given the costs and benefits of a high boundary layer resistance as outlined earlier, it could be possible to calculate an optimal canopy roughness for given environmental conditions (especially wind conditions). To our knowledge, such an optimality-based treatment of canopy roughness has not been done before, but this is beyond the scope of this study. It is however likely in our view that vegetation would have an advantage in avoiding large boundary layer resistances and maintaining a dynamic control on gas exchange by adjustments of stomata.

## CONCLUSIONS

A model based on the optimal water-use hypothesis performed better than one based on a constant stomatal conductivity and at least as well as a tuned empirical model. This suggests that the optimal water-use hypothesis is useful for modelling canopy gas exchange, and that it can reduce the need for model parameterization as only one parameter has to be estimated ( $\lambda$ ) if the photosynthetic properties of the canopy and atmospheric conditions are known. Furthermore, this one parameter is independent of scale and has a physiological meaning so that it can potentially be used to reconcile canopy-scale models with leaf-scale measurements.

We conclude by asserting that the organizing principle of natural vegetation that Cowan & Farquhar (1977) expressed in terms of the equation  $\partial E_t / \partial A_g = \text{constant}$ , is useful and perhaps more general than empirical equations (of increasing complexity) that are being developed to characterize the response of stomata to environmental forcing.

## ACKNOWLEDGMENTS

We thank Nigel Tapper for his support in the data acquisition, Erik Veneklas and Sandra Berry for providing useful literature references and John Evans and Susanne von Caemmerer for valuable insights into the physiology of photosynthesis. We also thank Graham Farquhar and an anonymous reviewer providing many constructive comments and suggestions, which substantially improved the presentation of the paper. The research was funded by the University of Western Australia, Perth; the Department for Education, Science and Training, Canberra; and the Cooperative Research Centre for Greenhouse Accounting, Canberra.

## REFERENCES

- Aalto T., Hari P. & Vesala T. (2002) Comparison of an optimal stomatal regulation model and a biochemical model in explaining  $\text{CO}_2$  exchange in field conditions. *Silva Fennica* **36**, 615–623.
- Baldocchi D., Hicks B.B. & Meyers T.P. (1988) Measuring biosphere–atmosphere exchanges of biologically related gases with micrometeorological methods. *Ecology* **69**, 1331–1340.
- Ball J.T., Woodrow I.E. & Berry J.A. (1987) A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. *Progress in Photosynthesis Research* **4**, 221–224.
- Beringer J., Hutley L.B., Tapper N.J., Coutts A., Kerley A. & O'Grady A.P. (2003) Fire impacts on surface heat, moisture and carbon fluxes from a tropical savanna in northern Australia. *International Journal of Wildland Fire* **12**, 333–340.
- Beringer J., Hutley L.B., Tapper N.J. & Cernusak L.A. (2007) Savanna fires and their impact on net ecosystem productivity in north Australia. *Global Change Biology* **13**, 990–1004.
- Berninger F. & Hari P. (1993) Optimal regulation of gas-exchange – evidence from field data. *Annals of Botany* **71**, 135–140.
- Berninger F., Mäkelä A. & Hari P. (1996) Optimal control of gas exchange during drought: empirical evidence. *Annals of Botany* **77**, 469–476.

- Buckley T.N., Farquhar G.D. & Mott K.A. (1999) Carbon–water balance and patchy stomatal conductance. *Oecologia* **118**, 132–143.
- von Caemmerer S. (2000) *Biochemical Models of Leaf Photosynthesis*, Vol. 2. CSIRO Publishing, Collingwood, Vic., Australia.
- Cernusak L.A., Hutley L.B., Beringer J. & Tapper N.J. (2006) Stem and leaf gas exchange and their responses to fire in a north Australian tropical savanna. *Plant, Cell & Environment* **29**, 632–646.
- Chen X.Y., Eamus D. & Hutley L.B. (2002) Seasonal patterns of soil carbon dioxide efflux from a wet–dry tropical savanna of northern Australia. *Australian Journal of Botany* **50**, 43–51.
- Cowan I.R. (1977) Stomatal behaviour and environment. *Advances in Botanical Research* **4**, 117–228.
- Cowan I.R. (1978) Water use in higher plants. In *Water: Planets, Plants and People* (ed. A. McIntyre), pp. 71–107. Australian Academy of Science, Canberra, Australia.
- Cowan I.R. (1982) Regulation of water use in relation to carbon gain in higher plants. In *Physical Plant Ecology II* (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), pp. 589–613. Springer, Berlin, Germany.
- Cowan I.R. (1986) Economics of carbon fixation in higher plants. In *On the Economy of Plant Form and Function* (ed. T.J. Givnish), pp. 133–171. Cambridge University Press, Cambridge, UK.
- Cowan I.R. (2002) Fit, fitter, fittest; where does optimisation fit in? *Silva Fennica* **36**, 745–754.
- Cowan I.R. & Farquhar G.D. (1977) Stomatal function in relation to leaf metabolism and environment. In *Integration of Activity in the Higher Plant* (ed. D.H. Jennings), pp. 471–505. Cambridge University Press, Cambridge, UK.
- Eamus D., Myers B., Duff G. & Williams D. (1999) Seasonal changes in photosynthesis of eight savanna tree species. *Tree Physiology* **19**, 665–671.
- Eamus D., Hutley L.B. & O'Grady A.P. (2001) Daily and seasonal patterns of carbon and water fluxes above a north Australian savanna. *Tree Physiology* **21**, 977–988.
- Farquhar G.D. & von Caemmerer S. (1982) Modeling of photosynthetic response to environmental conditions. In *Encyclopedia of Plant Physiology New Series* (eds O. Lange, P. Nobel, C. Osmond & H. Ziegler), pp. 550–587. Springer-Verlag, Berlin, Germany.
- Farquhar G.D., von Caemmerer S. & Berry S.L. (1980) A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* **149**, 78–90.
- Franks P.J., Cowan I.R. & Farquhar G.D. (1997) The apparent feedforward response of stomata to air vapour pressure deficit: information revealed by different experimental procedures with two rain forest trees. *Plant, Cell & Environment* **20**, 142–145.
- Givnish T.J. (1988) Adaptation to sun and shade – a whole-plant perspective. *Australian Journal of Plant Physiology* **15**, 63–92.
- Hall A.E. & Schulze E.-D. (1980) Stomatal response to environment and a possible interrelation between stomatal effects on transpiration and CO<sub>2</sub> assimilation. *Plant, Cell & Environment* **3**, 467–474.
- Hanan N.P., Kabat P., Dolman A.J. & Elbers J.A. (1998) Photosynthesis and carbon balance of a Sahelian fallow savanna. *Global Change Biology* **4**, 523–538.
- Hari P., Mäkelä A., Berninger F. & Pohja T. (1999) Field evidence for the optimality hypothesis of gas exchange in plants. *Australian Journal of Plant Physiology* **26**, 239–244.
- Hari P., Mäkelä A. & Pohja T. (2000) Surprising implications of the optimality hypothesis of stomatal regulation gain support in a field test. *Australian Journal of Plant Physiology* **27**, 77–80.
- Hutley L.B., O'Grady A.P. & Eamus D. (2001) Monsoonal influences on evapotranspiration of savanna vegetation of northern Australia. *Oecologia* **126**, 434–443.
- Hutley L.B., Leuning R., Beringer J. & Cleugh H.A. (2005) The utility of the eddy covariance techniques as a tool in carbon accounting: tropical savanna as a case study. *Australian Journal of Botany* **53**, 663–675.
- Jarvis A.J. (1976) The interpretation of leaf water potential and stomatal conductance found in canopies in the field. *Philosophical Transactions of the Royal Society of London, Series B* **273**, 593–610.
- Kelley G. (2002) *Tree water use and soil water dynamics in savannas of northern Australia*. PhD thesis, Northern Territory University, NT, Australia.
- Koskela J., Hari P. & Pipatwattanukul D. (1999) Analysis of gas exchange of Merkus pine populations by the optimality approach. *Tree Physiology* **19**, 511–518.
- van Kraalingen D.W.G. (1990) Implications of non-uniform stomatal closure on gas exchange calculations. *Plant, Cell & Environment* **13**, 1001–1004.
- Larcher W. (1995) *Physiological Plant Ecology*. Springer Verlag, Berlin, Germany.
- Lee T.J. & Pielke R.A. (1992) Estimating the soil surface specific-humidity. *Journal of Applied Meteorology* **31**, 480–484.
- Leuning R. (1990) Modeling stomatal behavior and photosynthesis of *Eucalyptus grandis*. *Australian Journal of Plant Physiology* **17**, 159–175.
- Leuning R. (1995) A critical appraisal of a combined stomatal–photosynthesis model for C<sub>3</sub> plants. *Plant, Cell & Environment* **18**, 339–355.
- Lloyd J. & Farquhar G.D. (1994) <sup>13</sup>C discrimination during CO<sub>2</sub> assimilation by the terrestrial biosphere. *Oecologia* **99**, 201–215.
- Lloyd J., Grace J., Miranda A.C., Meir P., Wong S.C., Miranda H.S., Wright I.R., Gash J.H.C. & McIntyre J. (1995) A simple calibrated model of Amazon rain forest productivity based on leaf biochemical properties. *Plant, Cell & Environment* **18**, 1129–1145.
- Mäkelä A., Berninger F. & Hari P. (1996) Optimal control of gas exchange during drought: theoretical analysis. *Annals of Botany* **77**, 461–467.
- Medlyn B.E., Dreyer E., Ellsworth D., et al. (2002) Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant, Cell & Environment* **25**, 1167–1179.
- Mercado L., Lloyd J., Carswell F., Malhi Y., Meir P. & Nobre A.D. (2006) Modelling Amazonian forest eddy covariance data: a comparison of big leaf versus sun/shade models for the C-14 tower at Manaus I. Canopy photosynthesis. *Acta Amazonica* **36**, 69–82.
- Monsi M. & Saeki T. (1953) Ueber den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung fuer die Stoffproduktion. *Japanese Journal of Botany* **14**, 22–52.
- O'Grady A.P., Eamus D. & Hutley L.B. (1999) Transpiration increases during the dry season: patterns of tree water use in eucalypt open-forests of northern Australia. *Tree Physiology* **19**, 591–597.
- Oren R., Hsieh C.I., Stoy P., Albertson J., McCarthy H.R., Harrell P. & Katul G.G. (2006) Estimating the uncertainty in annual net ecosystem carbon exchange: spatial variation in turbulent fluxes and sampling errors in eddy-covariance measurements. *Global Change Biology* **12**, 883–896.
- Pinker R.T. & Laszlo I. (1997) *Photosynthetically Active Radiation (PAR) and Conversion Factors (CF)*. NOAA National Geographical Data Center, Boulder, CO, USA.
- Roderick M.L. (1999) Estimating the diffuse component from daily and monthly measurements of global radiation. *Agricultural and Forest Meteorology* **95**, 169–185.
- Schymanski S.J. (2007) *Transpiration as the leak in the carbon*

- factory: a model of self-optimising vegetation. PhD thesis, University of Western Australia, Perth, Australia.
- Schymanski S.J., Roderick M.L., Sivapalan M., Hutley L.B. & Beringer J. (2007) A test of the optimality approach to modelling canopy properties and CO<sub>2</sub> uptake by natural vegetation. *Plant, Cell & Environment*, doi:10.1111/j.1365-3040.2007.01728.x
- Specht R.L. (1981) Foliage projective cover and standing biomass. In *Vegetation Classification in Australia* (eds A.N. Gillison & D.J. Anderson), pp. 10–21. ANU Press, Canberra, Australia.
- Spitters C.J.T., Toussaint H.A.J.M. & Goudriaan J. (1986) Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. 1. Components of incoming radiation. *Agricultural and Forest Meteorology* **38**, 217–229.
- Styles J.M., Raupach M.R., Farquhar G.D., *et al.* (2002) Soil and canopy CO<sub>2</sub>, <sup>13</sup>CO<sub>2</sub>, H<sub>2</sub>O and sensible heat flux partitions in a forest canopy inferred from concentration measurements. *Tellus Series B: Chemical and Physical Meteorology* **54**, 655–676.
- Thimijan R.W. & Heins R.D. (1983) Photometric, radiometric, and quantum light units of measure – a review of procedures for interconversion. *HortScience* **18**, 818–822.
- Thomas D.S., Eamus D. & Bell D. (1999a) Optimization theory of stomatal behaviour. I. A critical evaluation of five methods of calculation. *Journal of Experimental Botany* **50**, 385–392.
- Thomas D.S., Eamus D. & Bell D. (1999b) Optimization theory of stomatal behaviour. II. Stomatal responses of several tree species of north Australia to changes in light, soil and atmospheric water content and temperature. *Journal of Experimental Botany* **50**, 393–400.
- Williams W.E. (1983) Optimal water-use efficiency in a California shrub. *Plant, Cell & Environment* **6**, 145–151.
- Wilson K.B., Baldocchi D., Falge E., *et al.* (2003) Diurnal centroid of ecosystem energy and carbon fluxes at FLUXNET sites. *Journal of Geophysical Research Atmospheres* **108** doi:10.1029/2001JD001349
- Wong S.C., Cowan I.R. & Farquhar G.D. (1979) Stomatal conductance correlates with photosynthetic capacity. *Nature* **282**, 424–426.

*Received 5 July 2007; received in revised form 21 September 2007; accepted for publication 21 September 2007*

# ERRATA: A canopy scale test of the optimal water use hypothesis

Schymanski, S. J.; Roderick, M. L.; Sivapalan, M.; Hutley, L. B. & Beringer, J.  
A canopy scale test of the optimal water use hypothesis. *Plant Cell & Environment*, **2008**, 31, 97-111

1. In Equations (1) and (4), a minus sign is missing in the exponent. The correct Equation (1) should be:

$$J = J_{max} \left( 1 - e^{-\frac{0.3 I_t}{J_{max}}} \right)$$

The correct Equation (4) should be:

$$J_i = L_{Ashade,i} \left( 1 - e^{-\frac{0.3 I_{d,i}}{J_{max,i}}} \right) J_{max,i} + L_{Asun,i} \left( 1 - e^{-\frac{0.3 I_{sun,i}}{J_{max,i}}} \right) J_{max,i}$$

2. Equation (17) is only valid for  $\lambda \geq \frac{2a D_v}{C_a + 2\Gamma_*}$ . For  $\lambda < \frac{2a D_v}{C_a + 2\Gamma_*}$ , the sign before the square root in Equation (17) has to be reversed. The corrected Equation (17) is:

$$E_t = \begin{cases} \frac{a D_v (Y - 4 (J_A + 2 R_l) \Gamma_*)}{4 (C_a + 2 \Gamma_*)^2} - \frac{\sqrt{3 X Z}}{4 (C_a + 2 \Gamma_*)^2 X}, & \lambda < \frac{2a D_v}{C_a + 2 \Gamma_*} \\ \frac{a D_v (Y - 4 (J_A + 2 R_l) \Gamma_*)}{4 (C_a + 2 \Gamma_*)^2} + \frac{\sqrt{3 X Z}}{4 (C_a + 2 \Gamma_*)^2 X}, & \lambda \geq \frac{2a D_v}{C_a + 2 \Gamma_*} \end{cases}$$

For typical values of  $a$ ,  $D_v$ ,  $C_a$  and  $\Gamma_*$ , the correction would only be relevant for  $\lambda < 300$ , which was never found to be the case in the present study.