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# Transpiration, canopy conductance and the decoupling coefficient of a lowland mixed dipterocarp forest in Sarawak, Borneo: dry spell effects

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## Abstract

Tropical rainforests are among the most important biomes in terms of annual primary productivity and water cycling. However, the materials-exchange properties of Southeast Asian forests in their significant functions are less studied. We investigate key factors controlling materials-exchange, such as canopy ( $g_c$ ) and aerodynamic conductance ( $g_a$ ) and the decoupling coefficient ( $\Omega$ ) in an intact lowland mixed dipterocarp forest in Sarawak, Borneo. We operated an eddy covariance system above the canopy to measure canopy transpiration rate ( $E_c$ ) using an 80-m-tall canopy crane, and made concurrent meteorological measurements. In this region, solar radiation and air temperature have small seasonal variations, and annual rainfall is distributed evenly throughout the year, with some unpredictable intra-annual dry spells. We define three specific periods A, B and C as medium dry, heavy dry and wet periods, respectively, for analyses of the environmental control on  $E_c$ , according to their dryness level. The mean daily  $E_c$ ,  $g_c$  and  $\Omega$  were higher in the wet period C than in the dry periods A and B. Also, each  $g_c$  in its diurnal variation was much higher in the wet period C than in the dry periods A and B, where diurnal variations of  $g_c$  were almost the same. Both the value of  $g_c$  and its sensitivity to environmental variables were higher in the wet period C than in the dry periods A and B. The peak of  $\Omega$  was higher in the wet period C than in the dry periods A and B because of a higher value of  $g_c$  in period C. However, the higher values of  $g_c$  in the wet period C did not cause a higher  $E_c$  compared to in the dry periods A and B.

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**Keywords:** Transpiration; Canopy conductance; Aerodynamic conductance; Decoupling coefficient; Eddy covariance; Tropical rainforest

## 1. Introduction

Tropical rainforests are among the most important biomes in terms of annual primary productivity and evapotranspiration. Although these forests cover only

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about 12% of the global land surface (Food and Agriculture Organization, 1993), they are estimated to contain about 40% of the carbon in the terrestrial biosphere (Skole and Tucker, 1993) and are responsible for about 50% of terrestrial gross primary productivity (Grace et al., 2001). Tropical rainforests are also important latent energy sources, with large influences on the global and regional climate (Lean and Warrilow, 1989; Nobre et al., 1991). According to the results of some modeling, the deforestation of tropical rainforests is likely to reduce evapotranspiration and increase soil and air temperatures and runoff, but the long-term effects of deforestation have not been well determined experimentally.

The main tropical rainforest areas are in South America, Central Africa and Southeast Asia. Although tropical forests in Southeast Asia extend over only about 17% of the total tropical rainforest area (Food and Agriculture Organization, 1993), relative deforestation rates (Malhi and Grace, 2000) and estimated resulting CO<sub>2</sub> emissions (Houghton and Hackler, 1999; Malhi and Grace, 2000) are highest in this region. However, the materials-exchange properties of these forests are much less studied than those of Amazonian rainforest (Shuttleworth et al., 1984; Lloyd et al., 1995; Grace et al., 1996; Malhi et al., 1998; Williams et al., 1998). The studies on ecosystem fluxes of materials and energy in Southeast Asia have been poorly documented (Aoki et al., 1975): no published data, in particular, exist regarding long-term eddy covariance measurements in Southeast Asia.

The work described in this paper has been carried out as part of the project entitled 'Research and Observation on the Mechanisms of Atmosphere–Ecosystem Interaction in Tropical Forest Canopy' (Nakashizuka et al., 2001). The project site is an intact tropical rainforest in Borneo, Southeast Asia, which is characterized by tall stature and extremely rich floristic diversity compared to other tropical regions. This project has two main objectives: (1) to elucidate the mechanisms of general flowering, and (2) to scale-up the estimation of the carbon and water budgets in tropical rain forest. We have been conducting CO<sub>2</sub> and H<sub>2</sub>O flux measurements at this site since June 2001. This paper describes preliminary results from yearlong eddy covariance measurements.

The water vapor (H<sub>2</sub>O) exchange rate between the vegetated surface and the atmosphere is among the most important components of the energy exchange process at the air–land interface. The canopy conductance, which mainly depends on the physiological behavior of the plant, and the aerodynamic conductance, which represents the physical conditions of and over the canopy, and the control of the canopy transpiration as a whole (Jones, 1992) are the subject of this study. Our objectives are to examine the environmental and hydrologic controls on canopy transpiration, canopy conductance, and estimates of the decoupling coefficient,  $\Omega$ . Here,  $\Omega$  represents the magnitude of the coupling effect of the canopy and the aerodynamic conductance in controlling rates of canopy transpiration (Jarvis and McNaughton, 1986). In our study site, the solar radiation and the air temperature have small seasonal variations and the annual rainfall is distributed evenly throughout the year. However, there are some unpredictable intra-annual dry spells (Kuraji et al., 2001) and inter-annual dry sequences (Kumagai et al., 2001). Intra-annual dry spells, in particular, occur every year and often throughout the year. Therefore, canopy conductance is likely to be overly sensitive to the soil moisture condition. Our primary objective is to examine the environmental control on transpiration in prevailing environmental factors. Towards this end, we investigated the variation of  $\Omega$  and the sensitivities of canopy conductance to variations in environmental factors, such as solar radiation, atmospheric humidity deficit and, especially, soil moisture. An outcome of our study is used to provide an initial calibration of a simple, physically based model of materials exchange (Lloyd et al., 1995) for Southeast Asian rainforest.

## 2. Material and methods

### 2.1. Site description

The study was carried out in a natural forest in Lambir Hills National Park (4°12'N, 114°02'E), some 30 km south of Miri City, Sarawak, Malaysia. An experimental plot of 4 ha is used for this project. An 80-m-tall (at the base of the gondola) canopy crane with a 75-m-length rotating jib constructed

in the center of this plot enables us to gain access to the upper canopy of the trees. It includes observation stages at four levels (23.5, 38.5, 59.0, and 75.5 m above the ground), and an elevator to reach each stage. One stage (59.0 m high) was devoted to eddy covariance measurements. One subplot was used for soil and in-canopy micrometeorological measurements.

The mean annual rainfall at Miri Airport, 20 km from the study site, for the period 1968–1998 was around 2700 mm with no clear seasonal variation (Sakai et al., 1999). For the period 1999–2001, the mean monthly number of rain days near the study site ranged from 10 in August 2001 to 27 in January 2001. The average rainfall per rain day ranged from 7.2 mm in August 2001 to 21.3 mm in January 2001. Note that at this site August and January are not always the driest and wettest periods, respectively; when the driest period will actually be somewhat unpredictable. The mean annual temperature is around 27 °C with only a small seasonal variation (Yamakura et al., 1995).

The experimental plot is at an altitude of about 200 m, and the crane is situated on a gentle slope ( $<5^\circ$ ). The soils on the ridge with the gentle slope 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%) (Ishizuka et al., 1998; Sakurai, 1999). Borneo is covered primarily by hilly topography, most of whose soil type is ultisol. Ultisol is a typical soil of much of Southeast Asia, and its distribution corresponds to that of lowland and hill dipterocarp forest (Ohta and Effendi, 1992).

The rain forest in this park consists of two types of original vegetation common to the whole of Borneo, i.e. mixed dipterocarp forest and tropical heath forest (Yamakura et al., 1995). The former contains mainly various types of dipterocarp trees, which cover 85% of the total park area. The continuous canopy height of the forest surrounding the crane is about 40 m, but the height of emergent trees reaches 50 m. 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  $30 \times 30 \text{ m}^2$  subplot. The LAI ranged from 4.8

to  $6.8 \text{ m}^2 \text{ m}^{-2}$  and the mean LAI was  $6.2 \text{ m}^2 \text{ m}^{-2}$  (M. Yamashita, unpublished data). As the amount of litterfall in each month were evenly distributed throughout the year (M. Nakagawa, unpublished data), there could be little variations of LAI.

## 2.2. Meteorology and soil moisture

The following instruments were installed on the top of the crane, at 85.8 m: 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 tower located at about 100 m to the south from the crane, the upward short-wave radiation and long-wave radiation were measured using a solar radiometer (CM06E, Kipp and Zonen, Delft, The Netherlands) and an infrared radiometer (Model PIR, Epply, Newport, RI) installed upside down, during December 15–31, 2001. These measurements were used to compute net radiation. Samples were taken every 5 s and the averaging period was 10 min (CR10X datalogger, Campbell Scientific, Logan, UT).

At the subplot for the in-canopy microclimate measurements, we measured air temperature and humidity at heights of 41.5, 31.5, 21.5, 11.5, 6.5 and 1.5 m using a series of ventilated sensors with dataloggers (H0803208 and RS1, Onset, Pocasset, MA) at 10-min intervals.

Soil moisture (volumetric water content ( $\theta$ ) and matric potential ( $\psi$ )) was measured in the subplot at depths of 10, 20 and 50 cm at 10-min intervals (CR23X datalogger, Campbell Scientific, Logan, UT).  $\theta$  was measured with a time-domain reflectometer (TDR; CS615, Campbell Scientific, Logan, UT). A tensiometer (DIK3150, Daiki, Tokyo, Japan) was also used to measure  $\psi$  at the same depth as the volumetric water content was measured, and we could make soil water retention curves at each depth. The relative extractable water in the soil (REW;  $\text{m}^3 \text{ m}^{-3}$ ) was calculated using the average  $\theta$  in the 0–50 cm soil layer as:  $(\theta - \theta_r)/(\theta_s - \theta_r)$ , where  $\theta_s$  and  $\theta_r$  are the saturated water content and the residual water content, respectively.  $\theta_s$  was taken as the maximum observed  $\theta$  during the observation period (March 17, 2001–March 17, 2002), and  $\theta_r$  was estimated from the retention curves. Representative Elementary

Watersheds (REW) ranges from 0 (soil dry) to 1 (field capacity).

### 2.3. Eddy covariance measurement for transpiration

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. This was equipped with an open-path CO<sub>2</sub>/H<sub>2</sub>O analyzer (LI-7500, Li-Cor, Lincoln, NE) placed beside it, about 30 cm away. This open-path analyzer was mounted in an inclined orientation and its windows were coated with a wax, so as to reduce problems of rain and dew droplets sitting on the windows. There was, in addition, a ventilated psychrometer (MS020S, EKO, Tokyo, Japan) installed adjacent to the sonic anemometer and the open path analyzer for their calibration and correction for density effects (Webb et al., 1980).

The sensors were mounted 2.5 m apart from the crane leg by a horizontal boom. The boom was fixed on its southwest pointing corner, so as to minimize flow distortion by the crane when the wind was blowing from its prevailing northwesterly and southeasterly directions. When the crane was constructed, a gap with the crane at its center was formed. The largest radius of the gap was about 25 m. Moreover, while the fetch exceeded 1 km in the northwest sector, the minimum fetch, which was in the southwest sector, was about 200 m. The influences of the gap and the minimum fetch on the estimate of the flux were examined using a 2D analytic solution of the diffusion equation proposed by Schuepp et al. (1990), together with a stability dependency proposed by Lloyd (1995). As a result, we found that the wind flowed mostly from the northwest during the daytime, and that the maximum 80% effective fetch and the minimum 10% effective fetch were about 1500 m (12:30 h, June 18, 2001) and 50 m (2:00 h, June 13, 2001), respectively. Therefore, those influences could be neglected for the estimation of the flux during the daytime.

Wind speeds and gas concentrations were sampled at 10 Hz. Averages were computed at 30-min. They were detrended using a moving-average time constant of 200 s and the wind field ( $u, v, w$ ) (ms<sup>-1</sup>) coordinates were rotated so that the mean  $v$  and  $w$  were zero over 10 min periods. Note that the percentage

corrections for the coordinate rotations were less than 1%, probably because of the gentle slope. We applied the density fluctuation correction described by Webb et al. (1980). In this study, the flux data measured during rain events were abandoned. However, as the durations of the rain events in this study were short, gaps occurring because of this abandonment in the flux data were small.

Calibration for the open path analyzer was periodically performed using a dew point generator (LI-610, Li-Cor, Lincoln, NE): concerning the three specific periods for the analyses in this paper (see Fig. 1), the zero and span were checked at DOY 151, 254 and 342, 2001. Therefore, as very little drift in the analyzer concentration was noted on a week-to-week basis, drifts in measured gas concentrations had very little impact on the flux measurements during the above specific periods.

### 2.4. Calculation of canopy conductance, aerodynamic conductance and $\Omega$

To evaluate the response of the canopy conductance ( $g_c$ ; ms<sup>-1</sup>) to environmental driving variables, the actual  $g_c$  was calculated using the actual data of canopy transpiration ( $E_c$ ; ms<sup>-1</sup>) from the inverted Penman–Monteith equation (Dolman et al., 1991) as

$$g_c^{-1} = \left( \frac{\Delta}{\gamma} \beta - 1 \right) g_a^{-1} + \frac{\rho_a c_p}{\lambda \rho_w E_c \gamma} \delta_e \quad (1)$$

where  $\Delta$  is the rate of change of saturation water vapor pressure with temperature (Pa K<sup>-1</sup>),  $\gamma$  is the psychrometric constant (66.5 Pa K<sup>-1</sup>),  $\beta$  is the Bowen ratio,  $g_a$  is the aerodynamic conductance (m s<sup>-1</sup>),  $\rho_a$  is the density of dry air (kg m<sup>-3</sup>),  $c_p$  is the specific heat of air at constant pressure (J kg<sup>-1</sup>K<sup>-1</sup>),  $\lambda$  is the latent heat of vaporization of water (J kg<sup>-1</sup>),  $\rho_w$  is the density of water (1000 kg m<sup>-3</sup>) and  $\delta_e$  is the above-canopy atmospheric humidity deficit (Pa). From eddy covariance measurements, we obtain the surface conductance ( $g_s$ ), which is different from  $g_c$  because  $g_s$  includes the effect of soil surface evaporation (Raupach, 1995). However, as LAI in this site was in excess of 3,  $g_s$  and  $g_c$  are nearly identical because of the insignificant contribution of soil surface evaporation to the total flux (Kelliher et al., 1995). The actual  $g_a$

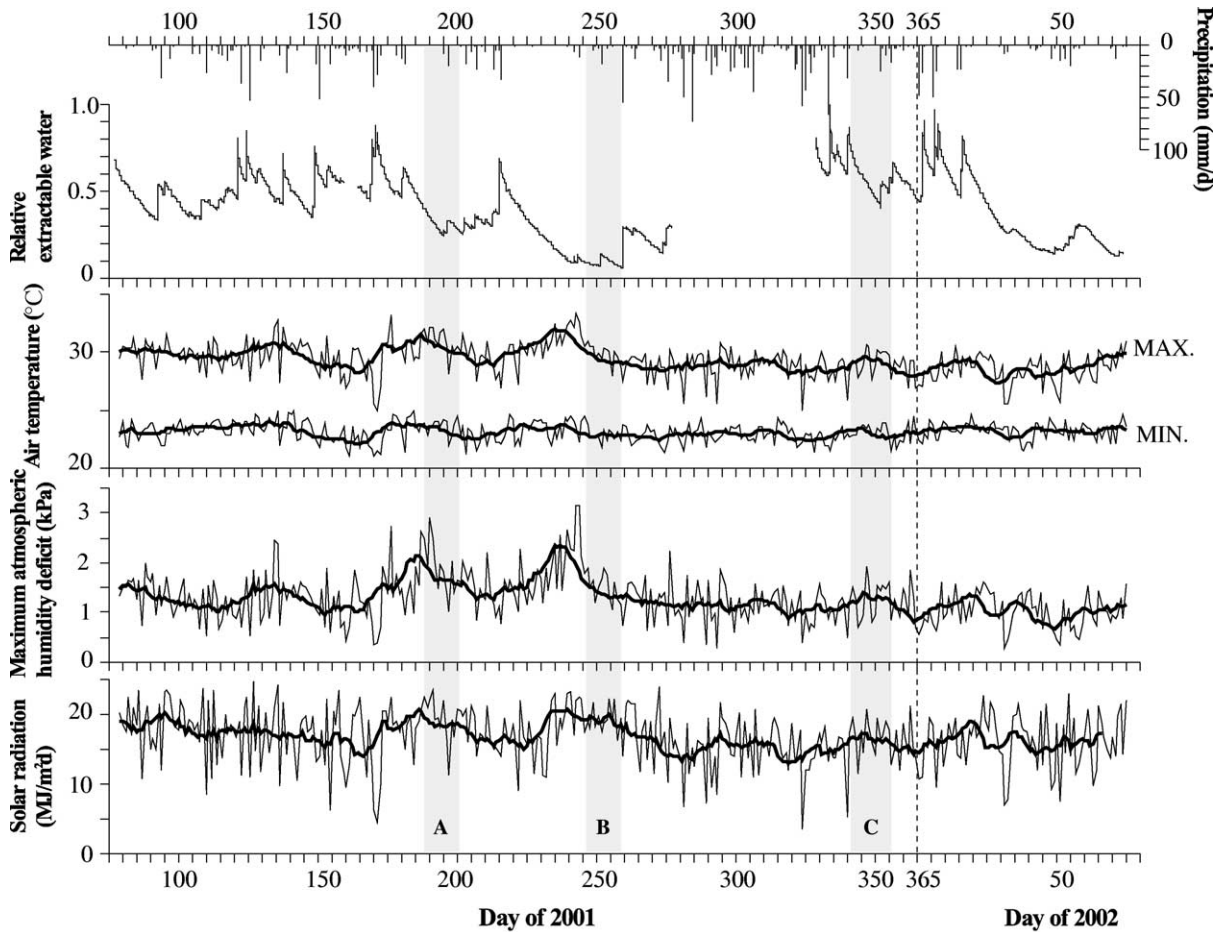


Fig. 1. Yearlong climatic data (DOY 76, 2001 to DOY 76, 2002, March 17, 2001 to March 17, 2002), reading from the top: daily precipitation (bars, right scale), relative extractable water in 30-min resolution (line, left scale), daily minimum and maximum air temperatures (thin line), daily maximum atmospheric humidity deficit (thin line), daily total solar radiation (thin line). Thick lines indicate 10-day moving average values. Shaded columns A, B and C represent the specific observation periods; medium dry, heavy dry and wet, respectively.

was estimated using the measured friction velocity ( $u_*$ ;  $\text{m s}^{-1}$ ), from

$$g_a = \frac{u_*^2}{u} \quad (2)$$

where  $u$  is the wind speed above the canopy ( $\text{m s}^{-1}$ ).

The net radiation above the canopy ( $R_n$ ;  $\text{W m}^{-2}$ ) was not measured but was derived from the measured solar radiation ( $R_s$ ;  $\text{W m}^{-2}$ ) using the relation  $R_n = 0.87R_s - 35.0$  ( $R^2 = 0.99$ ) obtained from the intensive observation. Using the eddy fluxes, the relation  $\lambda\rho_w E_c + H_c = 0.80R_n$  ( $R^2 = 0.81$ ) (where  $H_c$  is the sensible heat flux above the canopy ( $\text{W m}^{-2}$ ))

was achieved in this site. Assuming that the heat flux to soils ( $G$ ;  $\text{W m}^{-2}$ ) can be neglected, on a 1D scale the energy balance was not completely closed. Non-closure of the energy balance is a common feature of eddy covariance measurements above forest canopies, and the closure deficit of about 20% is comparative to what is obtained at most of the forested sites (Goulden et al., 1996; Ohta et al., 2001; Aubinet et al., 2001). This imbalance could be explained by a variety of processes, such as inadequate performance of the eddy covariance system, scale mismatches between the eddy fluxes and micrometeorological samples (McMillen, 1988). The energy balance relation in this site most likely means that the eddy fluxes were

underestimated by 20%; an underestimation that was in part caused by an insufficiency of the evaluation of the contribution of the relatively large-scale eddy (Lee, 1998). Although further analyses will be needed to resolve the reasons for the imbalance and the underestimation of the eddy fluxes, the degree of closure is well within the range reported for other forested site. In this study, we assumed that the eddy fluxes had been equally underestimated and added 20% to the flux.

The relative importance of radiative ( $E_{\text{eq}}$ ;  $\text{m s}^{-1}$ ) and advective ( $E_{\text{imp}}$ ;  $\text{m s}^{-1}$ ) energy for  $E_c$  were estimated using the equation

$$E_c = \Omega E_{\text{eq}} + (1 - \Omega) E_{\text{imp}} \quad (3)$$

where

$$E_{\text{eq}} = \frac{\Delta(R_n - G)}{\lambda \rho_w (\Delta + \gamma)} \quad (4)$$

$$E_{\text{imp}} = \frac{\rho_a c_p}{\lambda \rho_w \gamma} g_c \delta_e \quad (5)$$

(McNaughton and Jarvis, 1983). The equilibrium evaporation rate,  $E_{\text{eq}}$ , depends only on the energy supply (radiation) and would be obtained over an extensive surface of uniform wetness. The imposed evaporation rate,  $E_{\text{imp}}$ , is 'imposed' by the atmosphere on the natural canopy surface through the effect of  $\delta_e$ , so that evaporation is proportional to the physiological conductance. The decoupling coefficient,  $\Omega$ , was calculated according to Jarvis and McNaughton (1986)

$$\Omega = \frac{\Delta/\gamma + 1}{\Delta/\gamma + 1 + g_a/g_c} \quad (6)$$

The  $\Omega$  is a measure of the coupling between conditions at the surface and in the free air stream and can vary between 0 (for perfect coupling) and 1 (for complete isolation); stomatal control of transpiration grows progressively weaker as  $\Omega$  approaches 1. It is apparent from Eq. (6) that  $\Omega$  depends on the ratio between the surface conductance and that of the boundary layer, rather than on their absolute values (Jones, 1992).

Fig. 1 plots daily precipitation, 30-min values of REW, 24-h values of minimum and maximum air temperatures, maximum atmospheric humidity deficit, and total solar radiation. The climate in Borneo

shows very little seasonal variation in air temperature, atmospheric water content and solar radiation. Precipitation and soil water content also have no clear seasonal cycle. A noteworthy exception is some unsteady dry spells with various levels of dryness throughout the year. We defined three specific periods A, B and C as medium dry, heavy dry and wet periods, respectively, for analyses of the environmental control of transpiration, according to their dryness level (Fig. 1). These specific periods were determined by the measured REW. As the decreases in REW after major rainfall events were rapid, flux data during some steady state of REW were used for the analyses of the environmental control; REWs of specific periods A, B and C were 0.24–0.33, 0.05–0.09 and 0.47–0.66, respectively. Thanks to the abandonment in the eddy flux data during rainfall events and the use of the flux data during the steady state of REW, our analyses of the environmental control of transpiration could be performed for dry-canopy conditions. As a result, the number of flux data for the specific periods A, B and C were 218, 222 and 213, respectively.

As the amounts of litterfall in July, September and December 2001 were 61.0, 61.7 and 56.0  $\text{g m}^{-2}$ , respectively (M. Nakagawa, unpublished data), variations of LAI between periods A, B and C can be neglected. Therefore, comparisons of  $g_c$  between periods A, B and C mainly signify comparisons of leaf-level physiological behavior between these periods.

## 2.5. Canopy conductance model

To facilitate the interpretation of the influence of  $R_s$  and  $\delta_e$  on  $g_c$  for three specific periods A, B and C, we analyzed  $g_c$  using a multiplicative-type function (Jarvis, 1976), which is defined as follows

$$g_c = g_{c \text{ max}}(R_s)f(\delta_e) \quad (7)$$

where  $g_{c \text{ max}}$  is the canopy conductance, in the absence of limitation due to  $\delta_e$ , depending on  $R_s$ , and  $f(\delta_e)$ , the limiting functions of  $\delta_e$ . In general, stomatal conductance decreases exponentially with increasing vapor pressure deficit (VPD) between leaf and air (Meinzer et al., 1993; Monteith, 1995; Granier et al., 1996; Oren et al., 1999). Although in this study we used the relationship between  $g_c$  and  $\delta_e$  instead of stomatal conductance and VPD, respectively,

as Meinzer et al. (1993) reported that there was a clear response of  $g_c$  to variations in  $\delta_e$ , we used a Granier-type function (Granier et al., 1996) as  $f(\delta_e)$ . As a result, the following  $g_c$  model was selected

$$g_c = (aR_s + b)(1 - m \ln \delta_e) \quad (8)$$

where  $a$ ,  $b$  and  $m$  are parameters to be estimated through non-linear regression analysis for each specific period. Note that  $aR_s + b$  and  $m(aR_s + b)$  are the reference value of  $g_c$  (i.e. the value of  $g_c$  at  $\delta_e = 1$  kPa) and the sensitivity of  $g_c$  to  $\delta_e$  (i.e.  $-\partial g_c / \partial \ln \delta_e$ ), respectively.

### 3. Results

#### 3.1. Daily transpiration, canopy conductance and $\Omega$

Fig. 2 shows the diurnal variation of 30-min estimates of canopy transpiration ( $E_c$ ), solar radiation

( $R_s$ ), above-canopy atmospheric humidity deficit ( $\delta_e$ ), canopy conductance ( $g_c$ ), aerodynamic conductance ( $g_a$ ), and the decoupling coefficient ( $\Omega$ ) on given days (July 11–14, 2001). Estimates of  $E_c$  reached a maximum of  $0.72 \text{ mm h}^{-1}$ , and their pattern was similar to that of  $R_s$  (Fig. 2a and b). The maximum  $g_c$  and  $g_a$  values were  $1.91$  and  $17.9 \text{ cm s}^{-1}$ , respectively (Fig. 2c). The pattern of  $g_c$  had somewhat clear diurnal rhythm and was partly correlated with that of  $E_c$  (Fig. 2a and c). Estimates of  $\Omega$  ranged from  $0.1$  to  $0.4$  and had no clear diurnal cycle (Fig. 2d).

There were significant differences in mean daily  $E_c$ ,  $g_c$  and  $\Omega$  in the specific periods A, B and C (Table 1). The mean daily  $E_c$  and the level of environmental control of transpiration,  $\Omega$ , increased with soil moisture, with  $3.36 \text{ mm d}^{-1}$  and  $0.31$ ,  $2.86 \text{ mm d}^{-1}$  and  $0.24$  and  $3.48 \text{ mm d}^{-1}$  and  $0.43$  in the specific periods A, B and C, respectively. In period C, representing the wet period,  $E_c$  and  $\Omega$  were the highest. In period B, representing the heavy dry

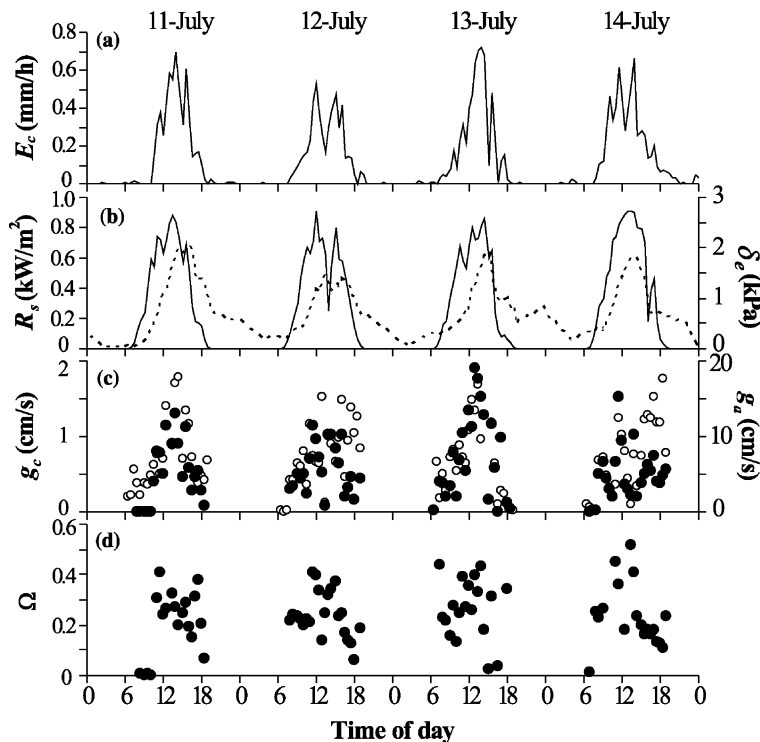


Fig. 2. Diurnal variations in (a) canopy transpiration ( $E_c$ ), (b) solar radiation ( $R_s$ ; solid line) and atmospheric humidity deficit ( $\delta_e$ ; dashed line), (c) canopy conductance ( $g_c$ ; solid circle) and aerodynamic conductance ( $g_a$ ; open circle), and (d) the decoupling coefficient ( $\Omega$ ; solid circle) for the period July 11–14, 2001.

Table 1  
Mean daily transpiration, canopy conductance and decoupling coefficient ( $\Omega$ ) for the three specific periods

Period	Canopy transpiration (mm d <sup>-1</sup> )	Canopy conductance (cm s <sup>-1</sup> )	$\Omega$
A	3.36 (0.26)	0.91 (0.14)	0.31
B	2.86 (0.29)	0.86 (0.11)	0.24
C	3.48 (0.31)	1.63 (0.23)	0.43

Standard errors are shown in parentheses. The decoupling coefficients were estimated using mean daily canopy conductance and aerodynamic conductance.

period,  $E_c$  was the lowest and the level of stomatal control of the transpiration ( $1 - \Omega$ ) was the highest. The mean daily  $g_c$  of the wet period C (1.63 cm s<sup>-1</sup>) was much higher than those of the dry periods A (0.91 cm s<sup>-1</sup>) and B (0.86 cm s<sup>-1</sup>), which were nearly identical.

### 3.2. Controls of canopy conductance

Fig. 3 compares the diurnal variations of  $g_a$  and  $g_c$  in periods A, B and C. Data were averaged within each 2-hour interval of the day. At this site, wind speed increases gradually from the early morning until noon, and is nearly constant in the afternoon. Therefore,  $g_a$  peaked at about noon in each period and was constant in periods B and C (Fig. 3a). As the wind was stronger in period B than in the other periods,  $g_a$  was higher. On the other hand, those of  $g_a$  in periods A and C were almost the same. The value of

$g_c$  peaked just before noon in all of the periods (Fig. 3b). The values of  $g_c$  were much higher in the wet period C than in the dry periods A and B, while the values of  $g_c$  at 12.00–14.00 h of period C were almost the same as those of the other periods. The diurnal patterns of  $g_c$  in the dry periods A and B were very similar, with both of their peaks at about 1.4 cm s<sup>-1</sup>.

Overall, for a given  $\delta_e$ , both  $g_c$  and the variability of  $g_c$  were significantly higher in the wet period C than in the dry periods A ( $P < 0.001$ ) and B ( $P < 0.0001$ ) (Fig. 4). Although during period B the conditions were drier than during period A, there were insignificant differences ( $P > 0.15$ ) in the values of  $g_c$  between dry periods A and B. Table 2 shows the parameters of Eq. (8) for the three specific periods. The modeled lines fitted for each period and given  $R_s$  classes are shown in Fig. 4 ( $R^2 = 0.35, 0.44$  and  $0.35$  for periods A, B and C, respectively). The parameters  $a$  and  $b$  were higher in the wet period C than in the dry periods A and B, and  $m$  in the wet period C was almost the same as in the heavy dry period B (Table 2). Consequently, the sensitivity of  $g_c$  to  $\delta_e$  ( $-\partial g_c / \partial \ln \delta_e$ ), which is represented as a function of  $R_s$ , is much higher in the wet period C than in the dry periods A and B, irrespective of the value of  $R_s$  (Fig. 5).

### 3.3. Canopy transpiration coupling or decoupling atmosphere

The relationships between  $\Omega$  and  $g_c$  were determined over the range of  $g_c$  measured in the dry

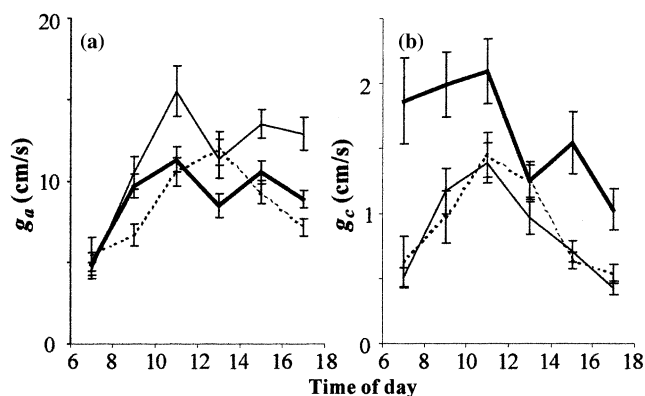


Fig. 3. Diurnal variations in (a) aerodynamic conductance ( $g_a$ ) and (b) canopy conductance ( $g_c$ ) for three specific periods A (dashed line), B (thin line) and C (thick line). Data are 2-h averages and error bars indicate  $\pm 1$  SE.



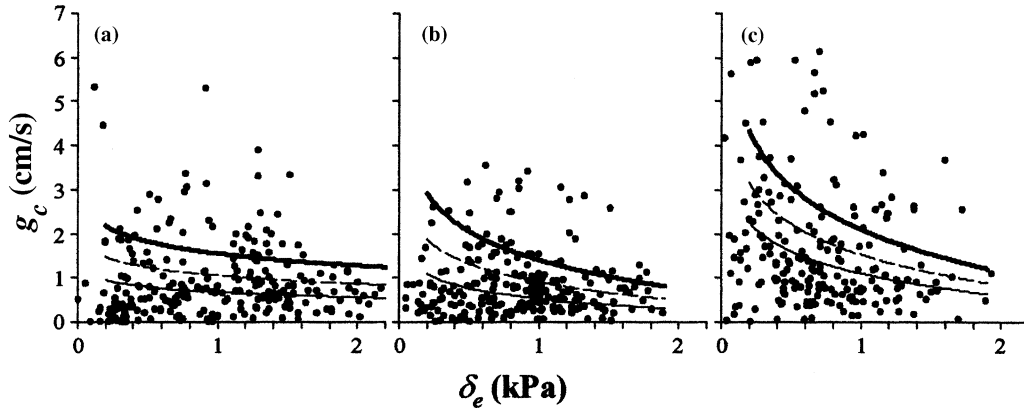


Fig. 4. Canopy conductance ( $g_c$ ) for three specific periods (a) A, (b) B and (c) C in relation to the above-canopy atmospheric humidity deficit ( $\delta_e$ ). The lines represent predicted  $g_c$  in three solar radiation ( $R_s$ ) classes  $300 \text{ W m}^{-2}$  (thin line),  $600 \text{ W m}^{-2}$  (dashed line) and  $900 \text{ W m}^{-2}$  (thick line).

periods A and B and the wet period C, in four  $g_a$  classes  $g_a < 5$ ,  $5 \leq g_a < 10$ ,  $10 \leq g_a < 20$  and  $20 \leq g_a$  (Fig. 6). As we used 30-min data, there was a wide range of ratios of  $g_c$  to  $g_a$ , and  $\Omega$  increased from 0. Therefore, during the dry periods A and B,  $\Omega$  varied between 0 and 0.6. However, during the wet period C, there were values of  $\Omega$  over 0.5 because of the higher  $g_c$ . When  $g_a < 5$ , the maximum  $\Omega$  in period C reached about 0.9 (Fig. 6a), and in the other  $g_a$  classes reached about 0.7 (Fig. 6b and c).

Fig. 7 shows the relationship between the actual  $E_c$  and  $g_c$  in three  $\Omega$  classes  $0 \leq \Omega < 0.2$ ,  $0.2 \leq \Omega < 0.4$  and  $\Omega \geq 0.4$ . When  $\Omega < 0.4$ , the  $E_c$  plotted by  $g_c$  were strongly correlated, regardless of the specific periods ( $R^2 = 0.67, 0.65$  and  $0.49$  for periods A, B and C, respectively). On the other hand, when  $\Omega \geq 0.4$ , there was a large scattering of the  $E_c$  plotted by  $g_c$ , regardless of the specific periods. However, as the values of  $\Omega$  were over 0.4, mainly in the wet

period C (Fig. 6), most of the scattering data of  $E_c$  plotted by  $g_c$  appeared in the wet period C (Fig. 7).

#### 4. Discussion

In Amazonian tropical rainforest with tree heights of about 30 m, the mean daily  $E_c$  collected during the dry season in which rainfall was anomalously high

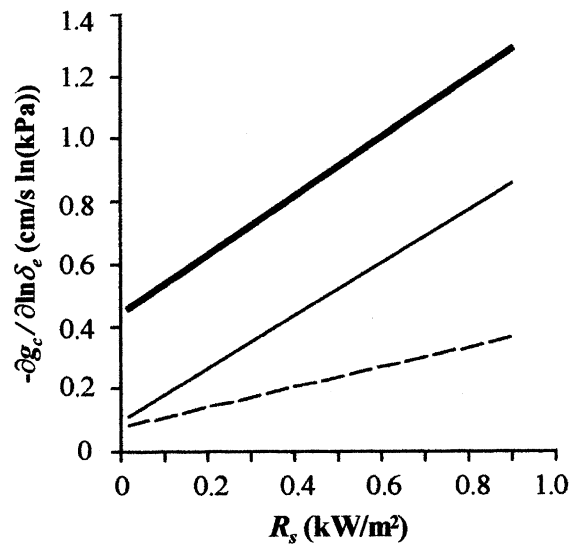


Fig. 5. The sensitivity of the canopy conductance ( $g_c$ ) to increasing above-canopy atmospheric humidity deficit ( $\delta_e$ ) ( $-\partial g_c / \partial \ln \delta_e$ ) as a function of solar radiation ( $R_s$ ) for three specific periods A (dashed line;  $y = 0.32x + 0.076$ ), B (thin line;  $y = 0.84x + 0.097$ ) and C (thick line;  $y = 0.94x + 0.42$ ).

Table 2

Parameters estimated for the multiplicative-type function for predicting canopy conductance ( $g_c$ ;  $\text{m s}^{-1}$ ) by solar radiation ( $R_s$ ;  $\text{W m}^{-2}$ ) and above-canopy atmospheric humidity deficit ( $\delta_e$ ; kPa) on  $g_c$  in three specific periods

Period	$a$	$b$	$m$	$a \times m$	$b \times m$
A	$1.25 \times 10^{-5}$	$2.99 \times 10^{-3}$	0.254	$3.18 \times 10^{-6}$	$7.58 \times 10^{-4}$
B	$1.27 \times 10^{-5}$	$1.46 \times 10^{-3}$	0.665	$8.42 \times 10^{-6}$	$9.69 \times 10^{-4}$
C	$1.43 \times 10^{-5}$	$6.71 \times 10^{-3}$	0.658	$9.42 \times 10^{-6}$	$4.42 \times 10^{-3}$

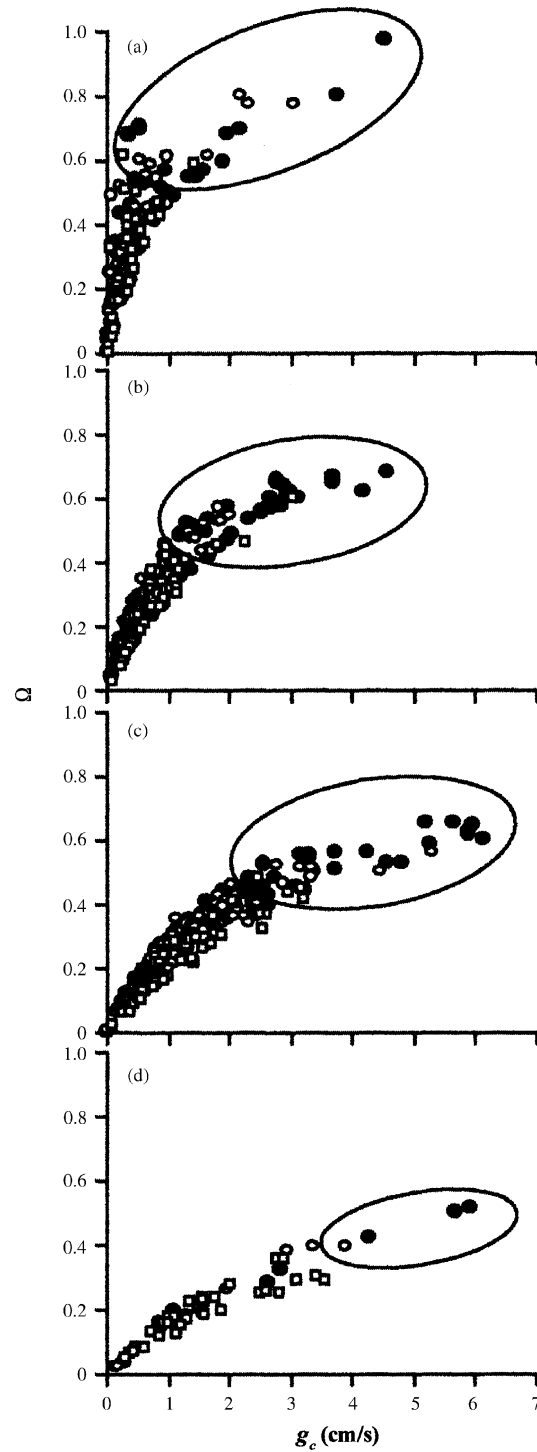


Fig. 6. The decoupling coefficient ( $\Omega$ ) over the range of canopy conductance estimated during period A (open circle), period B (open square) and period C (solid circle) in four aerodynamic conductance ( $g_a$ ;  $\text{cm s}^{-1}$ ) classes. (a)  $g_a < 5$ , (b)  $5 \leq g_a < 10$  (c)  $10 \leq g_a < 20$  and (d)  $20 \leq g_a$ .

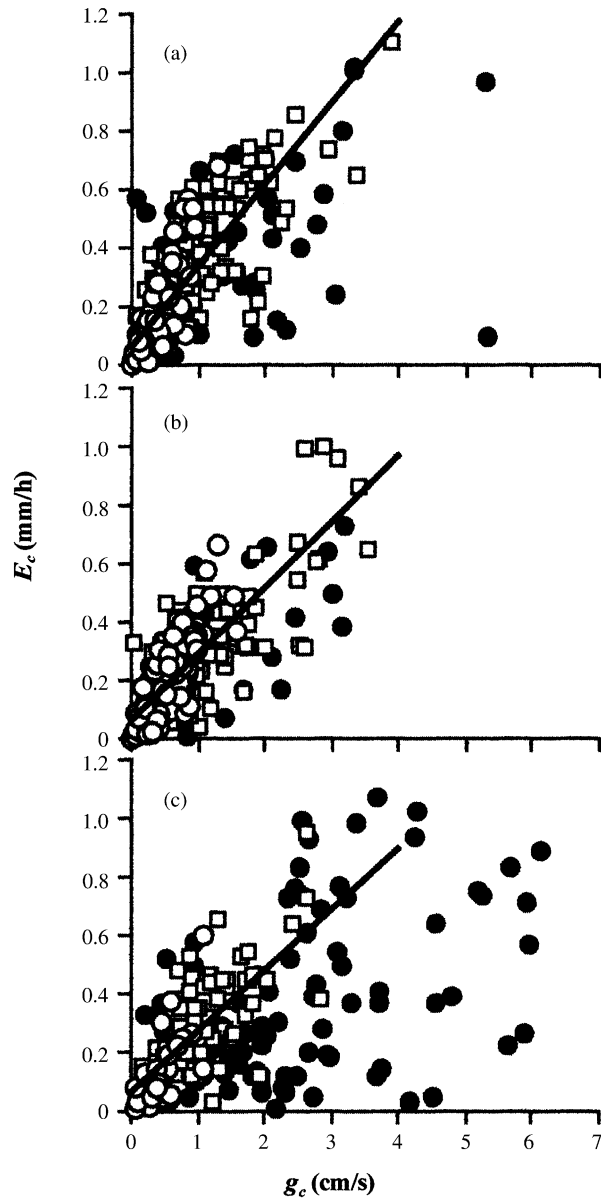


Fig. 7. The relationship between canopy transpiration ( $E_c$ ) and canopy conductance ( $g_c$ ) for three specific periods (a) A, (b) B and (c) C in three decoupling coefficient ( $\Omega$ ) classes  $0 \leq \Omega < 0.2$  (open circle),  $0.2 \leq \Omega < 0.4$  (open square) and  $0.4 \leq \Omega$  (solid circle). The lines represent the regression of the data of  $\Omega < 0.4$  for periods A ( $y = 0.28x + 0.068$ ,  $R^2 = 0.67$ ), B ( $y = 0.23x + 0.063$ ,  $R^2 = 0.65$ ) and C ( $y = 0.21x + 0.066$ ,  $R^2 = 0.49$ ).

was  $3.45 \text{ mm d}^{-1}$  (Shuttleworth et al., 1984). Also, Roberts et al. (1993) suggested that the mean daily  $E_c$  ranged from  $2.27 \text{ mm d}^{-1}$  in September to  $4.55 \text{ mm d}^{-1}$  in July–August. Cienciala et al. (2000) reported from their measurements during

a drier month that the mean daily  $E_c$  at two *Acacia mangium* (about 30 m tree height) plantations in Borneo were  $2.3$  and  $3.9 \text{ mm d}^{-1}$ . In our study, mean daily  $E_c$  in the specific periods A, B and C were  $3.36$ ,  $2.86$  and  $3.48 \text{ mm d}^{-1}$ , respectively; and were very

comparable to the daily values that have been reported for tropical rainforests (Table 1).

The mean daily  $E_c$ ,  $g_c$  and  $\Omega$  in each specific period were highly dependent on the soil moisture condition (Table 1). There is significant seasonal variation in rainfall in the Central Amazonian rainforest, and the variation of soil moisture is correlated with the seasonality in photosynthesis, partly explained by the response of stomatal conductance to soil moisture supply (Malhi et al., 1998). In fact, Roberts et al. (1990) reported that the stomatal conductance in the wet and dry seasons differed in Amazonian rainforest. There, given the convective nature of the rainstorms, the vegetation is thus unlikely to develop severe water stress, nor are substantial soil moisture deficits likely to be encountered (Dolman et al., 1991). On the other hand, at our site consisting of Southeast Asian tropical rainforest, there is little seasonal variation in rainfall, but with some short-term and unpredictable dry spells (Kuraji et al., 2001). The responses of stomatal conductance would have been highly influenced by these short-term spells throughout the year, instead of seasonal dry sequences, like in the Amazonian rainforest.

While  $\Omega$  in period B was lower than that in period A because of the highest  $g_a$  in the three specific periods,  $g_c$  in periods A and B were almost the same (Table 1, Figs. 3 and 4). In other words, the responses of stomatal conductance to soil moisture conditions were identical in both of the dry periods, that is, the medium dry period A and the heavy dry period B. The ultisols in this site, which is classified as an argillic soil, have a very high sand content (62–72%), so it might act like sand in terms of water movement at low tensions, but might hold water like clay soils at higher tensions. In fact, the drainage after rain events was indeed rapid (Fig. 1). Therefore, as Hodnett et al. (1995) reported about the oxisols in Amazonian rainforest, the ultisols in this site would have a very low available water capacity. Consequently, the very low available water capacity might have caused the low and almost same values of  $g_c$  in the medium dry period A and the heavy dry period B.

Each  $g_c$  in its diurnal variation was much higher in the wet period C than in the dry periods A and B except at noon;  $g_c$  at noon in the wet period C shows a midday depression (Fig. 3b). There are some studies on midday canopy-leaf stomatal closure in some tropical tree

species when the leaves are exposed to a high VPD (Roberts et al., 1990; Koch et al., 1994; Ishida et al., 1996). As those studies were carried out on an individual-leaf-level, our study cannot be directly compared with them. However, it is notable that although  $\delta_e$  was higher in the dry periods A and B than in the wet period C, the magnitude of the reduction in  $g_c$  with increasing  $\delta_e$  was higher in C than those in A and B throughout the range of  $R_s$  (Fig. 5), that is, the higher sensitivity of  $g_c$  to  $\delta_e$  in C might have caused the midday depression.

In their study in the Amazonian tropical rainforest, Roberts et al. (1990) showed that the response of stomatal conductance to VPD was more sensitive when  $R_s$  was high, but a higher sensitivity was observed in the March–April period when the soil was wettest. Our results agreed with those of Roberts et al. (1990) in that the decrease in  $g_c$  with increasing  $\delta_e$  was large when  $R_s$  was high and its sensitivity was higher in the wet period C (Fig. 5). Limited data suggest that tropical trees are particularly vulnerable to cavitation and must adjust their water-relations response to moisture conditions to avoid cavitation (Mulkey et al., 1996). In our results, the reference value of  $g_c$  (i.e.  $aR_s + b$ ) and the sensitivity of  $g_c$  to  $\delta_e$  (i.e.  $m(aR_s + b)$ ) were higher during the wet period C than in the dry periods A and B (Table 2 and Fig. 4). We interpret that under dry conditions,  $g_c$  is restricted to a low value and controlled by a low sensitivity to environmental variables, but that in wet conditions,  $g_c$  remains high and is controlled by the high sensitivity.

The role of  $g_c$  and  $g_a$  in controlling the rates of canopy transpiration varied with moisture condition (Fig. 6). Because of higher  $g_c$  values in the wet period C,  $\Omega$ , that is, the role of stomatal and environmental control in regulating transpiration varied between 0 and 0.8 compared with 0 and 0.6 during the dry periods A and B when the ratio of  $g_c$  to  $g_a$  was much lower. There were clear regions of higher values of  $\Omega$  during the wet period C in Fig. 6a–d. Some authors reported high values of  $\Omega$  and highly decoupled canopies for tropical trees (Meinzer et al., 1993, 1997; Wullschleger et al., 1998; Cienciala et al., 2000). Meinzer et al. (1993) concluded that tropical forests might be characterized by higher overall values of  $\Omega$  and considerable variation in the extent of stomatal control of

transpiration among upper canopy species. In our study, the maximum value of  $\Omega$  was close to the range of 0.68–0.81 reported by Meinzer et al. (1997), while the value of  $\Omega$  depended on the moisture condition.

Calculating  $E_c$  with  $\delta_e$  as the driving variables is commonly done for well-coupled canopies because  $\delta_e$  can approximate VPD (Schäfer et al., 2000). Also, this means that  $\delta_e$  is different from VPD when  $\Omega$  is high. When  $\Omega$  is high, the responses of stomatal conductance relate not to  $\delta_e$  but to VPD (Meinzer et al., 1997) and  $\delta_e$  is not the driving force of  $E_c$ . Therefore, while the relationships between  $E_c$  and  $g_c$  were almost linear when the values of  $\Omega$  were low, there were scattered  $E_c$  plotted by  $g_c$  when the values of  $\Omega$  were high; those high  $\Omega$  values appeared mainly during the wet period C (Fig. 7). Higher values of  $g_c$  during the wet period C compared to those in the dry periods did not generate higher  $E_c$  values.

## 5. Conclusion

In Bornean tropical rainforest, although annual rainfall is distributed evenly throughout the year and there is little seasonality like the dry and wet seasons in Amazonian tropical rainforest, there are some unpredictable intra-annual dry spells. From the standpoint of the dry spell effect on the canopy materials-exchange, we examined transpiration, canopy conductance and the decoupling coefficient of Bornean tropical rainforest using eddy covariance systems. The mean daily transpiration rate, canopy conductance and decoupling coefficient were higher in wet conditions than during dry spells. Both the value of canopy conductance and its sensitivity to micrometeorological variables were also higher in wet conditions than during dry spells. However, the higher values of canopy conductance in wet conditions did not cause higher transpiration rates compared to during dry spells.

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