Carbon and water cycling in a Bornean tropical rainforest under current and future climate scenarios

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Abstract

We examined how the projected increase in atmospheric CO2 and concomitant shifts in air temperature and precipitation affect water and carbon fluxes in an Asian tropical rainforest, using a combination of field measurements, simplified hydrological and carbon models, and Global Climate Model (GCM) projections. The model links the canopy photosynthetic flux with transpiration via a bulk canopy conductance and semi-empirical models of intercellular CO2 concentration, with the transpiration rate determined from a hydrologic balance model. The primary forcing to the hydrologic model are current and projected rainfall statistics. A main novelty in this analysis is that the effect of increased air temperature on vapor pressure deficit (D) and the effects of shifts in precipitation statistics on net radiation are explicitly considered. The model is validated against field measurements conducted in a tropical rainforest in Sarawak, Malaysia under current climate conditions. On the basis of this model and projected shifts in climatic statistics by GCM, we compute the probability distribution of soil moisture and other hydrologic fluxes. Regardless of projected and computed shifts in soil moisture, radiation and mean air temperature, transpiration was not appreciably altered. Despite increases in atmospheric CO2 concentration (Ca) and unchanged transpiration, canopy photosynthesis does not significantly increase if Ci/Ca is assumed constant independent of D (where Ci is the bulk canopy intercellular CO2 concentration). However, photosynthesis increased by a factor of 1.5 if Ci/Ca decreased linearly with D as derived from Leuning stomatal conductance formulation [R. Leuning. Plant Cell Environ 1995;18:339–55]. How elevated atmospheric CO2 alters the relationship between Ci/Ca and D needs to be further investigated under elevated atmospheric CO2 given its consequence on photosynthesis (and concomitant carbon sink) projections.

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1. Introduction

The projected growth in atmospheric greenhouse gases within the coming century, as summarized by the Intergovernmental Panel on Climate Change report (e.g., [19]), will significantly impact global and regional
temperatures with concomitant modifications to precipitation patterns. Tropical rainforests are among the most important biomes in terms of annual primary productivity and water cycling; hence, assessing their sensitivity to potential shifts in global and regional temperatures and precipitation patterns is a necessary first step to quantifying future local, regional, and global carbon and water cycling. Although these forests now cover only 12% of the total land surface [10], they contain about 40% of the carbon in the terrestrial biosphere [63] and are responsible for about 50% of terrestrial gross primary productivity [13]. Also, tropical rainforests are a major source of global land surface evaporation [5] with profound influences on both global and regional climate and hydrological cycling (e.g., [31,45]). This large latent energy fluxes from tropical rainforests is known to influence global atmospheric circulation patterns [50].

Although tropical forests in Southeast Asia are about 17% of the total tropical rainforest area [10], relative deforestation rates [38] and estimated resulting CO2 emissions [20,38] are highest in this region. These forests remain a viable resource for the economies of several Southeast Asian countries such as Malaysia, yet their potential as a carbon sink received much less attention than those of Amazonian rainforests (e.g., [9,12,14, 17,35,39,40,62,64,65]).

What is also lacking is an understanding of how hydrologic changes in future climates might impact the carbon cycling in these tropical rainforests, the subject of this investigation. Climate of the maritime environments in Southeast Asian tropics is quite different from those of environments of South American and Central African tropics. While there are clearly periodic dry periods in South American and Central African tropics, maritime Southeast Asian tropics do not have phase-locked dry period [29] because this climatic condition is formed by a combination of a summer monsoon from the Indian Ocean, a winter monsoon from the Pacific Ocean and the South China Sea, and Madden and Julian Oscillation (MJO). As a result, the solar radiation and the air temperature have small seasonal variations and the annual rainfall is evenly distributed throughout the year [22,29]. However, there are some unpredictable intra-annual dry spells [28] and inter-annual dry sequences [27] that may intensify in future climate.
Intra-annual dry spells, in particular, occur every year and often throughout the year.

Our goal is to investigate how carbon and water cycling of a lowland dipterocarp forest in Southeast Asian humid tropics will respond to current and projected atmospheric CO2 concentration and climate (i.e., air temperature and precipitation patterns). This work builds on an earlier study that investigated how the hydrologic budgets are altered by projected shifts in precipitation only using field measurements, Global Climate Model (GCM) simulation output, and a simplified hydrologic model [26]. In the present study, we go further and use these GCM simulation outputs of current and future air temperature and precipitation statistics, projected atmospheric CO2 concentration, a carbon flux model [24] combined with a simplified hydrological model described in [54,30,52], and field measurements conducted over a 2-year period to address the study goals. Prior to assessing the carbon and water budget for future climate scenarios, the model is first validated with field measurements conducted in a tropical rainforest in Lambir Hills National Park, Sarawak, Malaysia, over a 2-year period, described next.

2. Study site and measurements

While much of the site and instrument description relevant to the hydrologic cycle are presented in [26], a review and description of the carbon flux measurements are provided for completeness.

2.1. Site description

The experiment was carried out in a natural forest in Lambir Hills National Park (4°12’N, 114°02’E), 30 km south of Miri City, Sarawak, Malaysia (Fig. 1). A 4 ha experimental plot at an altitude of 200 m and on a gentle slope (<5°) was used in this project. An 80-m-tall canopy crane with a 75-m-length rotating jib was constructed in the center of this plot to provide access to the upper canopy. Observational stage at 59.0 m high was devoted to eddy-covariance flux measurements. The canopy height surrounding the crane is about 40 m but the height of emergent treetops can reach up to 50 m.

The mean annual rainfall at Miri Airport (4°19’N, 113°59’E), 20 km from the study site, for the period 1968–2001 was around 2740 mm with some seasonal variation. For example, the mean rainfall for September–October–November (SON) was around 880 mm and for March–April–May (MAM) was around 520 mm. The mean annual temperature is around 27 °C with little seasonal variation (e.g., [29]).

The rain forest in this park consists of two types of native vegetation common to the whole Borneo, i.e., mixed dipterocarp forest and tropical heath forest [68]. The former contains various types of dipterocarp trees, which cover 85% of the total park area. The soils consist of red–yellow podzonic soils (Malaysian classification) or ultisols (USDA Soil Taxonomy), with a high sand content (62–72%), an accumulation of nutrient content at the surface horizon, a low pH (4.0–4.3), and a high porosity (54–68%) [23,36].

The leaf area index (LAI) was measured in 2002 using a pair of plant canopy analyzers (LAI-2000, Li-Cor, Lincoln, NE) every 5 m on a 30 × 30 m² subplot. The LAI ranged from 4.8 to 6.8 m² m⁻² with a mean of 6.2 m² m⁻² [28]. The amount of monthly litter-fall was evenly distributed throughout the year suggesting minor variations in LAI.

2.2. Micrometeorological and soil moisture measurements

The following instruments were installed at the top of the crane, 85.8 m from the forest floor: a solar radiometer (MS401, EKO, Tokyo, Japan), an infrared radiometer (Model PIR, Epply, Newport, RI), and a tipping bucket rain gauge (RS102, Ogasawara Keiki, Tokyo, Japan). At a separate tower located some 100 m south from the crane, upward short-wave radiation and long-wave radiation were measured using a solar radiometer (CM06E, Kipp & Zonen, Delft, Netherlands) and an infrared radiometer (Model PIR, Epply, Newport, RI) installed upside down since December 15, 2001. Samples for radiation were taken every 5 s and an averaging period of 10 min was used (CR10X datalogger, Campbell Scientific, Logan, UT). These measurements were used to compute net radiation (Rn; W m⁻²). Maximum and average total daily solar radiation was 24.5 and 16.7 MJ m⁻² d⁻¹, respectively, and maximum and average total daily net radiation was 18.2 and 11.5 MJ m⁻² d⁻¹, respectively.

At the subplot for the in-canopy microclimate measurements, we sampled mean air temperature and humidity at heights of 41.5, 31.5, 21.5, 11.5, 6.5 and 1.5
A three-dimensional sonic anemometer (DA-600, Kaijo, Tokyo, Japan) was installed at 60.2 m, i.e., 20 m above the mean canopy height. Co-located with the sonic anemometer is an open-path CO2/H2O analyzer (LI-7500, Jo,Tokyo, Japan) was installed at 60.2 m, i.e., 20 m above

2.3. Flux measurements

A three-dimensional sonic anemometer (DA-600, Kaijo, Tokyo, Japan) was installed at 60.2 m, i.e., 20 m above

The CO2 concentration profile measurement within canopy was carried out about 70 m from the crane. Air samples were drawn at 1.5, 6.5, 11.5, 21.5, 31.5 and 41.5 m above ground level using diaphragm pumps and an auto solenoid switching system, and the CO2 concentration was measured using a closed-path CO2 infrared gas analyzer (LI-800, Li-Cor, Lincoln, NE). The CO2 channels were automatically calibrated every 10 Hz. All variances and covariances required for eddy-covariance flux estimates were computed over a 30-min averaging interval using the procedure described in [28].

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2.4. Derivation of canopy transpiration and photosynthetic rate

Canopy transpiration rate can be obtained as above-canopy H2O flux when the canopy was dry. Net ecosystem CO2 exchange (NEE) was derived as the sum of the above-canopy CO2 flux, which is obtained using the eddy covariance system above the canopy, and the within-canopy storage flux, which is determined by quantifying the rate of change of the CO2 concentration of the air column within the canopy. Maximum and average daily transpiration rates during the measurement period were 5.09 and 2.52 mm d⁻¹, respectively, and daytime average NEE and its maximum value were −7.06 and −12.74 μmol m⁻² s⁻¹, respectively (negative values denote net ecosystem CO2 uptake).

Power system failure and exclusion of unreliable data limited the amount of runs collected from the flux measurement system. Available data of the above-canopy CO2/H2O fluxes and the NEE were 41% and 30% of the total possible period between June 15, 2001 and November 15, 2002, respectively. We filled data gaps and replaced unreliable data (e.g., data obtained when rainfall occurred) using the light-response curve (Saitoh et al., unpublished data) and according to Kumagai et al. [29]. In addition, we obtained the daytime ecosystem respiration (Reco) from the intercept of the light-response curve (average daytime Reco: 8.83 μmol m⁻² s⁻¹) and then proceeded to derive a relationship between the daytime Reco and θ as given by (Saitoh et al., unpublished data): 0.36 mol m⁻² d⁻¹ (0 ≤ θ < 0.5) and 0.42 mol m⁻² d⁻¹ (0.5 ≤ θ ≤ 1.0).

At this site no above-ground biomass respiration (Rag) measurements were collected, and we used a daily average Rag of 1.9 μmol m⁻² s⁻¹ estimated using the functional model for tropical rainforest woody tissue respiration [42] and assuming that wood respiration is nearly equal to leaf respiration [37]. The daytime Reco expressed as Rsol + Rag was 7.6 μmol m⁻² s⁻¹. Taking uncertainties in estimating Rag into account, daytime Reco obtained from the result of eddy-covariance flux measurement (i.e., the light response curve) and from Rsol + Rag is sufficiently close. Hence, we concluded the Reco from the eddy-covariance flux measurement is representative of ecosystem-scale values. As a result, canopy photosynthetic rate can be obtained by subtracting the daytime Reco from the daytime NEE (note that negative values denote net ecosystem CO2 uptake).

While precipitation, solar radiation, and air temperature have small seasonal variations, intra-annual dry spells have been reported [28]. As the intra-annual dry spells often occur throughout the year, transpiration rate is likely to be overly sensitive to the soil moisture condition.
3. Methodology

We discuss first the carbon and water cycling model, as well as its parameterization and testing for this experiment, and then proceed to discuss its usage for assessing shifts in the carbon and water vapor fluxes following projected increases in atmospheric CO2 concentration and concomitant shifts in climatic factors such as precipitation, air temperature and humidity and net radiation. For the model testing, climatic factors time series were measured and used to drive the model calculations; however, in our model simulations for future climates, only precipitation statistics and potential increment in atmospheric CO2 concentration and temperature were available thereby necessitating a stochastic treatment. The generation of stochastic precipitation and the other climatic factors time series, and the connections to GCM simulation outputs are also discussed.

The structure of the carbon and water cycling model is schematically shown in Fig. 2a, illustrating all the linkages between meteorological inputs and model outputs.

3.1. Carbon flux modeling

The daily canopy photosynthetic rate $A$ (mol m$^{-2}$ d$^{-1}$) can be obtained from the water use efficiency (WUE; $\mu$molCO$_2$ mmol$^{-1}$H$_2$O) and the daily transpiration rate ($T_r$; mm d$^{-1}$) using [24]

$$A = \text{WUE} \cdot \kappa_1 T_r$$  \hspace{1cm} (1)

in which

$$\text{WUE} = \frac{C_i (1 - \frac{C_i}{C_a})}{1.6 \kappa_2 D}$$  \hspace{1cm} (2)

where $C_a$ and $C_i$ are the ambient and the bulk canopy intercellular CO2 concentration (ppmv), respectively, and $D$ is the vapor pressure deficit (kPa). $\kappa_1$ and $\kappa_2$ are unit adjustment coefficients ($5.56 \times 10^4$ mmol m$^{-2}$ mm$^{-1}$ and 9.87 mmol mol$^{-1}$ kPa$^{-1}$, respectively). The sign convention for photosynthesis is that CO2 uptake by plants is positive. With $T_r$ predicted from the hydrologic model (see next section) and measured $C_a$, the parameters $R_C$, $a$ and $b$ were estimated using non-linear least-squares regression between modeled and eddy-covariance observed $A$. Based on our regression analysis, we obtained $R_C$ of 0.88, $a$ of 0.99 and $b$ of 0.20. These values are reasonable for “canopy-scale surface” $C_i/C_a$ calculated from the relationship between maximum surface CO2 assimilation rate and maximum surface conductance for a wide range of vegetation types (see Fig. 3C in [60]). Also, as discussed in [24], $a$ must be unity, a fact that is independently reproduced by our optimization.

3.2. The hydrologic model

As evidenced from the above derivation, predicting $T_r$ is crucial for computing $A$. Much of the hydrologic model derivation, which was used to predict $T_r$, was presented in [26]; however, for completeness, we briefly recall here the relevant equations and assumptions.
For gentle slopes, where lateral movement can be neglected, the vertically integrated continuity equation is given by

\[ \frac{ds}{dt} = P - T_r - I_c - Q, \]  

(5)

where \( s \) is the volumetric soil moisture content averaged over the root zone (\( \text{mm} \)), \( t \) is the time (\( \text{day} \)), \( P \) is the precipitation (\( \text{mm} \text{d}^{-1} \)), \( T_r \) is, as before, the transpiration \( (\text{mm} \text{d}^{-1}) \), \( I_c \) is the interception \( (\text{mm} \text{d}^{-1}) \) and \( Q \) is the leakage loss \( (\text{mm} \text{d}^{-1}) \) from the soil layer. Given that the root zone is shallow, we assume that the top 50 cm soil layer captures much of the root zone water uptake activity. Also, we assume that \( Q \) includes runoff, and that soil evaporation is insignificant when compared to the total transpiration flux (given the high LAI at the site, this assumption is reasonable) (e.g., [25]). The parameterizations of \( T_r, I_c, \) and \( Q \) for the site are described next.

### 3.3. Transpiration modeling

The primary forcing variable for transpiration in the tropics is net available energy. Hence, we use a modified Priestley and Taylor [53] expression to compute daily transpiration rate \( T_r \) (\( \text{mm} \text{day}^{-1} \)) given by

\[ T_r = \kappa_3 f \Delta \frac{\Delta}{L \rho_w (\Delta + \gamma)} R_u, \]  

(6)

where \( \kappa_3 \) is the Priestley–Taylor coefficient, \( \Delta \) is the rate of change of saturation water vapor pressure with temperature \( (\text{Pa} \text{K}^{-1}) \), \( L \) is the latent heat of vaporization of water \( (\text{J} \text{kg}^{-1}) \), \( \rho_w \) is the density of water \( (1000 \text{ kg} \text{m}^{-3}) \), \( \gamma \) is the psychrometric constant \( (66.5 \text{ Pa} \text{K}^{-1}) \), and \( R_u \) is the daily net radiation above the canopy \( (\text{W} \text{m}^{-2}) \). \( \kappa_3 \) is a unit conversion factor \( (8.64 \times 10^7 \text{ mm} \text{s}^{-1} \text{ d}^{-1}) \). Thermodynamic variables \( \Delta \) and \( L \) are calculated based on mean air temperature averaged over daylight hours. Daily net radiation was obtained by averaging hourly values. In Eq. (6), \( f \) is the limiting factor related to a transpiration plateau at high \( D \) (e.g., [43]). Using a function for stomatal response to increasing \( D \) from [48,49], we assume a simplified form \( f \) given by

\[ f = \begin{cases} 1 & \text{for } D < 1, \\ 1 - 0.6 \ln D & \text{for } D \geq 1. \end{cases} \]  

(7)

The model formulation in [48,49] was shown to be reasonably accurate for a wide range of ecosystem types and \( D \) ranges. A major uncertainty in the transpiration model is which, for forested ecosystems, is usually less than its typical 1.26 value because of additional boundary layer, leaf, xylem, and root resistances. We conducted a detailed sensitivity analysis in [26] and demonstrated that the best estimator of \( \kappa_3 \) is

\[ \kappa_3 = 0.49 \Theta + 0.52 \]  

(8)

### 3.4. Interception modeling

In [26], the relationships between daily rainfall \( P \), throughfall \( TF \) and stemflow \( SF \) were described as linear regression equations, and daily interception \( I_c \) was related to \( P \) after subtracting both \( TF \) and \( SF \) from \( P \) to give

\[ I_c = \begin{cases} P & \text{for } 0 \leq P < 0.90, \\ 0.13P + 0.78 & \text{for } 0.90 \leq P < 3.91, \\ 0.084P + 0.96 & \text{for } 3.91 \leq P. \end{cases} \]  

(9)

### 3.5. Leakage losses modeling

In [26], the leakage loss rate \( Q \) was parameterized using

\[ Q = K_s \Theta^b, \]  

(10)

where \( K_s \) is the saturated hydraulic conductivity \( (\text{mm} \text{d}^{-1}) \) and \( b \) the fitted parameter. The parameters \( K_s \) and \( b \) were estimated using non-linear least-squares regression between \( s \) calculated from Eq. (5) and observed \( s \). Based on our regression analysis, we obtained a \( K_s \) of 33.4, typical for loam and sandy loam, and \( b \) of 5.3, typical for wet sandy clay loam and dry clay [4]. The minor differences between \( K_s \) and \( b \) computed here and those reported in [26] are strictly due to the differences in the \( T_r \) model.

Details on the ponding and infiltration calculations are discussed in [26]. When testing the model, measured time series of the climatic factors (precipitation, radiation, temperature, humidity and \( \text{CO}_2 \)) are used to drive the calculations. However, for future climate simulations, synthetic climatic drivers time series must be constructed as described next.

### 3.6. Simulations of precipitation

Current and future climatic factors time series were constructed using relationships between precipitation and other climatic factors obtained in the 2001–2002 observation period, rainfall records collected in 1968–2001 and GCM outputs for air temperature and precipitation for 2070–2100 (details described later). As a result, current and future time series (i.e., the 1968–2001 and the 2070–2100) of each hydrological component and carbon flow at the site can be computed. From the simulated time series of each hydrological components and carbon flow, their statistics for the period 1968–2001 and 2070 can then be calculated. We then examine shifts in the statistics of these hydrological components and carbon flows based on these anticipated changes in the climatic (or forcing) factors.

It is necessary to first construct the rainfall time series because they are needed for constructing other climatic
factors. Current and future rainfall time series (i.e., the 1968–2001 and the 2070–2100) were constructed as the series of random numbers generated according to probability distributions representing the 1968–2001 and the 2070–2100 rainfall characteristics at the site. As discussed in [26], we assumed the frequency and amounts of rainfall events to be stochastic variables, in which interval between precipitation events, \( \tau \) (day), is expressed as an exponential distribution given by

\[ f_\tau(\tau) = \lambda \exp(-\lambda \tau) \quad \text{for} \quad \tau \geq 0, \]  

(11)

where \( 1/\lambda \) is the mean interval time between rainfall events (day). The amount of rainfall when rainfall occurs, \( h \) (mm), is also assumed to be an independent random variable, expressed by an exponential probability density function [30]:

\[ f_h(h) = \frac{1}{\eta} \exp\left(-\frac{1}{\eta}h\right) \quad \text{for} \quad h \geq 0, \]  

(12)

where \( \eta \) is the mean depth of rainfall events (mm).

For the 1968–2001 rainfall scenario, a long-term data record obtained at Miri Airport was used to assess the descriptive skill of the above precipitation model. For the 2070–2100 rainfall scenarios, a number of transient climate GCM simulations from the Hadley Centre for Climate Prediction and Research, available through a public website, were used. The 2070–2100 time series of climatic factors at coordinates (2°30’–5°N, 112°30’–116°15’E) was constructed from the HadCM3 run (e.g., [11]). The Hadley Centre offers climate change predictions formulated as differences between current climate, conventionally defined as 1960–1990, and the climate at the end of the 21st century, taken to be 2070–2100. As in [26], we used average precipitation changes in the period 2070–2100 for each of the four seasons December–February (DJF), March–May (MAM), June–August (JJA) and September–November (SON) and obtained average rainfall in periods 1968–2001 and 2070–2100, respectively, for each season (Table 1). The Hadley Centre projected precipitation shifts for this region (i.e., comparing the climate in 1960–1990 with the climate in 2070–2100) are drier DJF (~180 mm), little change in MAM (~20 mm), wetter JJA (~70 mm), and wetter SON (~140 mm). Parameters \( 1/\lambda \) and \( \eta \) in 2070–2100 were obtained, using the total amount of rainfall \( P_{\text{season}} \) (mm) for each season using

\[ P_{\text{season}} = d_{\text{season}} \eta \lambda, \]

(13)

where \( d_{\text{season}} \) is the number of days in each season (day).

We constructed three types of rainfall scenarios for 2070–2100 (Table 1). Rainfall scenario 2070–2100 A, which computes \( 1/\lambda \) for the 2070–2100 precipitation, but retains \( \eta \) for 1968–2001. Rainfall scenario 2070–2100 B, which computes \( \eta \) for 2070–2100, but retains \( 1/\lambda \) as in 1968–2001. That is scenarios 2070–2100 A and B assume that future changes in rainfall are caused entirely by changes in rainfall frequency or rainfall depth. In reality, changes in precipitation are due to both frequency and depth. For simulation purposes, it is more constructive to evaluate these two “end members” as agents causing precipitation shifts by assigning the entire shift to be either frequency or depth. To ensure that “no surprises” exist at some intermediate state, we also constructed a rainfall scenario 2070–2100 C as the “intermediate” scenario between these two end members, which computes \( 1/\lambda \) and \( \eta \) as mean values between in 1968–2001 and in 2070–2100 A and B, respectively.

We assumed that a single storm event does not exceed a day, and that plural storm events during a day can be

Table 1

<table>
<thead>
<tr>
<th>Scenario</th>
<th>DJF</th>
<th>MAM</th>
<th>JJA</th>
<th>SON</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average rainfall (mm/d)</td>
<td>1.76</td>
<td>1.98</td>
<td>2.05</td>
<td>1.42</td>
</tr>
<tr>
<td>( 1/\lambda ) (day)</td>
<td>8.7</td>
<td>12.0</td>
<td>12.4</td>
<td>13.8</td>
</tr>
<tr>
<td>( \eta ) (mm)</td>
<td>14.5</td>
<td>12.0</td>
<td>14.1</td>
<td>15.3</td>
</tr>
<tr>
<td>1968–2001</td>
<td>3.87</td>
<td>5.85</td>
<td>7.70</td>
<td>9.72</td>
</tr>
<tr>
<td>Average rainfall (mm/d)</td>
<td>1.73</td>
<td>2.12</td>
<td>1.82</td>
<td>1.57</td>
</tr>
<tr>
<td>( 1/\lambda ) (day)</td>
<td>14.5</td>
<td>12.0</td>
<td>14.1</td>
<td>15.3</td>
</tr>
<tr>
<td>( \eta ) (mm)</td>
<td>12.8</td>
<td>12.0</td>
<td>14.7</td>
<td>16.5</td>
</tr>
<tr>
<td>2070–2100</td>
<td>6.37</td>
<td>5.65</td>
<td>8.45</td>
<td>11.22</td>
</tr>
<tr>
<td>Average rainfall (mm/d)</td>
<td>2.28</td>
<td>2.12</td>
<td>1.67</td>
<td>1.36</td>
</tr>
<tr>
<td>A</td>
<td>10.9</td>
<td>12.1</td>
<td>15.6</td>
<td>17.6</td>
</tr>
<tr>
<td>B</td>
<td>2.00</td>
<td>2.12</td>
<td>1.74</td>
<td>1.47</td>
</tr>
<tr>
<td>C</td>
<td>12.8</td>
<td>12.0</td>
<td>14.7</td>
<td>16.5</td>
</tr>
</tbody>
</table>

\( ^a \) See Eqs. (11) and (12). DJF, December–January–February; MAM, March–April–May; JJA, June–July–August; SON, September–October–November.

\( ^b \) The measurement period September 1, 2001 to August 31, 2002. Average annual rainfall is 2449.5 mm.

\( ^c \) Average annual rainfall is 2884.4 mm.

\( ^d \) Average annual rainfall is 2888.5 mm.

\( ^e \) Values of \( \eta \) are the same as in the 1968–2001 scenario.

\( ^f \) Values of \( 1/\lambda \) are the same as in the 1968–2001 scenario.
lumped together as a single daily storm. Such a simplifying assumption may be reasonable here because single storm events exceeding one day seldom occur at least in the historical record at Miri Airport.

3.7 Current climatic scenario

The current atmospheric CO$_2$ concentration (i.e., the 1968–2001) was assumed to be 360 ppmv. From the 2001–2002 observation results, we obtained relationships between precipitation, $P$, and the other climatic factors as follows (see Fig. 2b): (1) In [26], $R_n$ was related to $P$ via Gaussian random variables with parameters (mean, $\mu$, and standard deviation, $\sigma$) that vary with $P$, that is, $0 \leq P < 10$ ($\mu = 145.0$, $\sigma = 33.7$), $10 \leq P < 20$ ($\mu = 108.8$, $\sigma = 4.8$) and $20 \leq P$ ($\mu = 92.3$, $\sigma = 22.4$); (2) Daytime average air temperature, $T_a$ ($^\circ$C), and relative humidity, RH, were related to $R_n$ through linear regression models [$T_a = 0.0239R_n + 23.48$ ($R^2 = 0.65$) and $RH = -0.0015R_n + 1.0$ ($R^2 = 0.70$), respectively]. (3) An exponential model was fitted to related $D$ to $R_n$ ($D = 0.112 \exp(0.0118R_n)$, $R^2 = 0.75$). Using the above relationships between $P$ and other climatic factors and the 1968–2001 rainfall scenario, the 1968–2001 climatic factors time series was constructed.

3.8 Future climatic scenarios

The HadCM3 run assumes that future emissions of greenhouse gases will follow the IPCC-IS92a scenario [18], in which the atmospheric concentration of CO$_2$ increases by about 1% per year. According to the IPCC-IS92a scenario, the atmospheric CO$_2$ concentrations in 2070 and 2100 are 579.2 and 711.7 ppmv, respectively. Hence, we assumed the 2070–2100 atmospheric CO$_2$ concentration to be 645 ppmv, a mean value between in 2070 and 2100.

Comparing the climate in 1960–1990 with the climate in 2070–2100 for this region, the Hadley Centre projected that surface air temperature increases by 4 $^\circ$C for all of the four seasons DJF, MAM, JJA and SON. The warmer climate experiments using a wide variety of GCMs suggest that unchanged relative humidity is realistic [1,21,61,69]. Hence, the modified climate in 2070–2100 might consist of an attendant increase in atmospheric water vapor concentration but roughly retains its relative humidity as in 1960–1990.

For the 2070–2100 scenarios, we determined the climatic factors, such as $R_n'$, $T_a'$ and $D$ by following procedures (see Fig. 2b): (1) From the 2070–2100 A, B and C rainfall scenarios, $R_n'$ was estimated using the same method (i.e., the Gaussian random numbers generation) as when $R_n$ in the 1968–2001 climatic scenario was determined. (2) From this estimates of $R_n'$, $T_a'$ was initially estimated using the relationship between $T_a$ and $R_n$ derived from the 2001–2002 observations. Also, RH was estimated using the relationship between RH and $R_n$ (though the change in RH was minor). (3) In order to obtain elevated regional air temperature, new estimates of $T_a'$ were made by adding 4 $^\circ$C to the initial estimates of $T_a$. (4) From $D = e_{sat}(T_a')/(1 - RH)$ (where $e_{sat}(T_a)$ is the saturation vapor pressure at $T_a'$, in kPa), $D$ under the condition of air temperature increase was computed.

As a result, we obtained the 2070–2100 A, B and C scenarios as future climatic scenarios. Before discussing future carbon and water cycling simulations we evaluate the predictive skills of the simplified carbon and water cycling model next.

4. Model results

4.1 Model evaluation

Fig. 3 compares calculated cumulative $T_i$ ($\Sigma T_i$) and $A$ ($\Sigma A$) against measurements for June 15, 2001 to November 15, 2002. The model well reproduces measured $\Sigma T_i$ and $\Sigma A$ despite all the simplifying assumptions. Calculated $\Sigma T_i$ at the end of the observation period was only 4% higher than the observed value (Fig. 3a). While cal-

![Fig. 3. Comparisons between measured and modeled (a) cumulative transpiration rate and (b) cumulative photosynthetic rate (dotted line; the Norman model, solid line; the Leuning model) for June 15, 2001 to November 15, 2002.](image-url)
culated \( \Sigma A \) in the Norman model agreed well with the observed value (within 3%), the slope of calculated \( \Sigma A \) in the Leuning model was not statistically different from unity (Fig. 3b). This suggests that despite the small discrepancies between observed and calculated values in the Norman model, the calculation for \( A \) under current climatic conditions is robust to variations in \( D \).

Since the reproduction of \( s \) is important because \( s \) is fundamental to estimating \( A \) through its effect on \( a \) and \( T_r \), it is necessary to compare how well the measured and modeled \( s \) agree (Fig. 4).

### 4.2. Carbon and water balances

The model estimated annual \( T_r \) and \( I_c \) in the measurement period 2001–2002 to be 951.3 and 386.2 mm, respectively, suggesting that \( I_c \) can be up to 40% of \( T_r \) (Table 2). The ratio of \( I_c \) to annual precipitation (\( P \)) was 16%. Evapotranspiration, computed as the sum of \( T_r \) and \( I_c \) for the 1968–2001 scenario (hereinafter referred to as 1968) were 998.6 and 408.5 mm, respectively (Table 2). Note that total \( P \) in 2001–2002 was about 440 mm less than in 1968 scenario. As a result, evapotranspiration and its ratio to total \( P \) in 1968 scenario, which is the “standard” period, were 1407.1 mm and about 49%, respectively. Evapotranspiration studies by Brujinzeel [3] for humid tropical forests suggests that: (1) annual \( T_r \) was, on average, 1045 mm (range 885–1285 mm), (2) \( I_c \) was, on average, 13% of incident \( P \) (range between 4.5% and 22%), and (3) annual evapotranspiration ranged from 1310 to 1500 mm. Our values for evapotranspiration and interception losses for both 2001–2002 and 1968 scenario are comparable to those reported values. Although the majority of \( R_n \) was transformed into latent heat (LE) for both 2001–2002 (78%) and 1968 scenario (82%), LE positively correlated with \( P \) (Table 2). Interestingly, most measurements on the fraction of \( R_n \) converted to LE = (LE/\( R_n \) reported for other tropical forests did not consider the evaporation from the wet canopy. Our results included wet canopy evaporation in the energy partitioning. When we calculated LE using only \( T_r \), annual averaged LE/\( R_n \) in 2001–2002 and 1968 scenario were 0.55 and 0.58, respectively. Our LE/\( R_n \) for the dry year (i.e., 2001–2002) and the standard year (i.e., 1968 scenario) correspond to LE/\( R_n \) measurements collected during the dry and the transition seasons in the Amazonian tropical forests [40,65], respectively.

There were little changes in annual \( P \) between the scenario 1968 and in the future scenarios 2070–2100A, 2070–2100B and 2070–2100C (hereinafter referred to as A, B and C, respectively) thereby in annual \( I_c \), while annual \( T_r \) decreased by about 20 mm and annual \( Q \) increased by about 30 mm in the future scenarios: some compensation emerged (Table 2). According to Kumagai et al. [26], seasonal shift in each hydrologic component for the future scenarios introduced some cancellation, that is, on annual timescales, all hydrologic components experienced minor changes under projected precipitation scenarios. However, in the future scenarios of this study, owing to a minor decrease in annual \( T_r \) caused by an increase in \( D \), annual \( Q \) mildly increased. Furthermore, the computed \( R_n \) for all the scenarios were comparable. Hence, the year total LE/\( R_n \) for future scenarios hardly changed (Table 2). Although some differences in hydrologic components among the future scenarios were observed at seasonal timescales, they dis-

<table>
<thead>
<tr>
<th>Scenario</th>
<th>( P ) (mm)</th>
<th>( T_r ) (mm)</th>
<th>( I_c ) (mm)</th>
<th>( Q ) (mm)</th>
<th>( R_n ) (MJ/m² d)</th>
<th>LE/( R_n )</th>
<th>( A ) (tC/ha y)</th>
</tr>
</thead>
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<tr>
<td>2001–2002</td>
<td>2449.5</td>
<td>951.3</td>
<td>386.2</td>
<td>1041.4</td>
<td>11.50</td>
<td>0.78</td>
<td>33.3</td>
</tr>
<tr>
<td>1968–2001</td>
<td>2884.4</td>
<td>998.6</td>
<td>408.5</td>
<td>1477.5</td>
<td>11.48</td>
<td>0.82</td>
<td>32.4</td>
</tr>
<tr>
<td>2070–2100A</td>
<td>2891.5</td>
<td>975.9</td>
<td>408.1</td>
<td>1507.5</td>
<td>11.50</td>
<td>0.80</td>
<td>36.4</td>
</tr>
<tr>
<td>2070–2100B</td>
<td>2891.5</td>
<td>978.8</td>
<td>408.9</td>
<td>1504.0</td>
<td>11.49</td>
<td>0.81</td>
<td>36.5</td>
</tr>
<tr>
<td>2070–2100C</td>
<td>2891.5</td>
<td>976.4</td>
<td>406.9</td>
<td>1507.9</td>
<td>11.49</td>
<td>0.80</td>
<td>36.4</td>
</tr>
</tbody>
</table>

\( ^a \) See Table 1.

\( ^b \) Latent heat flux.

\( ^c \) NR, the Norman model; LU, the Leuning model.
appeared at annual timescales (see [26]). An immediate consequence of the computed $T_r$ not significantly changing in all three future climate scenarios is that all the changes in photosynthesis are attributed to changes in WUE, discussed next.

Annual $A$ estimated using the Norman model [46] and the Leuning model [33] for the measurement period 2001–2002 (33.3 and 32.3 tC ha$^{-1}$ yr$^{-1}$, respectively) were not significantly different from those for scenario 1968 (32.4 and 33.7 tC ha$^{-1}$ yr$^{-1}$, respectively) (Table 2). Those values are comparable to the 30.4 tC ha$^{-1}$ yr$^{-1}$ reported for an Amazonian tropical rainforest [37]. Annual $A$ in the scenario 1968 calculated using the Norman and the Leuning models were also comparable (Table 2). However, when using the Norman model for the future scenarios a slight increase in annual $A$ was obtained. On the other hand, annual $A$ calculated by the Leuning model markedly increased for the future scenarios (Table 2). For $A$ in the future scenarios computed by the Norman model, marked increases in $D$ reduced WUE thereby eliminating the expected enhancement in WUE attributed to increased $C_a$. Mathematically, if $R_C$ ($\approx 0.88$) is constant,

$$WUE = \frac{C_a(1 - R_C)}{1.6 \times 9.87 D} = \frac{C_a}{1.6 \times 9.87} \cdot \frac{0.12}{D}.$$ 

In the Leuning model, $C_l/C_a$ linearly decreases with increasing $D$ thereby offsetting the expected reduction in WUE by increased $D$. Hence, for the Leuning model, WUE was primarily affected by an increase in $C_a$ only. Mathematically, the Leuning model with parameters $a \approx 1$ and $b = 0.2$ leads to a WUE that is independent of $D$ and is given by

$$WUE = \frac{C_a(1 - (0.99 - 0.2D))}{1.6 \times 9.87 D} = \frac{C_a}{1.6 \times 9.87} \cdot \frac{0.2}{D}.$$ 

which linearly increases with increasing $C_a$.

Again, on annual timescales, the differences in annual $A$ among scenarios A, B and C were negligible.

### 4.3. Soil moisture

Ensemble seasonal probability distributions of soil moisture content ($p(s)$) for scenarios 1968, A, B and C are compared in Fig. 5. $p(s)$ for the measurement period 2001–2002 is also compared. Note that for SON in scenario 1968 and 2001–2002 which have similar rainfall (see Table 1), $p(s)$ is about the same despite lower $s$ tail in 2001 caused by preceding drought (Fig. 5d). Departures in Fig. 5 for the DJF, JJA and whole year $p(s)$ are primarily due to the frequent droughts in 2001–2002 (i.e., flatter tails) when compared to ensemble record of scenario 1968 (see Table 1).

Decrease in heavy rainfall under scenario B does not affect $p(s)$, while decrease in rainfall frequency increases the dry mode (Fig. 5a). Under the condition of increased rainfall, some cancellations occur—for example, storms with smaller (but more frequent) depths are likely to be intercepted; however, storms with bigger depths (but less frequent) contribute to the drainage. Hence, $p(s)$ appears more robust to future shifts in precipitation when compared to interception or drainage (see [26]).

### 4.4. Evapotranspiration

Seasonal cumulative $T_r$ ($\Sigma T_r$) and $T_r + I_c$ ($\Sigma (T_r + I_c)$) for the measurement period 2001–2002, current scenario 1968, and future scenarios A, B and C are compared in Fig. 6.
\( \Sigma T_r \) and \( \Sigma (T_r + I_c) \) calculated for 2001–2002 were almost within the range of those calculated using 1968 scenario. However, owing to the frequent droughts in 2001–2002, \( \Sigma T_r \) and \( \Sigma (T_r + I_c) \) calculated for 2001–2002 were almost identical to the lower values of \( \Sigma T_r \) and \( \Sigma (T_r + I_c) \) for scenario 1968 in DJF and JJA (Fig. 6).

For any future scenario, \( \Sigma T_r \) was not appreciably altered in each of the four seasons (Fig. 6).

Decrease in rainfall amount in DJF reduced \( I_c \) under the future scenarios A, B and C (Fig. 6). For scenario A, the more frequent light rainfall events were almost perfectly intercepted by the canopy, while under scenario B, the heavier (though less frequent storms) increased \( I_c \) (for SON in Fig. 6). For DJF, decreases in \( I_c \) determined decreases in \( \Sigma (T_r + I_c) \), while for each of the other seasons, \( \Sigma (T_r + I_c) \) was not appreciably altered.

4.5. Canopy photosynthesis

Figs. 7 and 8 show seasonal cumulative \( A \) (\( \Sigma A \)) for the measurement period 2001–2002 and scenarios 1968, A, B and C, calculated using the Norman and the Leuning models, respectively.

While \( \Sigma A \) calculated by the Leuning model for 2001–2002 was almost within the range of those for scenario 1968 in any season (Fig. 8), in MAM and JJA there were large discrepancies between \( \Sigma A \) calculated by the Norman model for 2001–2002 and for scenario 1968 (Fig. 7). Note that for either model, considering annual \( \Sigma A \), the discrepancies are reduced because parameter \( C_i/C_a \) was determined using yearlong climatic data. Also, on seasonal timescale, using the Leuning model, the discrepancies between \( \Sigma A \) in 2001–2002 and in scenario 1968 were minimized because the \( C_i/C_a \) can respond to seasonal variations in \( D \).

For either model, the projected growth in \( C_a \) (i.e., 645 ppmv) increased \( \Sigma A \) for all seasons. However, when using the Norman model, \( \Sigma A \) did not increase under future scenarios (Fig. 7). The \( \Sigma A \) calculated by the Leuning model increased up to 170% (Fig. 8). This suggests that for the Norman model (and constant transpiration), an increase in \( D \) roughly cancels the increase.
in WUE due to increased $C_a$ thereby resulting in a near-constant $\Sigma A$.

The $C_i/C_a$ estimated using the Norman model under all scenarios for $A$ estimates was 0.88 (Table 3). However, using the Leuning model, although the estimated $C_i/C_a$ in scenario 1968 for $A$ were almost the same as values estimated using the Norman model (0.87 ± 0.056), the $C_i/C_a$ in future scenarios A, B and C were significantly reduced (0.81 ± 0.059) because of increases in $D$ (Table 3). As a result, using the Leuning model for future scenarios, increases in $\Sigma A$ for all season were very large (Fig. 8).

5. Discussion and conclusions

In a previous study [26], how future shifts in precipitation resulting from an increase in global temperature affected water reservoirs and fluxes within an Asian tropical rainforest was examined using a combination of field measurements, simplified water balance models, and GCM projections of precipitation. In the present study, we have examined how the projected increase in atmospheric CO$_2$ and its concomitant shifts in air temperature, added to shifts in precipitation affect both water fluxes and photosynthesis within an Asian tropical rainforest. We used carbon flux model combined with a simplified hydrological model already developed and tested for this region and GCM projections of air temperature to address the study objective. The field measurements permitted us to derive key relationships for present-day climate that tie the “forcing” term with parameters or state variables. For example, the field data were used to derive relationships between precipitation and variability in net radiation, air temperature and air humidity, between transpiration and extractable water content, between precipitation and interception, the drainage flow parameters, and the parameters for describing $C_i/C_a$.

The Hadley Centre projected precipitation shifts for this region in 2070–2100 are drier DJF, little change in MAM, wetter JJA, and wetter SON compared to the climate in 1968–2001. We assumed that this shift occurs in one of the two ways: change in precipitation depth or change in precipitation frequency. In reality, both frequency and depth are likely to change; thus, by exploring the “end members” and an “intermediate” precipitation shift scenarios, we can quantify the expected changes in hydrologic fluxes and reservoirs. Based on climate models relative humidity appears invariant to changes in greenhouse warming (e.g., [1,21,61,69]). This invariance in relative humidity, when combined with a 4 °C temperature increase leads to a concomitant increase in water vapor pressure deficit that affects both water use efficiency, and, to a lesser extend transpiration for the site.

The probability distribution of soil moisture ($p(s)$) is sensitive to a decrease in precipitation, in part because smaller depth (but more frequent) precipitation events are efficiently intercepted by the ecosystem. On the other hand, $p(s)$ is robust to an increase in precipitation because larger depth (but less frequent) precipitation events increase primarily the drainage. Regardless of shifts in precipitation (and hence shifts in soil moisture), radiation and mean air temperature, transpiration is not appreciably altered. This lack of sensitivity of transpiration to increases in vapor pressure deficit ($D$) is due to
the fact that only a $D$ exceeding 1 kPa will reduce stomatal conductance. Despite increases in atmospheric CO$_2$ concentration and unchanged transpiration, the results for canopy photosynthesis strongly depend on how $C_i/C_a$ will respond to $D$. In the case of a constant $C_i/C_a$ or even a $C_i/C_a$ that varies with relative humidity (RH) [24] as is the case with the widely used Ball–Berry formulation [6], given by

$$\frac{C_i}{C_a} \approx 1 - \frac{1}{m \cdot RH}$$  \hspace{1cm} (14)

(where $m$ is the Ball–Berry slope parameter), much of the water use efficiency (WUE) enhancement due to elevated atmospheric CO$_2$ will be counteracted by the increase in $D$. The latter increase is attributed to a constant RH and a 4 °C warmer climate. On the other hand, if $C_i/C_a$ linearly varies with $D$, as is the case for the Leuning model, WUE becomes independent of $D$ and any increase in atmospheric CO$_2$ results in a proportional increase in WUE and photosynthesis if transpiration is unaltered.

In general, under elevated CO$_2$, CO$_2$ uptake of forest canopies is expected to increase as demonstrated by the FACE experiment in a Southeastern United States pine forest (Duke Forest) (e.g., [47,58]). In the Duke Forest FACE experiment with ambient +200 ppm CO$_2$, the simpler model (i.e., the Norman model) was sufficient for reproducing the photosynthesis rate enhancement through modeling appropriate $C_i/C_a$ [24]. Katul et al. [24] suggested that the CO$_2$ concentration enhancement is 1.55 and the computed enhancement in photosynthesis from the Norman model is also 1.55. This estimate is in agreement with leaf-level measurements of photosynthesis enhancement by Ellsworth (1.56; [7]). It is important to note that FACE experiments are generally designed to maintain similar microclimatic conditions for ambient and CO$_2$ enriched conditions; hence, differences between $D$ (or RH) for ambient and enriched plots is minimum. Schäfer et al. [59] showed that for this Duke Forest FACE experiment, $D$ for ambient and enriched plots was similar (see e.g., their Fig. 2). In this study, however, our values of CO$_2$ uptake estimated using the Norman model under current +300 ppm CO$_2$ were not much altered when compared to the ambient state mainly because of the ratio of $C_a/D$ was not altered. Furthermore, our values of CO$_2$ uptake calculated using the Norman and the Leuning models were considerably different, because the Leuning model takes the effect of $D$ into consideration, while the Norman model does not. It is interesting to note that no FACE experiments currently exist that take into consideration increase in $D$ caused by an increase in air temperature attendant on the projected growth in CO$_2$.

An important consequence of a change in $D$ but constant RH in a future climate scenario is that if the Ball–Berry model [6] was used for computing $C_i/C_a$, future photosynthesis rate would be similar to those calculated using the Norman model and would not be appreciably altered from their present value. For the Leuning model, photosynthesis increased by a factor of 1.5 when comparing current and future climate. Although the Leuning model is generally regarded as a Ball–Berry type model, this study highlights a fundamental difference between the two approaches. From a physiological point of view, stomata respond to $D$ not RH [49].

Although warmer temperatures could increase rates of all chemical and biochemical processes in plants and soils up to a point where enzymes disintegrate (e.g., [57]), the uncertainty over the interaction between elevated CO$_2$ and temperature (e.g., [16]) is not small. In general, under elevated CO$_2$, enhancements of photosynthetic rate are observed (e.g., [7]). However, in a few instances, increasing atmospheric CO$_2$ has been shown to cause down-regulation of photosynthetic rate (e.g., [67]) through a reduction in stomatal conductance (e.g., [36]). Furthermore, increase in atmospheric CO$_2$ can increase interception by increasing LAI (e.g., [34]).

On much longer time scales, increases in atmospheric CO$_2$ can induce higher soil water holding capacity because of an increase in soil organic matter content resulting from increased litter production (e.g., [44,59]). In the Duke Forest FACE experiment, however, it is suggested that LAI, stomatal conductance, $C_i/C_a$ and bulk canopy conductance are, to a first order, unaltered by elevated CO$_2$ [8,24,51,59]. Thus, the effects of elevated CO$_2$, including its attendant shifts in the other climatic factors, on numerous factors in forest ecosystems still remain uncertain. Further research is now required on the effects of elevated CO$_2$ on Southeast Asian rainforest ecosystems using extensive and technically difficult experiments.

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Appendix A. The Norman and the Leuning models for stomatal conductance

The photosynthetic rate \( A \) can be described as

\[
A = g_c(C_a - C_i) = g_c C_a \left(1 - \frac{C_i}{C_a}\right),
\]

where \( g_c \) is the stomatal conductance, and \( C_a \) and \( C_i \) are the ambient and the intercellular \( \mathrm{CO}_2 \) concentration, respectively.

Wong et al. [66] have shown that the \( C_i \) can be approximated by \( C_i = 0.80C_a \) for \( \mathrm{C}_3 \) plants, for a wide range of environmental conditions, but that this relationship varies from species to species. According to Wong et al. [66], Norman [46] assumed that \( A \) resulted from changes in which attempt to hold \( C_i/C_a \) constant (= \( R_C \)) for a wide range of environmental conditions (see Eq. (3)).

One widely used \( g_c \) model is the Ball–Berry model (see [6]), given by

\[
g_c = m \frac{A \, \mathrm{RH}}{C_S} + g_0,
\]

where \( m \) and \( g_0 \) are empirical parameters, and \( \mathrm{RH} \) and \( C_S \) are relative humidity and \( \mathrm{CO}_2 \) concentration at the leaf surface, respectively. Eq. (A.2) is an empirical relationship that incorporates the often-observed correlation between \( A \) and \( g_c \), and includes the effects of \( \mathrm{RH} \) and \( C_S \) on \( g_c \). Using Eqs. (A.1) and (A.2) and upon neglecting the leaf boundary layer resistance relative to \( g_c^{-1} \) (i.e., \( C_a \approx C_S \)), a closure model for \( C_i/C_a \), given by Eq. (14), can be derived if \( g_0 \) is neglected [24].

However, it is widely accepted that stomata respond to humidity deficit, \( D \), rather than to surface \( \mathrm{RH} \) (e.g., [2]). Furthermore, since \( A \) approaches zero when \( C_S \) approaches the \( \mathrm{CO}_2 \) compensation point, and Eq. (A.2) cannot describe stomatal behavior at low \( \mathrm{CO}_2 \) concentration [32]. Leuning [32,33] accounted for those observations by replacing \( \mathrm{RH} \) and \( C_S \) in Eq. (A.2) with a vapor pressure deficit correction function \( f \) (\( D \)) and \( C_S - D \) respectively, i.e.,

\[
g_c = m \frac{A f(D)}{C_S - D} + g_0; \quad f(D) = \left(1 + \frac{D}{D_0}\right)^{-1},
\]

where \( D_0 \) is the empirical parameter. Using the same approach for deriving a closure model for \( C_i/C_a \) described by Eq. (14), the Leuning [33] model reduces to

\[
\frac{C_i}{C_a} = 1 - \frac{1}{m} \left(1 - \frac{f}{C_c}\right) \left(1 + \frac{D}{D_0}\right), \quad (A.4)
\]

\[
= \left[1 - \frac{1}{m} \left(1 - \frac{f}{C_c}\right)\right] - \frac{1}{mD_0} \left(1 - \frac{f}{C_c}\right) D. \quad (A.5)
\]

Note that Eq. (A.5) is synonymous with Eq. (4).

References

[16] Hikosaka K, Murakami A, Hirose T. Balancing carboxylation and regeneration of ribulose-1,5-bis-phosphate in leaf photosyn-


