

## Evaluating the models of stomatal conductance response to humidity in a tropical rain forest of Xishuangbanna, southwest China

Zhiheng Li, Yiping Zhang, Shusen Wang, Guofu Yuan, Yan Yang, Guiri Yu and Xiaomin Sun

### ABSTRACT

The ecosystem-level fluxes of water vapour and carbon dioxide were measured from 2003 to 2006 at a tropical rain forest in Xishuangbanna, southwest China, using the eddy covariance (EC) technique. These flux measurements allowed the canopy-level evaluation of stomatal conductance ( $g$ ) response to humidity models. The results showed that both the BWB model and the Leuning model discussed here underestimated  $g$  at high humidity and overestimated  $g$  at the mid-to-low range of humidity. In contrast, the Wang models discussed here (model- $h_a$  and model- $D_a$ ) perfectly described the relationship of  $g$  response to humidity. The model comparison results also demonstrated high consistency over all the observation years. The good performance of the Wang model- $h_a$  and model- $D_a$  indicated that stomatal conductance responds more sensitively to humidity deficit or water vapour pressure deficit than to relative humidity itself at canopy level.

**Key words** | evaluation, humidity, response, stomatal conductance models, tropical rain forest

**Zhiheng Li**

**Yiping Zhang** (corresponding author)  
Xishuangbanna Tropical Botanical Garden,  
Chinese Academy of Sciences,  
Kunming, Yunnan 650223,  
China  
E-mail: yipingzh@xtbg.ac.cn

**Shusen Wang**

**Yan Yang**  
Canada Centre for Remote Sensing,  
Natural Resources Canada,  
Ottawa ON K1A 0Y7,  
Canada

**Guofu Yuan**

**Guiri Yu**

**Xiaomin Sun**

Institute of Geographic Sciences and Natural  
Resources Research,  
Chinese Academy of Sciences,  
Beijing 100101,  
China

### INTRODUCTION

The stomatal behaviour is an important physiological process that controls CO<sub>2</sub> and water vapour exchanges between plant leaves and atmosphere. These two fluxes largely determine the carbon and water cycles in the vegetated land surface and have profound impacts on the regional and global climate (Sellers *et al.* 1986; Margolis & Ryan 1997). It is therefore imperative to understand stomatal conductance and its mechanisms in ecological and climate studies. Stomata respond to environmental variables in an extremely complex way. Numerous laboratory and field studies have shown that light, air temperature, humidity and soil water status can directly modulate stomatal conductance (Cowan 1977; Jarvis & Mansfield 1981; Willmer 1988; Lloyd 1991; Franks *et al.* 1997; Schultz 2003).

Models in different forms have been used to simulate stomatal behaviour. The first stomatal conductance model

was proposed by Jarvis (1976). This model empirically determines the response of stomata to environmental factors using the nonlinear least-squares analysis. But it ignores the linkage between leaf photosynthesis ( $A$ ) and stomatal conductance ( $g$ ). Ball *et al.* (1987) incorporate this linkage into their model (hereafter termed as the BWB model), which is given by

$$g = mh_s A / C_s + g_0 \quad (1)$$

where  $h_s$  (dimensionless) and  $C_s$  ( $\mu\text{mol mol}^{-1}$ ) are the relative humidity and CO<sub>2</sub> concentration at the leaf surface,  $g_0$  is the leaf minimum (residual)  $g$  ( $\text{mol m}^{-2} \text{s}^{-1}$ ) when  $A$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) reaches 0 and  $m$  is a dimensionless parameter. The BWB model was subsequently modified by

Leuning (1995) who found stomatal conductance responds more closely to water vapour pressure deficit ( $D_s$ ). The model is represented by:

$$g = a_1 A / [(C_s - \Gamma)(1 + D_s/D_0)] + g_0 \quad (2)$$

where  $a_1$  (dimensionless) and  $D_0$  (Pa) are empirical coefficients and  $\Gamma$  ( $\mu\text{mol mol}^{-1}$ ) represents the  $\text{CO}_2$  compensation point.

The main difference between the BWB model and the Leuning model is the humidity response function  $f(H)$  (Equation (3)). The  $f(H)$  equals  $mh_s$  in the BWB model and  $a_1/(1 + D_s/D_0)$  in the Leuning model. Some investigators suggest that the BWB model performs better (Collatz *et al.* 1991; Sellers *et al.* 1996; Betts *et al.* 1999; Gutschick 2007), while other literatures show that the Leuning model is preferable in simulating stomatal conductance (Leuning 1995; Van Wijk *et al.* 2000; Mo & Liu 2001; Arora 2003). Independent evaluations of the two models are not always consistent and there is no compelling evidence in favour of either approach. In Wang *et al.* (2009a), they developed a diagnostic approach (Equation (5)) to calculate  $f(H)$  through coupling canopy transpiration equation (Equation (4)) with photosynthesis-based stomatal model (Equation (3)). The  $f(H)$  and transpiration equation are given by

$$f(H) = (C_s - \Gamma)(g - g_0)/A \quad (3)$$

$$LE_{can} = L\rho_s(q_{sat}(T_c) - q_s)g_{H_2O} \quad (4)$$

$$f(H) = \frac{(C_s - \Gamma)LE_{can}}{v\delta L\rho_s(q_{sat}(T_c) - q_s)A} \quad (5)$$

where  $LE_{can}$  ( $\text{W m}^{-2}$ ) is canopy latent heat exchange due to transpiration,  $L$  ( $\text{J kg}^{-1}$ ) is the latent heat of vaporization of water,  $\rho_s$  ( $\text{kg m}^{-3}$ ) and  $q_s$  ( $\text{kg kg}^{-1}$ ) are the density and specific humidity of the air at leaf surface,  $q_{sat}(T_c)$  ( $\text{kg kg}^{-1}$ ) is the saturated specific humidity at leaf temperature  $T_c$  ( $^{\circ}\text{C}$ ),  $g_{H_2O}$  ( $\text{m s}^{-1}$ ) is the canopy  $g$  to water vapour ( $g_{H_2O} = \delta g$ ),  $\delta$  is a parameter accounting for the difference of stomatal conductance to water vapour and to  $\text{CO}_2$  and  $v$  is the volume of gas per mole. Note that the second item in the original equation

(Equation (6)) of Wang *et al.* (2009a) is small and excluded in this study.

This diagnostic approach enables us to examine the response of  $g$  to humidity without requiring the leaf-level stomatal measurement which is tedious and costly. It could also test various stomatal conductance models at canopy level. The main difficulties in using Equation (5) are that it needs variables such as humidity and  $\text{CO}_2$  concentration at the leaf surface, while most sites measure their values of the ambient air.

In Wang *et al.* (2009b), leaf surface variables (i.e.  $\rho_s$ ,  $q_s$ ,  $q_{sat}(T_c)$  and  $C_s$ ) were replaced by their corresponding ambient air variables ( $\rho_a$ ,  $q_a$ ,  $q_{sat}(T_a)$  and  $C_a$ , which are the density, specific humidity, saturated specific humidity and  $\text{CO}_2$  concentration of the ambient air, respectively) in Equation (5). It was found that these treatments only induced very small differences in predicting the response of  $g$  to humidity. As such, the ambient air variables can be used in Equation (5) to assess the canopy  $g$ -humidity relationships with acceptable accuracy. Based on this approach, Wang *et al.* (2009b) assessed the performance of the BWB model and Leuning model at the canopy level of three boreal forests in Canada. It was found that both of the two models could not adequately express canopy  $g$ -humidity relationships particularly at high humidity. They proposed the following canopy stomatal conductance models that were based on  $h_s$  (Equation (6), hereafter termed as Wang model- $h_a$ ) and  $D_s$  (Equation (7), hereafter termed as Wang model- $D_a$ ), and concluded that the two equations significantly outperformed the BWB and Leuning models:

$$\text{Wang model-}h_a: g = \alpha(1.0 - h_s)^\beta A / (C_s - \Gamma) + g_0 \quad (6)$$

$$\text{Wang model-}D_a: g = \alpha D_s^\beta A / (C_s - \Gamma) + g_0 \quad (7)$$

where  $\alpha$  and  $\beta$  are parameters. (Note that they have different values in Equations (6) and (7), and the humidity response function  $f(H)$  equals  $\alpha(1.0 - h_s)^\beta$  in Wang model- $h_a$  and  $\alpha D_s^\beta$  in Wang model- $D_a$ .)

The large difference between the four models (the BWB mode, the Leuning model, the Wang model- $h_a$  and Wang model- $D_a$ ) occurs at high humidity. The latter two models can best predict the  $g$ -humidity relationships at high

humidity. This indicates that the diagnostic theory and the stomatal conductance models depend closely on humid conditions of the site.

Xishuangbanna in southwest China is located on the northern edge of the tropical zone in southeast Asia (Figure 1). Despite its relatively high latitude, Xishuangbanna has a tropical moist climate due to the impact of the Himalayan Mountains. The Himalayas lead to the penetration of warm and moist tropical air from the Indian Ocean to Xishuangbanna in summer, and blockade cold air from the north to the region in winter (Cao et al. 2006). To aim at long-term measurements of energy, water vapour and CO<sub>2</sub> fluxes in the tropical rain forest in Xishuangbanna, a tower flux measurement station was initiated by the Chinese Terrestrial Ecosystem Flux Research Network (CTEFRN, ChinaFlux) in the year 2002.

The humid conditions and present measurements at the site allowed us to validate the above diagnostic theory and to assess the canopy  $g$ -humidity relationships at the tropical site. Based on this, we calculated the diagnostic parameter  $f(H)$  using Equation (5), the canopy flux measurements and the measurements of ambient air variables and then critically examined the performance of the four models (BWB, Leuning, Wang model- $h_a$  and Wang model- $D_a$ ) of stomatal conductance response to humidity at canopy level in the tropical rain forest.

## MATERIALS AND METHODS

### Site description

The measurement station (21° 55' 39"N, 101° 15' 55"E) is located at a National Natural Reserve in Xishuangbanna, Yunnan Province, southwest China (Figure 1). This site is a permanent observation plot dedicated to long-term forest ecosystem research, managed by the Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies (XSTRFES), Chinese Academy Sciences (CAS). The annual mean air temperature at the site is 21.7 °C, with a maximum monthly temperature of 25.7 °C for the hottest month (June) and a minimum monthly temperature of 15.9 °C for the coldest month (January). The annual mean precipitation is 1507 mm, 87% of which occurs in the rainy season (from May through October; Liu et al. 2008). The annual mean relative humidity is 86%.

The soil at the site is latosol developed from siliceous rocks, which is a dark-red clay soil with high organic matter content (about 20 g kg<sup>-1</sup>; Sha et al. 2005). The typical vegetation in this area is represented by tropical seasonal rain forest with a canopy height of about 35 m. The dominant species are *Pometia tomentosa*, *Terminalia myriocarpa*, *Girardiniera subaequalis*, *Barringtonia macrostachya*, *Garcinia cowa*, *Knema erratica*, *Ardisia tenera*, *Mezzettiopsis creaghii*

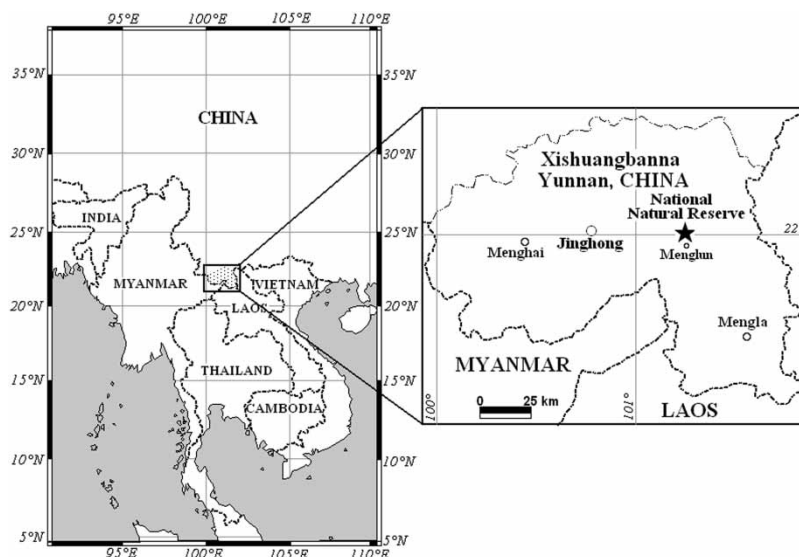


Figure 1 | Location of the National Natural Reserve (21°55'39"N; 101°15'55"E) in Xishuangbanna, Yunnan Province, southwest China.

and *Dichapetalum gelonioides*. The stands are mainly evergreen although there are some deciduous trees. Total canopy leaf area index (LAI) is about  $5.58 \text{ m}^2 \text{ m}^{-2}$ , with variations between  $3.56 \text{ m}^2 \text{ m}^{-2}$  in the hot-dry season (March and April) and  $6.34 \text{ m}^2 \text{ m}^{-2}$  in the rainy season (from May to October; Zhang *et al.* 2006). More detailed descriptions of vegetation at the site can be found in Cao *et al.* (1996, 2006) and Zhu *et al.* (2006).

### Field measurements

The  $\text{CO}_2$  and water vapour fluxes were measured at the site using the eddy covariance (EC) technique, which consists of a three-dimensional sonic anemometer-thermometer (Model CSAT-3, Campbell Scientific Inc., Logan, USA) and an open-path infrared gas analyzer (Model LI-7500, Licor Inc., Lincoln, NE, USA). All sensors were installed on a tower 48.8 m above the ground surface and about 10 m above the canopy. To minimize the potential disturbance of the tower on measurements, these sensors were oriented in the direction of the upwind side ( $210^\circ$  from north). Data were recorded at 10 Hz by a data logger. To eliminate horizontal and vertical advection, the coordinate system rotation for the 3D wind speed was applied according to the approach of Tanner & Thurtell (1969). Fluxes were also corrected for the effects of variation in air density using the method of Webb *et al.* (1980). Details of the instrumentations and data quality control are available from Zhang *et al.* (2006) and Dou *et al.* (2007).

Ambient air variables in the rain forest such as air temperature, relative humidity (RH) and wind speed were measured at the heights of 4.2, 16.3, 26.2, 36.5, 42.0, 48.8 and 69.8 m above the ground surface using platinum resistance thermometers (PRT), capacitive RH chips (Model HMP45C, Vaisala Inc., Finland) and anemometers (Model A100R, Vector Inc., UK), respectively. Net radiation ( $R_n$ ) was measured on the tower at 41.6 m above the ground using a four-component net radiometer (Model CNR-1, Kipp & Zonen Inc., Netherlands), which consists of downwards and upwards short-wave and long-wave radiations. Soil temperature was measured at depths of 0, 5, 10, 15, 20, 40, 60, 80, 100 cm using thermocouple probes (Model 105T, Campbell Scientific Inc., USA). Soil volumetric water content was measured at depths of 5, 20 and 40 cm using water content reflectometers (Model CS-616-L, Campbell Scientific Inc., USA). Rain was measured

on the top of the tower about 70.2 m above the ground using a rain gauge (Model 52203, RM Young, Inc.). All these data were collected using a data logger.

### Parameters calculation

Details of the  $f(H)$  calculations in Equation (5) were largely based on data from field measurements at the ecosystem level. The 30 min values of ambient air variables (i.e.  $\rho_a$ ,  $q_a$ ,  $q_{sat}(T_a)$ ,  $C_a$ ,  $h_s$  and  $D_s$ ) were obtained from micrometeorological measurements. The 30 min values of  $A$  and  $LE_{can}$  were estimated by using empirically based corrections of ecosystem- to canopy-level fluxes.

The canopy photosynthesis rate ( $A$ ) was obtained by

$$A = -F_{NEE} + F_{RE} \quad (8)$$

where  $F_{NEE}$  and  $F_{RE}$  are the net ecosystem  $\text{CO}_2$  exchange ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) and ecosystem respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ). Note that the positive sign represents  $\text{CO}_2$  release into the atmosphere (and vice versa). The net ecosystem  $\text{CO}_2$  exchange ( $F_{NEE}$ ) was computed from

$$F_{NEE} = F_c + F_s \quad (9)$$

where  $F_c$  is the 30 min averaged  $\text{CO}_2$  fluxes above the canopy measured by EC instruments and  $F_s$  is the  $\text{CO}_2$  storage in the canopy layer, which was estimated by the changes of  $\text{CO}_2$  concentration measured by EC instruments. Ecosystem respiration ( $F_{RE}$ ) was measured directly at the tower during night-time periods (Falge *et al.* 2002), and extrapolated over other periods by using exponential regressions of measured  $F_{RE}$  with air or soil temperature. The Lloyd and Taylor respiration equation (Lloyd & Taylor 1994) was used here for this exponential regression:

$$F_{RE,night} = F_{NEE,night} \\ = F_{RE,298.16} \exp\left(E_0 \left(\frac{1}{298.16 - T_0} - \frac{1}{T_k - T_0}\right)\right) \quad (10)$$

where  $T_k$  is air or soil temperature (K),  $E_0$  is set to 309 K,  $F_{RE,298.16}$  ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) is the ecosystem respiration rate at reference temperature (298.16 K) and  $T_0$  (K) is the fitted parameters.

The canopy latent heat exchange ( $LE_{can}$ ) was calculated by

$$LE_{can} = F_{LE} - LE_{soil} \quad (11)$$

where  $F_{LE}$  is the storage-corrected latent heat fluxes above the canopy and  $LE_{soil}$  is soil latent heat exchange.  $F_{LE}$  was estimated from

$$F_{LE} = LE_c + LE_s \quad (12)$$

where  $LE_c$  is the 30 min averaged latent heat fluxes above the canopy measured by the EC instruments and  $LE_s$  is the latent heat storage in the canopy layer.  $LE_s$  was computed here (Blanken et al. 1998; Oliphant et al. 2004) as:

$$LE_s = \rho_a L \sum_{i=1}^n \left( \frac{\Delta q_i}{\Delta t} \Delta z_i \right) \quad (13)$$

where  $L$  ( $\text{J kg}^{-1}$ ) is the latent heat of vaporization,  $\rho_a$  ( $\text{kg m}^{-3}$ ) and  $q_i$  ( $\text{kg kg}^{-1}$ ) are the density and specific humidity of the air in the six layers below the EC measurements,  $\Delta q_i/\Delta t$  is the layer-average changes of specific humidity and  $\Delta z_i$  is the height difference between two adjacent layers.

Soil latent heat exchange ( $LE_{soil}$ ) due to soil evaporation was estimated based on other studies. Liu et al. (2005) estimated the soil evaporation at the same site using stable isotopic techniques, and found that soil evaporation was 5.1% of the total evapotranspiration in 2002 and 3.1% in 2003. The low soil evaporation would have a small impact on the calculation of the canopy transpiration (canopy latent heat exchanges,  $LE_{can}$ ). As such,  $LE_{soil}$  was estimated as 4% of  $F_{LE}$  in this study which means that soil evaporation is proportionally related to total evapotranspiration.

### Data processing

This study analyzed the four years (2003–2006) of observation data from the study site. To better evaluate the response of canopy-level stomatal conductance to humidity, measurement data were filtered as follows.

1. Daylight hours when canopy photosynthesis and transpiration were strong ( $A$  was above  $5 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $LE_{can}$  was above  $40 \text{ W m}^{-2}$ ). At this time period, the

canopy  $\text{CO}_2$  and latent heat exchanges have the largest contributions in the measured ecosystem  $\text{CO}_2$  and latent heat fluxes so that the impacts of uncertainties in  $F_{RE}$  and  $LE_{soil}$  on the estimations of  $A$  and  $LE_{can}$  are minimized.

2. Daylight hours when incoming shortwave radiation was above  $150 \text{ W m}^{-2}$ . Stomatal activities have minimal impact on canopy water and  $\text{CO}_2$  exchanges when radiation is low.
3. Time periods when there is no water on the canopy (e.g. intercepted rain) to avoid the complication in canopy transpiration estimate.

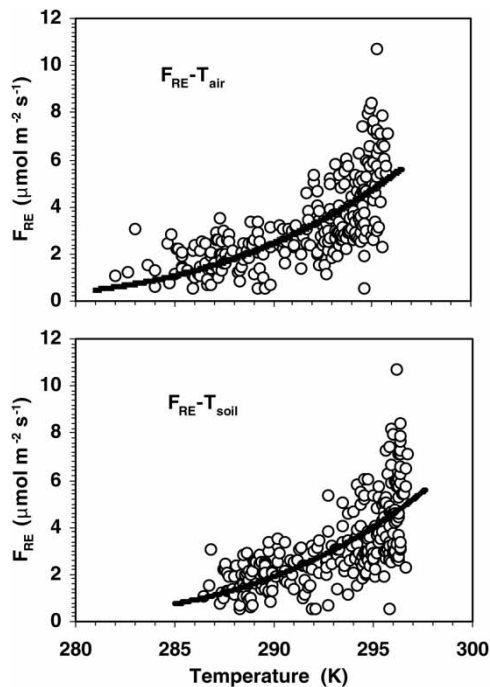
## RESULTS AND DISCUSSION

### Analysis of the $f(H)$ calculation

According to Equation (5), the values of the diagnostic parameter  $f(H)$  are mainly determined by the ratio of  $LE_{can}/A$ . The canopy-level  $A$  and  $LE_{can}$  were obtained by correcting the measured ecosystem-level fluxes of  $\text{CO}_2$  and latent heat using the estimated  $F_{RE}$  and  $LE_{soil}$ . The impact of soil latent heat flux ( $LE_{soil}$ ) on  $LE_{can}$  had been estimated in the preceding section. Here we discussed the impact of ecosystem respiration ( $F_{RE}$ ) on  $A$ , and then analyzed the impact of uncertainties in both  $F_{RE}$  and  $LE_{soil}$  on  $f(H)$  values.

The daytime ecosystem respiration ( $F_{RE}$ ) could be estimated by the relationship between night-time  $F_{RE}$  and temperature (in air or in soil, Falge et al. 2002). Figure 2 shows the relationships between ecosystem respiration ( $F_{RE}$ ) and air temperature ( $T_{air}$ ) and soil temperature ( $T_{soil}$ ) at the study site for all the 2003–2006 night-time data. In order to reduce the impact of high-frequency noise in the night-time flux measurements, 5 day night-time averaged data were used. It can be seen that there was an exponential increase in  $F_{RE}$  with response to the increasing  $T_{air}$  or  $T_{soil}$ . The parameters (such as  $F_{RE,298.16}$  and  $T_0$ ) best fitted between the  $F_{RE}$  and  $T_{air}$  using the Lloyd & Taylor Equation (10) were very close to those best fitted between  $F_{RE}$  and  $T_{soil}$ . In this study, the night-time  $F_{RE} - T_{air}$  relationships were used to estimate the daytime  $F_{RE}$  since it could provide us with a reasonable explanation for ecosystem respiration,

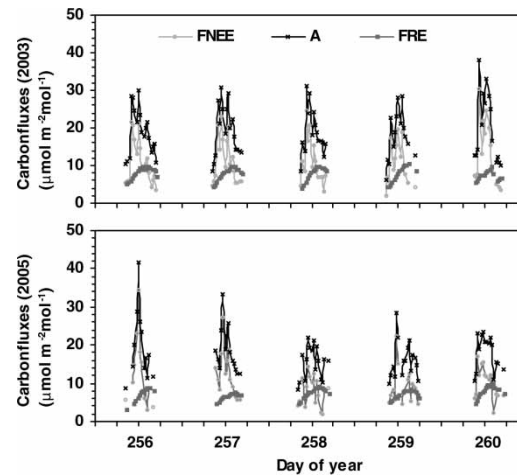




**Figure 2** | Relationship between night-time ecosystem respiration and temperature (in air and in soil) during the study periods from 2003 to 2006 at Xishuangbanna tropical rain forest, southwest China, using the Lloyd & Taylor model (Equation (10)). Here five-day means for night-time 30-min data were used for analysis. In the relationship of  $F_{RE} - T_{air}$  (top panel), the fitted parameter  $F_{RE,298.16}$  and  $T_0$  are  $6.73 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and  $244.12 \text{ K}$ , respectively, ( $r = 0.70$ ); and in the relationship of  $F_{RE} - T_{soil}$  (bottom panel), the fitted parameter  $F_{RE,298.16}$  and  $T_0$  are  $5.97 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and  $246.89 \text{ K}$ , respectively, ( $r = 0.68$ ).

which not only includes soil respiration but also contains stems, branches and leaves respiration.

Figure 3 showed the 30-min values of carbon flux components over five consecutive days in 2003 and 2005. It could be seen that the relative magnitudes of the flux components varied similarly between the two years. The canopy photosynthesis ( $A$ ) exhibited a distinct diurnal pattern. The large variations in  $A$  at midday were mainly due to the high-frequency fluctuations in the measured  $F_{NEE}$ , since the ecosystem respiration ( $F_{RE}$ ) was smooth. Moreover, the values of  $A$  were much higher than the ecosystem respiration ( $F_{RE}$ ) in midday. This caused a much smaller ratio of  $F_{RE}$  to  $A$ , and could minimize the impact of the estimated  $F_{RE}$  on the accuracy of  $f(H)$  estimations. Overall, during the study period over the four years, the ratios of total  $F_{RE}$  to total  $A$  were 0.41 (2003), 0.45 (2004), 0.41 (2005) and 0.39 (2006). The ratio differences between the four years were small (less than 0.10). The estimated  $F_{RE}$  was comparable with results from other



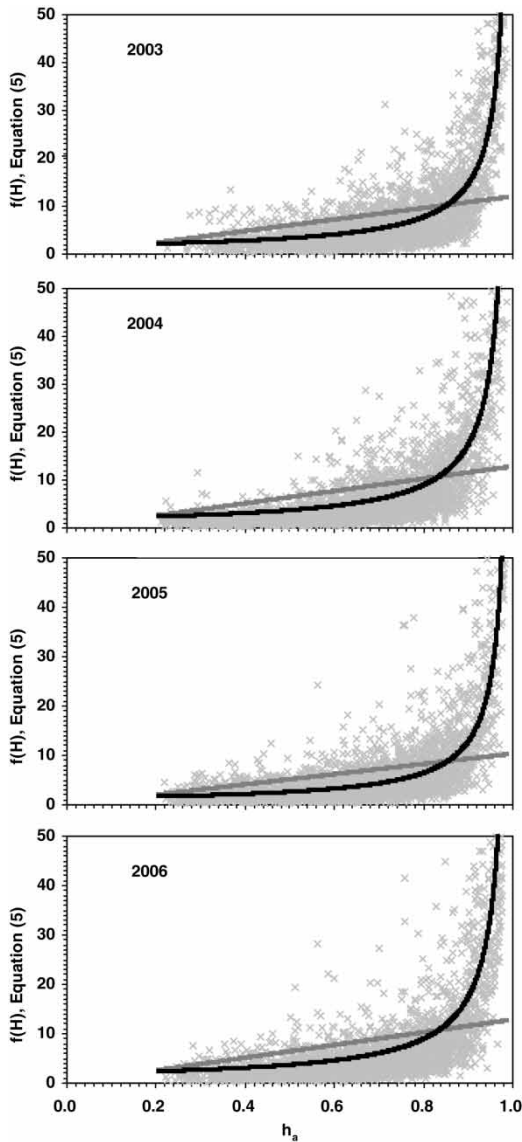
**Figure 3** | The 30-min  $\text{CO}_2$  flux components for five consecutive days in 2003 (top panel) and 2005 (bottom panel) in the canopy of Xishuangbanna tropical rain forest, southwest China ( $F_{NEE}$ : the net ecosystem  $\text{CO}_2$  exchange;  $F_{RE}$ : ecosystem respiration estimated using the empirical relationship of air temperature;  $A$ : canopy photosynthesis calculated as the sum of  $F_{NEE}$  and  $F_{RE}$ ).

studies. Measurements of soil, litter and low vegetation respiration at the same site were conducted using the static opaque chamber techniques during a rain-free period every week of 2003 (Sha *et al.* 2005). The ratio of total daytime soil, litter and low vegetation respiration to total photosynthesis ( $A$ ) was 0.46, which is close to the Lloyd & Taylor equation estimation.

The uncertainties in the estimation of ecosystem respiration and soil evaporation are difficult to quantify precisely due to data limitations. Considering the average quantities of  $F_{RE}/A$  and  $LE_{soil}/LE_{can}$  ratios stated above, errors of 10% in estimated  $F_{RE}$  and  $LE_{soil}$  will result in the estimate error of  $f(H)$  less than 5.1%, 5.6%, 5.2% and 4.9% in 2003, 2004, 2005 and 2006, respectively.

### Evaluating the models of stomatal conductance response to humidity

Evaluations of the BWB model, Leuning model, Wang model- $h_a$  and Wang model- $D_a$  at the tropical forest site were conducted using the diagnostic parameter  $f(H)$  (Equation (5)). Figure 4 shows the distribution of  $f(H)$  with  $h_a$  together with the BWB model and Wang model- $h_a$  for 2003, 2004, 2005 and 2006. The response of  $f(H)$  to  $h_a$  exhibited great consistency in the four years. The  $f(H)$  values increased in response to  $h_a$  increase, especially at



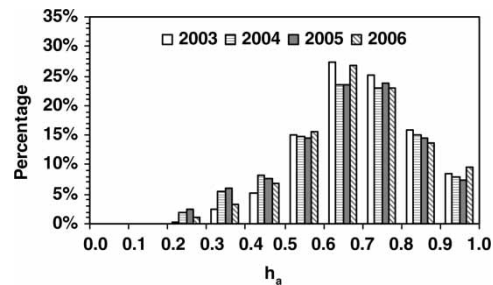
**Figure 4** | The response of stomatal conductance to relative humidity ( $h_a$ ) in the canopy of the tropical rain forest, southwest China. The scattered spots represent the 30 min values of the diagnostic parameter  $f(H)$  calculated by Equation (5) in 2003, 2004, 2005 and 2006. The gray line and the black curve are the best fit performances according to the form of BWB model and Wang model- $h_a$  when regressing the  $f(H)$  against  $h_a$ .

high humidity where the response between them was more sensitive. The scattered spots of  $f(H)$  versus  $h_a$  in Figure 4 were best fitted based on the least-squares regression analysis according to the form of BWB model (Equation (1)) and Wang model- $h_a$  (Equation (4)), respectively. The fit performance by the BWB model (gray line in Figure 4) did not work well for the relationships between stomatal conductance and  $h_a$ . It made  $g$  overestimation at the mid-to-low range

of humidity ( $h_a < 80\%$ , Figure 4; approximately 75% of total data, Figure 5) and  $g$  underestimation at high humidity values ( $h_a > 80\%$ , Figure 4; approximately 25% of total data, Figure 5). In contrast, the curvilinear fit by the Wang model- $h_a$  (black curve in Figure 4) provided better estimations at any range of humidity.

Table 1 compared the statistical results of the two model performances in the four years from 2003 to 2006. The fit performance by the form of Wang model- $h_a$  obtained a higher correlation coefficient and smaller standard deviation compared to that by the form of BWB model. This indicated that the  $g$ -humidity relationships depended on the curvilinear variation more strongly than on the linear variation.

Experiment on model parameterization showed that the parameters fitted by the BWB model varied more strongly than those fitted by Wang model- $h_a$  over the four years. In the BWB model, the parameter  $m$  changed from 10.35 to 12.88 at this site (Table 1). The  $m$  is often near 10 among diverse  $C_3$  species (Ball *et al.* 1987; Leuning 1990; Collatz *et al.* 1991). The larger  $m$  in our analysis may be mainly due to the rapid increase of  $f(H)$  with the increasing  $h_a$  at high humidity. In the Wang model- $h_a$ , the  $\alpha$  values varied from 1.34 to 1.92 and the  $\beta$  values changed from  $-0.92$  to  $-1.02$  (Table 1). The slight variation in  $\alpha$  and  $\beta$  over the four years indicated the great stability of model performance when predicting the  $g$ -humidity relationships using the Wang model- $h_a$ . We also made an analysis of all the available data taken together to define the best estimate of these parameters. We found that the best estimates of  $\alpha$  and  $\beta$  were 1.66 and  $-0.94$ , respectively, during the study period from 2003 to 2006 at this tropical site (Table 1).



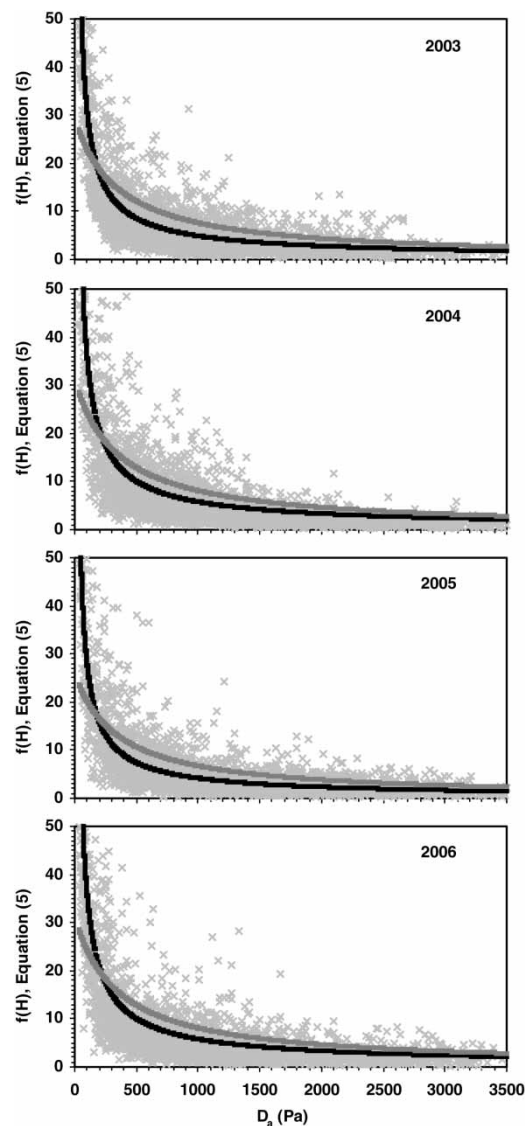
**Figure 5** | Frequency distributions of relative humidity ( $h_a$ ) in the period from 2003 to 2006 at Xishuangbanna tropical rain forest, southwest China.

**Table 1** | The regression analysis results according to the form of the BWB model, Leuning model, Wang model- $h_a$  and Wang model- $D_a$ 

Year	BWB $\alpha h_a$	Leuning $\alpha / (1 + D_0/\beta)$	Wang model- $h_a \alpha (1-h_a)^\beta$	Wang model- $D_0 \alpha D_0^\beta$	
2003	$\alpha$	12.06	29.44	1.78	1227
	$\beta$	–	350	–0.92	–0.80
	$r$	0.37	0.67	0.84	0.86
	$\sigma$	10.30	8.08	5.96	5.69
	$n$	4227	4277	4277	4277
	2004	$\alpha$	12.88	31.30	1.92
$\beta$		–	350	–0.96	–0.79
$r$		0.39	0.66	0.88	0.87
$\sigma$		10.93	8.71	6.62	6.36
$n$		3544	3590	3544	3590
2005		$\alpha$	10.35	25.98	1.34
	$\beta$	–	350	–0.98	–0.83
	$r$	0.36	0.65	0.88	0.89
	$\sigma$	9.07	7.27	4.53	4.45
	$n$	3781	3781	3781	3781
	2006	$\alpha$	11.44	28.35	1.38
$\beta$		–	350	–1.02	–0.80
$r$		0.37	0.66	0.86	0.86
$\sigma$		9.92	7.86	5.52	5.53
$n$		4045	4045	4045	4045
2003–2006		$\alpha$	11.68	28.79	1.66
	$\beta$	–	350	–0.94	–0.79
	$r$	0.37	0.66	0.85	0.86
	$\sigma$	10.08	8.01	5.65	5.55
	$n$	15,647	15,647	15,647	15,647

Note:  $\alpha$ ,  $\beta$  are the best-fit parameters when regressing the diagnostic parameter  $f(H)$  against relative humidity or vapour pressure deficit in terms of the BWB model, Leuning model, Wang model- $h_a$  and Wang model- $D_a$ .  $r$ ,  $\sigma$  are the correlation coefficient and standard deviation, respectively.  $n$  is the total number of samples used in the analysis. Data with  $f(H) > 100$  were excluded.

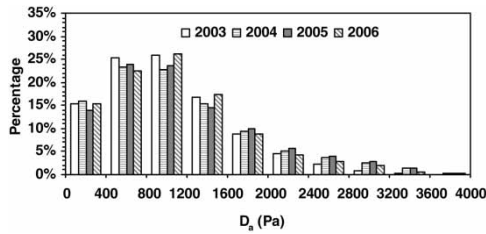
Figure 6 showed the distribution of  $f(H)$  with  $D_a$  together with the Leuning model and Wang model- $D_a$  for the years 2003, 2004, 2005 and 2006. It can be seen that the response of  $f(H)$  to  $D_a$  displayed a similar trend over the four years. The  $f(H)$  values decreased as the  $D_a$  increased, and dropped rapidly when the  $D_a$  values were low (the humidity was high). The scattered spots in Figure 6 were best fitted using the nonlinear least-squares regression analysis based on the form of the Leuning model (Equation (2)) and Wang model- $D_a$  (Equation (5)), respectively. In the Leuning model, some studies found that a value for  $D_0$  of 350 Pa provided the best fit to most of the data, with  $D_0$  values of up to 1500 Pa for some data sets (Leuning 1995). In this study, we obtained the best-fit relationships between  $f(H)$  and  $D_a$  by constraining  $D_0$  in the range of 350–1500 Pa.



**Figure 6** | The response of stomatal conductance to water vapour pressure deficit ( $D_a$ ) in the canopy of the tropical rain forest, southwest China. The scattered spots represent the 30 min values of the diagnostic parameter  $f(H)$  calculated by Equation (5) in 2003, 2004, 2005 and 2006. The gray curve and the black curve are the best fit performances in terms of the Leuning model and Wang model- $D_a$  when regressing the  $f(H)$  against  $D_a$ .

Results of the nonlinear regression analysis for the  $f(H)$  and  $D_a$  are also presented in Table 1. It was found that the fit performance using Leuning model accounted better (higher  $r$  and lower  $\sigma$ ; Table 1) for the  $g$ -humidity relationships than that using the BWB model. The fit curve (gray curve in Figure 6) by the Leuning model reduced the overestimation bias at mid-to-low range of humidity and the underestimation bias at high humidity. Nevertheless, it still could not





**Figure 7** | Frequency distributions of water vapour pressure deficit ( $D_a$ ) in the four years from 2003 to 2006 at Xishuangbanna tropical rain forest, southwest China.

capture the  $f(H)$  rapid decrease with the increasing  $D_a$  at high humidity ( $D_a < 600$  Pa, Figure 6; approximately 25% of total data, Figure 7). In contrast, the response relationship between  $f(H)$  and  $D_a$  was best expressed by the form of Wang model- $D_a$  (the highest  $r$  and the lowest  $\sigma$ ; Table 1), as was shown in Figure 6 (black curve).

Model parameterization showed that the parameters in the Leuning model and Wang model- $D_a$  were generally stable over the four years. In the Leuning model, the parameter  $D_0$  was the same 350 Pa (Table 1) for each year. This was in good agreement with the studies of Leuning (1995) and Wang *et al.* (2009a, b). The parameter  $a_1$  in the Leuning model changed from 25.98 to 31.30 at this site (Table 1). The larger  $a_1$  in the analysis may be responsible for the overestimation at the mid-to-low range of humidity. In the Wang model- $D_a$ , the parameter  $\alpha$  values varied from 1211 to 1390 (Table 1) over the four years. In fact, these values would become small if  $D_a$  was measured in kPa when fitting the relationships between  $f(H)$  and  $D_a$  using the Wang model- $D_a$ . By comparison, the  $\beta$  values displayed small difference over the four years (from  $-0.79$  to  $-0.83$ ; Table 1). The analysis of the 4-year available data taken together defined the best estimate of the parameter  $\alpha$  and  $\beta$  in Wang model- $D_a$ , which were 1.66 and  $-0.94$ , respectively, during the study period from 2003 to 2006 at this tropical site (Table 1).

## CONCLUSIONS

Stomatal conductance responding to humidity was studied in the tropical rain forest in southwest China using the diagnostic approach (Wang *et al.* 2009a) and the eddy covariance fluxes data measured at the canopy level. Our study showed the weak correlations between  $f(H)$  and  $h_a$  when fitting this relationship by the BWB model, in which  $g$  was

underestimated at high humidity and overestimated at the mid-to-low range of humidity. The fit of  $f(H)$  to  $D_a$  by the form of Leuning model reduced this bias, but it still could not fully capture the response of  $g$  to  $D_a$  at high humidity. In contrast, The Wang model- $h_a$  and Wang model- $D_a$  that employed the power functions of  $1-h_a$  and  $D_a$  (Equations (4) and (5)) perfectly expressed the relationships of stomatal conductance response to humidity. The model comparison results demonstrated high consistency over the four years from 2003 to 2006. Our results are in general agreement with those in Wang *et al.* (2009a, b) where the latter two models have been tested in three boreal forests in Canada.

The diagnostic theory provides a practical approach to evaluate the models of stomatal conductance response to humidity. Since it is based on the ratio of canopy latent heat and  $\text{CO}_2$  fluxes rather than their real quantities (Stewart 1988; Ewers & Oren *et al.* 2000; Blanken & Black 2004), this reduces the impacts of measurement accuracies and energy closure problems which existed in flux measurements using the eddy-covariance (EC) technique (Barr *et al.* 2006). It works at canopy level which is beneficial for most land surface and hydrology schemes as they operate at canopy level. In our study, we successfully validated this theory in a tropical forest in southwest China. It is worth noting that, in this study, the evaluations of the BWB model and Leuning model were also conducted at the canopy level.

As mentioned earlier, the two models have been tested among diverse species in various biomes. They were both developed based on the data measured at the leaf level in laboratory-controlled environments. This made it difficult to extrapolate them to the canopy level which has a complex structure, heterogeneity of leaf physiological features and spatial variations in canopy microclimate. Although these stomatal conductance models had been up-scaled from leaf to canopy or larger scale for hydrological or climate modelling (Sellers *et al.* 1996; Cox *et al.* 1999), they also involved substantial simplifications and assumptions which could lead to large uncertainties. This is why the BWB model and Leuning model did not perform well in our study.

Furthermore, the model parameters were obtained through best fitting the relationship between the  $f(H)$  and  $h_a$  or  $D_a$ ; it did not consider the fact that the weightings of  $g$  in controlling leaf transpiration and  $\text{CO}_2$  influx varied with environmental conditions. In other words, the same error in

g estimation would have a much larger impact on transpiration simulations under low humidity than under high humidity. The specific humidity deficit, which is the main force in driving leaf transpiration, was large at low humidity. As a result, the best fit between  $f(H)$  and humidity variables made the BWB model and the Leuning model perform poorly.

On the other hand, the main differences between the Wang model- $h_a$  and Wang model- $D_a$  are the forms of  $g$  responding to humidity (use  $1-h_a$  in Wang model- $h_a$  and  $D_a$  in Wang model- $D_a$ ). The forms of both  $1-h_a$  and  $D_a$  represent the differences of humidity to saturated conditions, which reflect the ability of atmospheric evaporative demand. The good performance of the Wang model- $h_a$  and Wang model- $D_a$  implied that stomatal conductance may be much more sensitive to the humidity deficit or water vapour pressure deficit than to the relative humidity itself. Our results were in general agreement with those studies in Lloyd (1991), Wu *et al.* (2000), Blanken & Black (2004), in which  $g$  could be better predicted when replacing  $h_s$  by  $D_s$  in the stomatal conductance models.

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