

Environmental control of canopy stomatal conductance in a tropical deciduous forest in northern Thailand



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ABSTRACT

Tropical seasonal forests in Southeast Asia are among the most important biomes in terms of global and local hydrologic and carbon fluxes, and their vulnerability to climate change. We conducted eddy flux measurements in a teak (*Tectona grandis* Linn. f.) plantation in northern Thailand over a 6-year period; this forest undergoes a drastic seasonal change in foliage with somewhat constant incident radiative energy. We used a combination of actual evapotranspiration (ET) flux data and an inverted version of a simple two-layer ET model for estimating the mean canopy stomatal conductance (g_s). The main novelty of this analysis is that canopy conductance can be extracted from total surface conductance (including the canopy and forest floor effects), and thus environmental and biological controls of g_s are explicitly compared among seasons and years. The relationship between seasonal variations in the leaf area index (LAI) and g_s revealed an apparent effect of leaf age on leaf gas exchange capacity: within a year, g_s peaked earlier than full-leaf expansion and abruptly declined after the peak of LAI. We used this result to classify three leaf age stages: leaf-out, mid-growing, and leaf-senescence seasons. Then, two ecophysiological parameters, the reference value of g_s (g_{sref}), and the sensitivity of g_s to atmospheric demand (m), as well as their proportion (m/g_{sref}), were derived from the logarithmic response curve of g_s to vapor pressure deficit (VPD) for each season. We showed seasonal variation in g_{sref} as follows: leaf-out season \approx mid-growing season $>$ leaf-senescence season. m demonstrated little seasonality and little interannual variation was observed in either parameter. This resulted in a value of almost 0.6 for m/g_{sref} during the leaf-senescence season and of less than 0.6 in the leaf-out and mid-growing seasons, which suggests that the teak trees had strict stomatal regulation to prevent excessive xylem cavitation during the leaf-senescence season (i.e., under drought conditions) and less strict stomatal regulation during the leaf-out and mid-growing seasons (i.e., under moist conditions) when little risk of water stress-induced hydraulic failure would occur. In addition, we obtained a simple linear relationship between soil moisture and g_{sref} , which can be a powerful tool for further research of land–atmosphere interactions using global climate and vegetation dynamics models.

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1. Introduction

Tropical forests receive high radiative energy and play an important role in the global carbon budget (Melillo et al., 1993; Field et al., 1998; Malhi and Grace, 2000; Grace et al., 2001). They are a major source of global hydrological fluxes, profoundly influencing both global and regional climates (Lean and Warrilow, 1989; Nobre et al., 1991; Kanae et al., 2001; Avissar and Werth, 2005;

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Kumagai et al., 2013). Furthermore, recent evidence shows that unprecedented climates will occur first in the tropics, implying the vulnerability of tropical forest ecosystems (Mora et al., 2013). Although those in Southeast Asia represent only ~11% of the world's tropical forests in terms of area (World Resource Institute, 2007), they have undergone the highest relative deforestation rate in the tropics (Houghton and Hackler, 1999; Laurance, 1999; Malhi and Grace, 2000; Canadell et al., 2007); thus, their impacts on global and regional climates, and on hydrological cycling, are an important concern (Kanae et al., 2001; Malhi and Wright, 2004; Mabuchi et al., 2005; Werth and Avissar, 2005; Spracklen et al., 2012).

Tropical moist deciduous forests and tropical dry forests represent 55.9% of the total area of tropical forests (Food and Agriculture Organization, 2009). Furthermore, the area consisting of tropical deciduous forests is estimated to be larger than that of temperate deciduous forests (see Melillo et al., 1993). In deciduous forests, transpiration and primary productivity are significantly affected by large seasonal changes in leaf area, as well as physiological factors such as stomatal control (e.g., Wilson et al., 2001). Partitioning of net radiation into sensible and latent heat fluxes and the carbon exchange balance are considerably different between the growing and leafless seasons due to the lack of tree transpiration and photosynthesis during the latter (Moore et al., 1996; Schmid et al., 2000; Wilson and Baldocchi, 2000; Saigusa et al., 2002). In deciduous forests of temperate and boreal zones, incident radiative energy and atmospheric evaporative demands are smaller in fall/winter than in spring/summer. However, unlike in temperate and boreal forests, the impact of leaf phenology modification (i.e., the timing of leaf-out and leaf-fall, and the length of the physiological active season) on the annual energy and carbon cycle in tropical deciduous forests is likely to be critical because of the large annual and seasonal energy fluxes.

Previous studies (Yoshifuji et al., 2006, 2014) suggest that a teak (*Tectona grandis* Linn. f.) plantation as a typical Southeast Asian tropical deciduous forest in northern Thailand has much larger interannual variations in canopy duration and the transpiration (T_r) period (i.e., the periods between leaf-out and leaf-fall, and between the commencement and decline of tree T_r , respectively) than temperate and boreal deciduous forests (Black et al., 2000; Wilson and Baldocchi, 2000; Granier et al., 2002; Barr et al., 2004). Studies have also found that the major determining factor of these tropical deciduous forests is soil moisture, which is affected by interannual variation in rainfall regimes. Notably, a remarkable difference exists in the teak canopy between canopy duration and the leafless season (Fig. 1).

Vourlitis et al. (2008) reported that in a semi-deciduous forest in the southern Amazon basin, T_r was correlated to the leaf area index (LAI) during the dry-wet season transition period, while evapotranspiration (ET) changed little throughout the year. This shows that values of T_r and estimated canopy conductance (G_c) are

significantly smaller in the dry season than in the wet season. The authors attributed the difference to the inclusion of an evaporation component in the estimates of ET. In Southeast Asian tropical deciduous forests, the energy balance, and water and material cycling dynamics are less certain. As Vourlitis et al. (2008) pointed out, detailed long-term studies on the vegetation–atmosphere exchange of energy, water, and materials are needed in such ecotonal forests, which are being endangered by both human activity and climate change.

The goal of this study, therefore, was to examine the seasonal and interannual variations in canopy exchange traits of teak, a major tropical deciduous plantation tree, and to determine the environmental and biological factors that cause such variations. Toward this goal, we conducted eddy flux measurements over a 6-year period and compared the estimated mean canopy stomatal conductance (g_s) among seasons and years. Prior to assessing the environmental control of stomatal conductance, a simple two-layer model (Kelliher et al., 1995), which considers a whole ecosystem ET as a sum of canopy ET and vegetation floor evaporation, was first used to extract G_c from surface conductance (G_s).

2. Materials and methods

2.1. Site description

The experiments were carried out in an even-aged teak plantation in Mae Moh district, Lampang province, northern Thailand (18° 25' N, 99° 43' E; 380 m a.s.l.). Teak plantations are widely established throughout the tropics, especially in Indochina and India, due to their market value (Kollert and Cherubini, 2012). In Thailand, as a result of significant decreases in forest area until the 1980s, forest rehabilitation and plantations have been promoted, resulting in the establishment of teak plantations by the Forest Industry Organization (FIO), mainly in northern regions. The Mae Moh teak plantation was established by the FIO in ~1968.

Tree density in the study site was 440 trees ha⁻¹ in 2005 and 433 trees ha⁻¹ in 2012 due to tree mortality. Mean stem diameter at breast height (DBH) was 22.4 ± 7.3 cm (mean ± SD; $n = 308$) in November 2005, and increased to 24.2 ± 8.3 cm ($n = 303$) in February 2012. Mean tree height was 19.9 ± 3.5 m ($n = 308$) in November 2005, and 23.8 ± 5.4 m ($n = 303$) in February 2012. Various species of herbaceous plants and shrubs, at a moderate density, occupied the understory. The study site was located on an area of flat land with an almost homogeneous stand structure. The soil was classified as Loamy Paleustults (Thai classification) or Ultisols (U.S. Department of Agriculture Soil Taxonomic Classification), with 35.5% sand, 43.5% silt, and 21.0% clay, and a total porosity of 35–40%. Most fine and coarse roots were detected in the top 0.4 m of soil (Kume et al., 2013).

(a) Wet season



(b) Dry season



Fig. 1. Photographs of the studied teak plantation canopy in northern Thailand, during a wet season (a) and a dry season (b).

The climate is governed by the Asian Monsoon, with two distinct seasons: a wet (~May–October) and a dry (~November–April) season. The mean annual precipitation in the period 1986–2010 was 1231 mm. The mean annual temperature in the period 2001–2010 was 25 °C, with a minimum monthly mean of 21–22 °C in December–January, and a maximum monthly mean of 29.5 °C in April.

2.2. Meteorological measurements

A 40-m-tall scaffold tower was constructed in the study site for micrometeorological and eddy flux measurements. Incident solar radiation above the canopy (R_s ; W m^{-2}) and downward longwave radiation were measured with a pyranometer (CMP21: Kipp & Zonen, Delft, The Netherlands) and an infrared radiometer (model PIR: Epply, Newport, RI, USA, and CG4: Kipp & Zonen, before and after February 2007, respectively), respectively, at a height of 41 m. Upward shortwave and longwave radiation were measured using a solar (CMP21) and an infrared (model PIR) radiometer, respectively, installed upside down at a height of 35 m. The sensors were mounted roughly 3 m apart from the tower by a horizontal boom. The boom was fixed on its south corner to minimize the effect of the tower. These four radiation components were used to calculate the net radiation (R_n ; W m^{-2}). Air temperature (T_a ; °C) and relative humidity above the canopy were measured with an air temperature and humidity sensor (HMP45A: Vaisala, Helsinki, Finland) at a height of 39 m. Solar (S_b ; W m^{-2}) and the net radiation below the canopy was measured on the forest floor at heights of ~0.5 and 1.2 m, respectively, 30 m away from the tower, with a pyranometer (MS401: EKO, Tokyo, Japan, and the CMP21, before and after August 2008, respectively) and a net radiometer (CNR1: Kipp & Zonen). All samples were scanned every 5 s and their 10-min averages were recorded on data loggers (CR10X, CR23X, and CR1000: Campbell Scientific, Logan, UT, USA).

Rainfall (P_r ; mm) was measured every day with a self-made storage-type rain gauge in an open site ~500 m away from the tower. A tipping bucket (no. 34T: Ohta Keiki, Tokyo, Japan) with a data logger (Hobo Event: Onset Computer, Bourne, MA, USA) was also installed beside the rain gauge, and the time of tip was recorded to obtain the time distribution of rainfall.

Volumetric soil water content (θ ; $\text{m}^3 \text{m}^{-3}$) and soil heat flux (G ; W m^{-2}) were measured ~40 m away from the tower at depths of 10, 20, 40, and 60 cm with time domain reflectometers (TDR, CS-615: Campbell Scientific) and at a depth of 3 cm with a soil heat flux plate (MF-180: EKO). The data were recorded with a data logger (CR10X) at 10-min intervals. The weighted average of θ in the 0–60-cm soil layer was calculated by considering each TDR sensor's control domain as $\theta_{0-60} = (10\theta_{10} + 20\theta_{20} + 20\theta_{40} + 10\theta_{60})/60$, where θ_{10} , θ_{20} , θ_{40} , and θ_{60} are θ at depths of 10, 20, 40, and 60 cm, respectively, in $\text{m}^3 \text{m}^{-3}$. The relative extractable water in the soil (Θ_{0-60} ; $\text{m}^3 \text{m}^{-3}$) was calculated using θ_{0-60} as $\Theta_{0-60} = (\theta_{0-60} - \theta_r)/(\theta_s - \theta_r)$, where θ_s and θ_r are the saturated water content and the residual water content, respectively, averaged in the 0–60-cm layer. The θ_s and θ_r were taken as the maximum and minimum observed θ_{0-60} during the experimental period (January 2006–March 2011).

2.3. Eddy covariance measurements

The latent heat flux (LE ; W m^{-2}) and sensible heat flux (H ; W m^{-2}) were measured via the eddy covariance technique. A three-dimensional sonic anemometer (USA-1: METEK, Elmshorn, Germany) and an open-path $\text{CO}_2/\text{H}_2\text{O}$ analyzer (LI-7500: Li-Cor, Lincoln, NE, USA) were installed 28 m above the ground. Wind speeds and gas concentration time series were sampled and stored at 10 Hz (CR5000 and CR1000 data loggers: Campbell Scientific). First, spikes, outliers, possible sensor/logger malfunctions, and data

discontinuities in the raw 10-Hz data were detected and removed (e.g., Moncrieff et al., 2005). The double rotation method was applied to the sonic anemometer velocities (Kaimal and Finnigan, 1994; McMillen, 1988). Here, linear trends in sonic air temperature and water vapor concentration were not removed because the differences in the flux values between detrending and non-detrending fluxes were less than 3%. Then, H and LE were computed using the 30-min averaged covariances of the rotated 10-Hz vertical wind velocity with the 10-Hz sonic temperature and water vapor concentration, respectively, with corrections for density effects (Webb et al., 1980). Note that two large data gaps (March 2007–January 2008 and April–November 2009) occurred in the 6-year observation campaign due to equipment failures following lightning strikes and electric power supply problems.

The influences of the minimum fetch (~500 m) on the flux estimate were examined using a two-dimensional analytic solution of the diffusion equation proposed by Schuepp et al. (1990). We found that 81.3% of the observed fluxes during the daytime originated within the teak plantation. Therefore, those influences could be neglected for estimating the flux during the daytime. The stationarity test (Foken and Wichura, 1996) was employed, and if a difference of more than 30% existed between the 30-min averaged covariance and an average of six 5-min averaged covariances within the 30-min run, the flux calculated in the 30-min run was rejected. In addition, we discarded H and LE values that were measured during rain events and when the friction velocity was less than 0.22 m s^{-1} (see Saleska et al., 2003; Miller et al., 2004), as well as those originating from a direction of 270–360° (when the wind flow was distorted by the tower). In this study, we did not take into consideration the effect of the storage flux on the available energy and the scalar fluxes because the midday storage flux is generally lower than the morning flux due to the active turbulent mixing due to the unstable midday conditions, and because the storage flux cannot be large under small stem density, moderate LAI, and moderate canopy height conditions (see Ohkubo and Kosugi, 2008).

Using the eddy fluxes, the relationship $H + LE = 0.68 (R_n - G)$ ($R^2 = 0.79$) was achieved at this site, indicating that on a one-dimensional scale, the energy balance was not completely closed. This is a common feature of eddy covariance measurements above forest canopies, and a closure deficit of 10–35% is comparable to what is obtained at most forested sites (e.g., Aubinet et al., 2000; Wilson et al., 2002). Thus, we employed the “Bowen-ratio closure” method (see Twine et al., 2000) for closing the surface energy balance for each 30-min interval. This method assumes that H and LE are the sources of closure error in a correctly estimated Bowen ratio ($=H/LE$) and in the closure deficit to the flux. LE data gaps were filled with values estimated from the relationship between actual LE and $R_n - G$.

2.4. LAI estimate

According to Beer's law, the silhouette area index of leaves, plus stems and branches (plant area index, PAI), can be expressed as (Holst et al., 2004)

$$\text{PAI} = \text{LAI} + b = -\frac{1}{k} \ln(R_t), \quad (1)$$

where b is an empirical constant representing the contribution of stems and branches to radiation extinction, k is the extinction coefficient, and R_t is the radiative transmittance defined as S_b/R_s . Once the parameters b and k are determined, the temporal variation in LAI can be produced by Eq. (1) with continuous monitoring of R_t (see Holst et al., 2004; Maass et al., 1995; Wang et al., 2004).

The parameters b and k were determined to be 1.03 and 0.52, respectively, using the least squares linear regression in Eq. (1) between periodic data of LAI estimated from litter-fall collection

and R_t observation (Yoshifuji et al., 2014). The parameter k is known to vary with zenith angle and cloudiness (Baldocchi et al., 1984; Holst et al., 2004), so to reduce this effect, we took the 15-day moving average of daily R_t ($R_{td,ave}$) as an input into Eq. (1), calculated by averaging R_t values measured during the period when the zenith angle was greater than 75° . The periodic LAI data were calculated for dates on which we measured litter-fall, during the period from the day of the maximum R_t in the dry season to the day of the minimum R_t in the previous rainy season. Since the teak canopy was completely dormant (i.e., LAI = 0) on the day with the maximum R_t , the LAI for each day on which we measured litter-fall was calculated by multiplying the total dry weight of the litter lost from the canopy during the period between that day and the day of the maximum R_t with the specific leaf area. Here, the specific leaf area was estimated to be $87.6 \text{ cm}^2 \text{ g}^{-1}$ from the measurements of 40 sample leaves.

Using a plant canopy analyzer (LAI-2000: Li-Cor), we periodically checked whether the LAI estimates from Eq. (1) were reasonable and determined that no large discrepancies existed between the two readings throughout the study period.

2.5. Calculation of canopy stomatal conductance

The surface conductance (G_s ; m s^{-1}), representing the efficiency of exchange between the top vegetation surface and atmosphere, was calculated using the actual data on LE from the inverted Penman–Monteith equation as (Dolman et al., 1991)

$$G_s^{-1} = \left(\frac{\Delta}{\gamma} \beta - 1 \right) G_a^{-1} + \frac{\rho C_p \text{VPD}}{LE \gamma} \quad (2)$$

where Δ is the ratio of the charge of saturation water vapor pressure to temperature (Pa K^{-1}), γ is the psychrometric constant (Pa K^{-1}), β is the Bowen ratio, ρ is the density of dry air (kg m^{-3}), C_p is the specific heat of air at a constant pressure ($\text{J kg}^{-1} \text{K}^{-1}$), and VPD is the vapor pressure deficit above the canopy (Pa). G_a is the aerodynamic conductance (m s^{-1}), and assuming that the roughness length for momentum and heat fluxes are the same, was estimated as u_*^2/u , where u_* is the friction velocity (m s^{-1}) and u is wind speed (m s^{-1}) above the canopy.

Canopy conductance (G_c ; m s^{-1}), representing the efficiency of canopy transpiration (LE_c ; W m^{-2}), was also calculated from the inverted Penman–Monteith equation implemented in a simple two-layer model (Kelliher et al., 1995) with some modification:

$$G_c^{-1} = \left[\frac{\Delta}{\gamma} \left(\frac{A_c}{LE_c} - 1 \right) - 1 \right] G_a^{-1} + \frac{\rho C_p \text{VPD}}{LE_c \gamma} \quad (3)$$

in which

$$A_c = [1 - \exp(-c_A \text{LAI})] A \quad (4)$$

where A is the total available energy ($=R_n - G$) (W m^{-2}), A_c is the A absorbed by the canopy (W m^{-2}), and c_A is the extinction coefficient. The c_A was determined to be 0.7 ($R^2 = 0.89$) from the field measurements of net radiation above and below the canopy throughout the period from leafless to leafed seasons ($0 \leq \text{LAI} \leq 2.7$) according to Baldocchi et al. (1984). The c_A value of 0.7 is comparable to the values reported in some previous studies (e.g., Baldocchi et al., 1984; Kelliher et al., 1995). LE_c can be expressed as a contribution from the canopy to the total vegetation latent heat flux:

$$LE_c = LE - LE_s \quad (5)$$

in which

$$LE_s = 1.26 \frac{\Delta}{\Delta + \gamma} A_s (1 + d \ln \Theta_{0-60}) \quad (6)$$

and

$$A_s = A - A_c, \quad (7)$$

where LE_s and A_s are the latent heat flux (W m^{-2}) and available energy (W m^{-2}), respectively, at the forest floor, and d is an empirical parameter representing the effect of soil moisture deficit on LE_s . Here, the LE_s in the wet season was assumed to be the potential evaporation described by Priestley and Taylor (1972) ($E_{PT} = 1.26 \Delta A_s / (\gamma + \Delta)$) because of the low wind speed (=low VPD) at the vegetation floor and moist soil condition. In the dry season, the E_{PT} would be enhanced by increased A_s and would be reduced by the soil moisture deficit, resulting in an LE_s throughout the year as described by Eq. (6). The parameter $d = 0.295$ ($R^2 = 0.83$) was estimated using a nonlinear least squares regression between LE_s calculated from Eq. (6) and LE observed under leafless (i.e., LAI = 0) conditions, where LE can be assumed to be equal to LE_s .

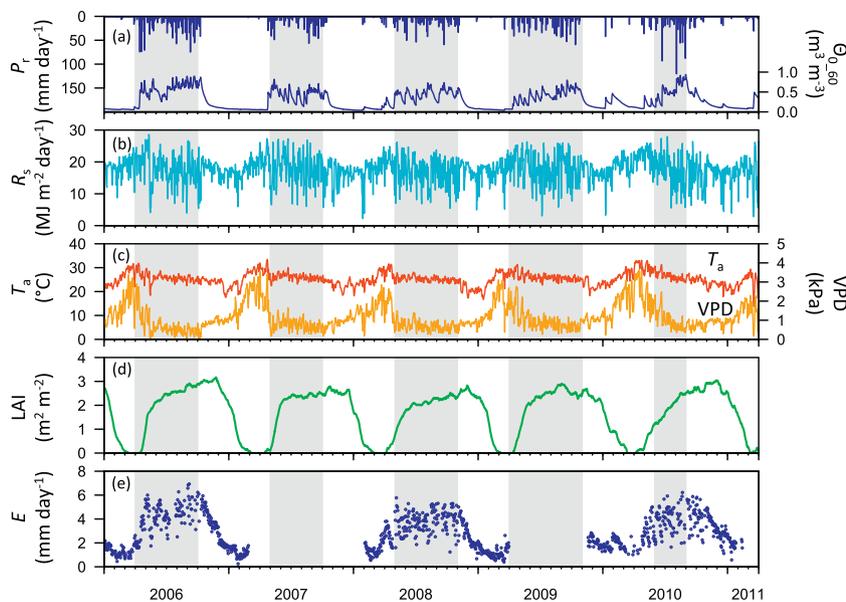


Fig. 2. A year's data on (a) daily precipitation (P_r ; bars, left scale) and relative extractable water in the 0–60-cm soil layer (Θ_{0-60} ; line, right scale), (b) daily total solar radiation (R_s), (c) daily mean air temperature (T_a , left scale) and vapor pressure deficit (VPD, right scale), (d) leaf area index (LAI), and (e) daily total evapotranspiration from a whole ecosystem (ET). Shaded columns represent periods of wet seasons.

We assumed that G_c can be regarded as the parallel sum of the individual leaf's stomatal conductance (e.g., Raupach and Finnigan, 1988; Raupach, 1995), giving

$$g_s = \frac{G_c}{LAI}, \quad (8)$$

where g_s is the mean canopy stomatal conductance per unit leaf area (m s^{-1} ; see Pataki and Oren, 2003). Note that for quality control, we removed g_s values obtained on rainy days and when $VPD \leq 0.6 \text{ kPa}$ (cf. Ewers and Oren, 2000) and $LAI < 1.0$ (cf. Kelliher et al., 1995).

2.6. Stomatal conductance model

To facilitate interpretation of the influence of environmental variables on stomatal behavior, a multiplicative-type function is commonly used, where parameters contained in each function are determined by appropriate nonlinear regression analysis (see Jarvis et al., 1976). Oren et al. (1999b) focused on the relationship between stomatal conductance and VPD as follows (cf. Kumagai, 2011):

$$g_s = g_{sref} - m \ln(VPD), \quad (9)$$

where g_{sref} and m are the reference value of g_s (i.e., the value of g_s at $VPD = 1 \text{ kPa}$) and the sensitivity of g_s to VPD (i.e., $-dg_s/d\ln(VPD)$), respectively. A VPD and g_s data set was subjected to a boundary line analysis designed to select data representing the maximum conductance without the effects of light and soil moisture along the range of VPD (e.g., Martin et al., 1997). We used the boundary line analysis of the relationships between VPD and g_s , to determine the parameters g_{sref} and m (e.g., Schäfer et al., 2000; Ewers et al., 2001, 2005). The upper boundary line was derived by regressing Eq. (9) with data obtained as follows: (1) partitioning the g_s response to VPD into 0.5-kPa VPD intervals, (2) calculating the mean and standard deviation of the g_s data within each interval of VPD, (3) removing outliers ($P < 0.05$, Dixon's test; see Sokal and Rohlf, 1995), (4) selecting data above the mean plus 1 standard deviation of g_s , and (5) averaging the selected data for each VPD interval.

Oren et al. (1999b) fitted Eq. (9) to literature data from porometry-based leaf-level measurements, and regressed with m and g_{sref} . As a result, they found that the interspecific response of m ($= -dg_s/d\ln(VPD)$) to g_{sref} was well correlated with a slope of 0.6. Note that this result generalized the previous findings, where the sensitivity of g_s to VPD increased with g_{sref} regardless of whether the variation in g_{sref} was related to some other environmental variables.

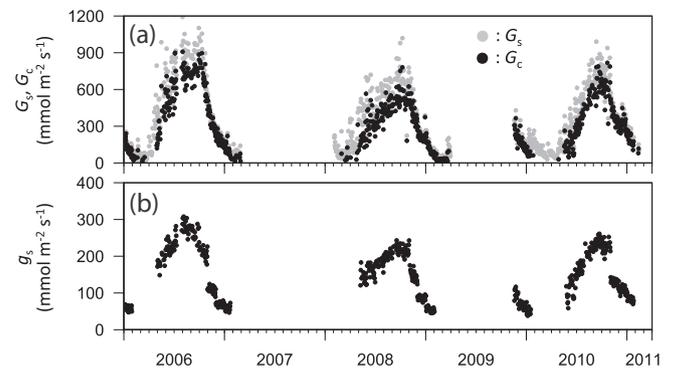


Fig. 3. Seasonal patterns of midday (1000–1500 LT) averaged (a) surface conductance (G_s) and canopy conductance (G_c), and (b) canopy stomatal conductance (g_s).

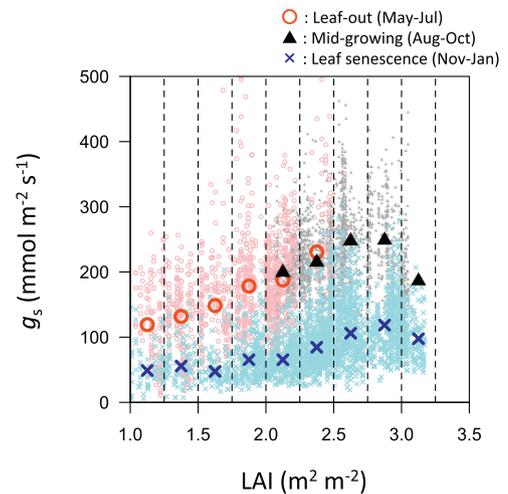


Fig. 4. The relationship between the leaf area index (LAI) and canopy stomatal conductance (g_s). Smaller and larger marks represent 30-min data (1000–1500 LT) and their averages in bins of $LAI = 0.25$, respectively.

3. Results

3.1. Environmental and eddy flux data

Daily data of environmental factors, LAI, and whole ecosystem ET for the study period 2006–2011 are shown in Fig. 2. The mean annual rainfall during 2006–2010 was $1326 \pm 243 \text{ mm}$

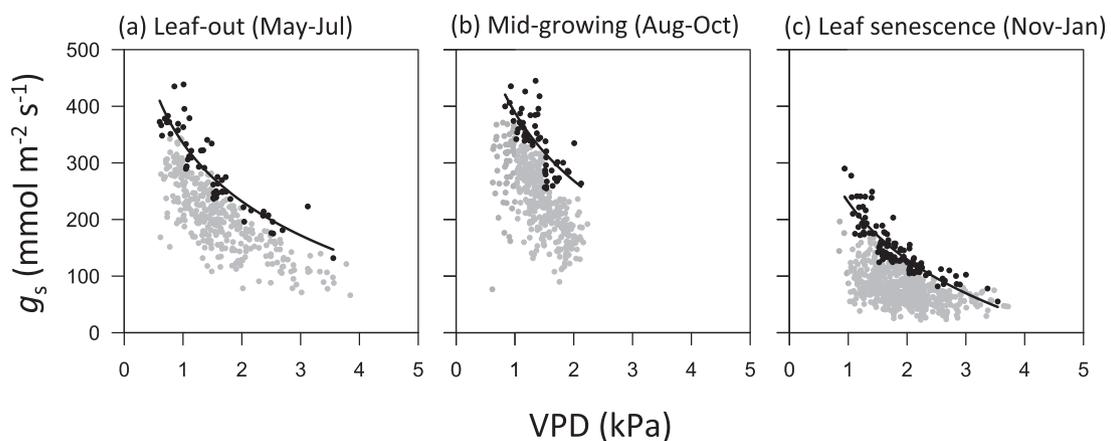


Fig. 5. Representative relationships between vapor pressure deficit (VPD) and canopy stomatal conductance (g_s) on a 30-min basis (1000–1500 LT) for the (a) leaf-out (May–July), (b) mid-growing (August–October), and (c) leaf-senescence (November–January) seasons in 2006. Thick circles and lines represent the selected data and results from the boundary line analysis (see text).

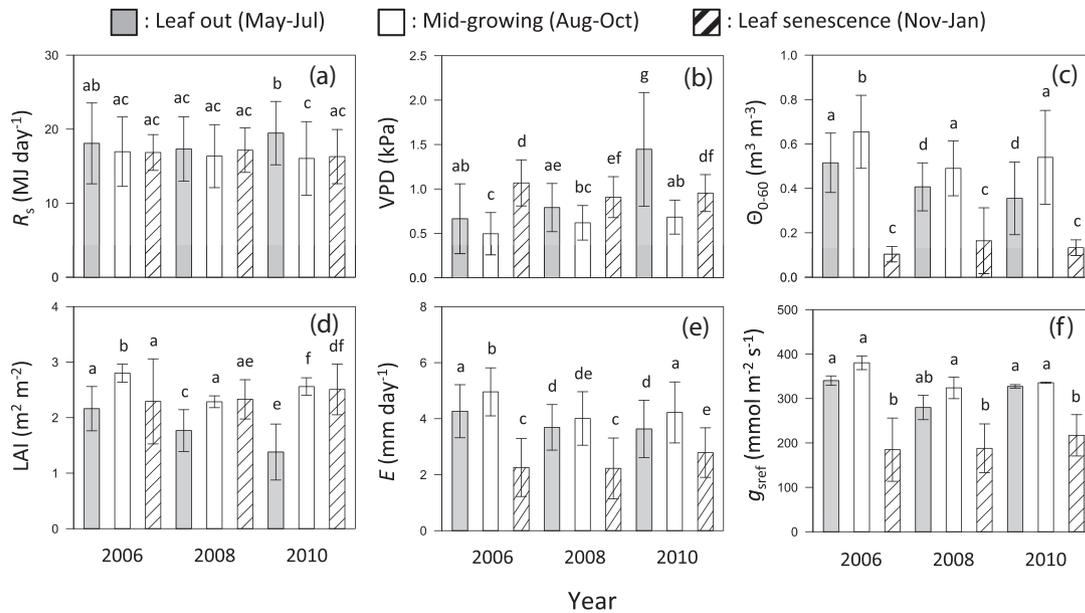


Fig. 6. (a) Daily total solar radiation (R_s), (b) daily mean vapor pressure deficit (VPD), (c) relative extractable water in the 0–60-cm soil layer (Θ_{0-60}), (d) leaf area index (LAI), (e) daily total canopy evapotranspiration (E), and (f) seasonal analysis (see Fig. 5) results in canopy stomatal conductance at VPD = 1 kPa (g_{sref}) for each study period. Values are averaged over each study period, and vertical bars represent the standard deviation. Different letters indicate significant differences among periods within each panel ($P < 0.05$, Tukey's test).

(mean \pm SD). Clear seasonal variation in rainfall was observed around the study area, and we classified wet (monthly $P_r \geq 100$ mm) and dry (monthly $P_r < 100$ mm) seasons according to the “Humid Month” definition by the International Hydrological Program (IHP) of UNESCO (Chang and Lau, 1993; Fig. 2). On average, the wet season occurred during May–October, but distinct interannual variation was detected in the length of the wet season: the shortest and longest seasons during the study period were 3 months in 2010 and 7 months in 2009, respectively. Additionally, on average, Θ_{0-60} was $>0.5 \text{ m}^3 \text{ m}^{-3}$ in wet seasons and $\sim 0.1 \text{ m}^3 \text{ m}^{-3}$ in dry seasons, with interannual variation in the seasonal soil moisture rhythm. Note that Θ_{0-60} reached $0.5 \text{ m}^3 \text{ m}^{-3}$ after heavy rainfall in February 2010, despite the dry season.

The mean annual R_s was $17.6 \pm 4.2 \text{ MJ day}^{-1}$, with a clear seasonal variation: a decrease in R_s caused by cloud cover in the wet season was compensated for by the maximal solar elevation during the wet season, and thus the maximum R_s occurred during the wet season, and mean values in the wet and dry seasons were similar. Maximum daily mean T_a surpassed 30°C in the late dry seasons, with a minimum of $\sim 20^\circ\text{C}$ in the early dry seasons. VPD showed a distinct seasonal variation: the highest daily mean VPD ($\sim 3.0 \text{ kPa}$) occurred in the late dry seasons because the highest T_a and the lowest values ($\leq 1.0 \text{ kPa}$) were detected throughout the wet seasons.

Seasonal variation in LAI and canopy duration can be explained by seasonal variation in soil moisture availability; the LAI values reached a plateau in the early wet seasons. Notably, the timing of leaf-out and leaf-fall, i.e., canopy duration, were considerably different between years. The eddy ET flux (i.e., the whole ecosystem ET including ET from canopy trees and the forest floor) also showed a clear seasonal variation similar but not perfectly corresponding to that in LAI because of seasonal variation in leaf physiology and the effect of the forest floor ET in leafless periods. The whole ecosystem ET reached a plateau at $\sim 6.0 \text{ mm day}^{-1}$ in the wet seasons.

3.2. Seasonal variation in stomatal control

Seasonal patterns in averaged G_s , G_c , and g_s at midday (1000–1500 LT) are compared in Fig. 3. During the study period,

G_s reached $900 \text{ mmol m}^{-2} \text{ s}^{-1}$ in wet seasons and a minimum of $\sim 100 \text{ mmol m}^{-2} \text{ s}^{-1}$ in dry seasons (Fig. 3a). Maximum and minimum values of G_c were $\sim 800 \text{ mmol m}^{-2} \text{ s}^{-1}$ in wet seasons and almost zero in the dry (i.e., leafless) seasons, respectively. Differences between G_s and G_c due to the contribution of forest floor ET to total ET were somewhat constant ($\sim 100 \text{ mmol m}^{-2} \text{ s}^{-1}$), and thus, we considered that the forest floor ET did not vary appreciably. Maximum values of G_s ($\sim 700 \text{ mmol m}^{-2} \text{ s}^{-1}$) and G_c ($\sim 600 \text{ mmol m}^{-2} \text{ s}^{-1}$) in 2008 were less than the maximum values in other years mainly because of the lower maximum LAI (see Fig. 2d). Although g_s was estimated as G_c/LAI (see Eq. (8)), the seasonal variation in g_s was similar to that in G_c in that the maximum g_s in 2008 was less than that in other years (Fig. 3b). This implies that the reduction in g_s in 2008 might have been affected by physiological status at the leaf-scale.

The hysteretic relationship between LAI, whose intra-annual variation can be an index for changing seasons, and the 30-min

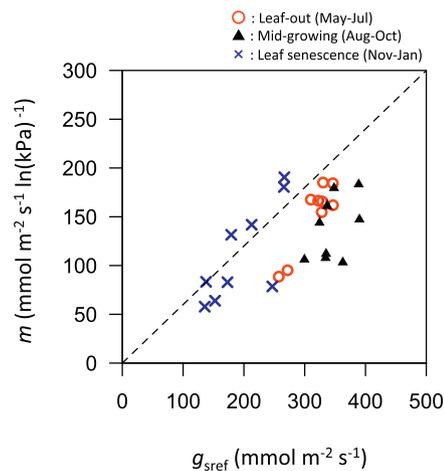


Fig. 7. Relationship between the monthly canopy stomatal conductance (g_s) at vapor pressure deficit (VPD) = 1 kPa (g_{sref}) and sensitivity of g_s to VPD [$-dg_s/d\ln(\text{VPD})$; m]. The theoretical proportion 0.60 (Oren et al., 1999b) is shown by a dashed line.

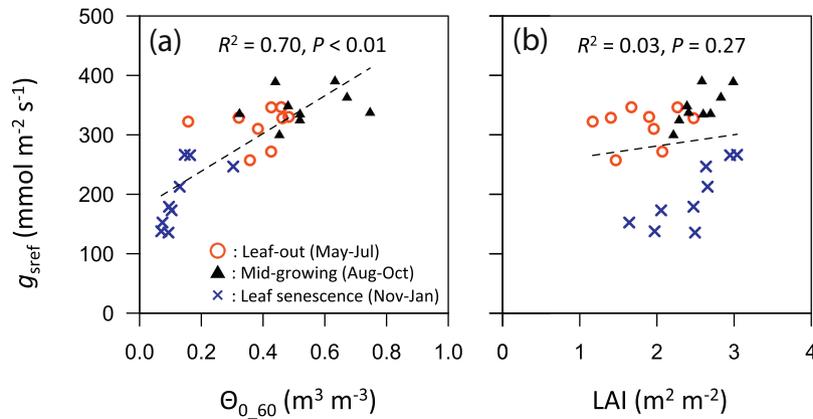


Fig. 8. Monthly canopy stomatal conductance at vapor pressure deficit = 1 kPa (g_{sref}) as a function of (a) relative extractable water in the 0–60-cm soil layer (Θ_{0-60}) and (b) leaf area index (LAI). Lines denote linear regressions for all data.

midday g_s (Fig. 4), enabled us to define the phenological periods as leaf-out (May–July), mid-growing (August–October), and leaf-senescence (November–January) seasons. This relationship also showed that although the forest had the same LAI in both the leaf-out and leaf-senescence seasons, g_s was higher in the former. The parameter g_s was the highest in the mid-growing season, when LAI reached its highest value of the year. When LAI began declining after its peak, g_s suddenly decreased (Fig. 4), suggesting that the leaf-level gas exchange ability is higher during the leaf-out and mid-growing seasons and lower during the leaf-senescence season.

3.3. Controlling factors for seasonal and interannual variations in g_s

The representative relationship between VPD and g_s for each season is shown in Fig. 5. We obtained the reference conductance, g_{sref} , and the rate of decline in g_s , m , by fitting Eq. (9) to the upper boundaries of the VPD – g_s data. In all seasons in 2006, g_s declined with increasing VPD, but neither g_{sref} nor m was significantly different between the leaf-out and mid-growing seasons, but were higher in these seasons than in the leaf-senescence season.

To further investigate factors affecting seasonal and interannual variations in g_s , we performed the seasonal analysis used in Fig. 5 for all years; data, including some environmental factors, are shown in Fig. 6. The seasonality of g_{sref} was as follows: leaf-out season \approx mid-growing season $>$ leaf-senescence season, and we found no significant interannual difference in seasonality (Figs. 5 and 6f). Note the nonsignificant seasonal and interannual variations in m (data not shown). However, seasonal variations in E , their controlling factors, VPD, Θ_{0-60} , and LAI, and their interannual variations were apparent (Fig. 6b–e). Conversely, seasonal and interannual variations in R_s were unclear and seasonal averages were approximately constant (Fig. 6a).

The proportion $m/g_{sref} \approx 0.6$ results from the regulation of the minimum leaf water potential (ψ_L) to prevent excessive xylem cavitation, and a value <0.6 denotes less strict regulation of ψ_L (Oren et al., 1999a; Ewers et al., 2005, 2007). Using the same analysis as in Fig. 5 but on a monthly basis, we plotted monthly values of g_{sref} and m with the 0.6 proportion in Fig. 7. While the leaf-senescence season data fell almost along the 0.6 line (m/g_{sref} : 0.56 ± 0.05 , mean \pm SD), the leaf-out (0.48 ± 0.06) and mid-growing (0.40 ± 0.03) seasons had lower proportions. This implies that teak trees allow the minimum ψ_L to drop with increasing VPD in the leaf-out and mid-growing seasons, and that during the leaf-senescence season, they have strict stomatal regulation of the minimum ψ_L .

The mean values of g_{sref} differed significantly among the three seasons (ANOVA, $P < 0.05$), and no significant difference was observed in the mean m among seasons and years (ANOVA, $P = 0.36$). However, the m/g_{sref} averaged for all pooled data was 0.48 (Fig. 7), and seasonal estimates of m/g_{sref} did not significantly differ among seasons and years (ANOVA, $P = 0.25$) despite the significant g_{sref} and nonsignificant variation in m .

Again, the m/g_{sref} proportions in the leaf-out and mid-growing seasons were <0.6 and almost 0.6 in the leaf-senescence season, but no significant difference occurred among seasons, implying the existence of partial cancelations; although the seasonal variation in m was not significant, m depended weakly on environmental factors. It would be informative to investigate how the large seasonal and interannual variations in g_{sref} correspond to those in environmental and biological factors (i.e., Θ_{0-60} and LAI; Fig. 6). Notably, little variation occurred in R_s , and the effect of VPD was already taken into account for the variation in g_s (Fig. 6). As a result, a significant linear relationship was observed between Θ_{0-60} and g_{sref} (Fig. 8a), but no clear relationship was detected between LAI and g_{sref} (Fig. 8b). This suggests that when considering seasonal and interannual variations (see Fig. 3), a teak tree's stomatal conductance can be described first by soil moisture and then by additional minor factors such as VPD (see Eq. (9)).

4. Discussion and conclusions

Yoshifuji et al. (2014) provided us with the phenological responses of our teak forest to seasonal and interannual climatic fluctuations: leaf-out and onset of transpiration generally occur on day of year 90–100. However, when the initial date of $\Theta_{0-60} > 0.2$ ($ID_{0.2}$) is later than day of year 90, the dates of leaf-out and onset of transpiration are equivalent to $ID_{0.2}$. However, Yoshifuji et al. (2014) did not clarify the cause of leaf-senescence timing and variations in leaf physiological traits, both critical parameters for delineating forest canopy gas exchange. In this study, we used a combination of the actual ET flux data from 6-year period of field measurements and the inversed version of a simple 2-layer ET model (Kelliher et al., 1995) for estimating mean canopy stomatal conductance (g_s). This analysis enabled us to extract the teak canopy conductance from total surface conductance, including the canopy and forest floor effects. Finally, we examined how environmental and biological factors affected g_s in a tropical seasonal forest of Southeast Asia, allowing us to consider hydrologic and energy fluxes in this region.

Promising indexes are available for the purposes of examining the environmental and biological control of stomatal behavior, i.e.,

the reference value of g_s and the sensitivity of g_s to VPD, which are g_{sref} and m in Eq. (9), respectively (Oren et al., 1999b). We derived seasonal and interannual variations in g_{sref} and m by fitting the long-term g_s estimate to Eq. (9) and found seasonal variation in g_{sref} to be as follows: May–July \approx August–October $>$ November–January (Fig. 6f).

The start of an increase or decrease in g_s was initiated by the expansion or falling of leaves, respectively (Fig. 4). Hysteresis was also evident in the LAI– g_s relationship, suggesting that in any given year, g_s peaks come about one or two months earlier than full-leaf expansion and declines after the peak of LAI. This temporal change in g_s might be related to the effects of soil moisture on stomatal aperture and/or the effects of leaf age on the decline in photosynthetic capacity. The linear relationship between soil moisture and g_{sref} found in this study (Fig. 8a) is key for understanding the g_s dynamics, which correspond to the temporal variation in soil moisture. However, Wilson et al. (2000, 2001) reported that, in a temperate deciduous forest, maximum carboxylation rate was maximized ($\sim 55 \mu\text{mol m}^{-2} \text{s}^{-1}$) rapidly following the start of leaf development (day of year = 90–130) and decreased in the middle and late summer (day of year = 180–290), depending on leaf age, even when leaf nitrogen does not show significant seasonal variation. Kitajima et al. (2002) reported that nitrogen use efficiency changes to about one half or one-third in 90 days after full leaf expansion for tropical pioneer tree species in a seasonally dry forest in Panama. These imply that a seasonal change in the fractional allocation of leaf nitrogen to Rubisco may be occurring (see Niinemets and Tenhunen, 1997) and that the g_s dynamics could be attributable to such a leaf-scale “inside job”. Further research on leaf-scale ecophysiology, such as the seasonal variation in the leaf nitrogen content and the maximum rate of carboxylation is required.

In addition to the significant seasonal variation in g_{sref} , we found a nonsignificant seasonality in m and little interannual variation in both g_{sref} and m . This results in a m/g_{sref} of almost 0.6 in November–January (leaf-senescence season) and a value less than 0.6 in May–July (leaf-out season) and August–October (mid-growing season). A proportion of 0.6 was predicted from the results of the plant transpiration model coupled with the hydraulic constraint model in which plants control their transpiration rate via stomatal regulation to protect the transport system from excessive loss of hydraulic function (Oren et al., 1999b; Cochard et al., 2002; Ewers et al., 2005; Katul et al., 2009). Thus, we demonstrated that teak trees in our study area have strict stomatal regulation to maintain a constant difference between leaf water potential (ψ_L) and soil water potential during the leaf-senescence season; they seem to have less strict stomatal regulation during the leaf-out and mid-growing seasons (see Herbst et al., 2008; Kumagai et al., 2008; Naithani et al., 2012). Kumagai et al. (2008) hypothesized that a proportion of <0.6 for Japanese cedar would confer a carbon uptake advantage to tree species adapted to moist soil conditions, as little risk of water stress-induced hydraulic failure would exist and g_s would not need to decrease with increasing atmospheric demand. In this study, the proportion m/g_{sref} was ~ 0.6 during the leaf-senescence season and less than 0.6 in the leaf-out and mid-growing seasons, when the trees were under drought and moist conditions, respectively (see Fig. 6c); thus, our results are consistent with the hypothesis of Kumagai et al. (2008). Note that these characteristics are realized by a linear decrease in g_{sref} with soil moisture (Fig. 8a) and a nonsignificant variation in m .

Regarding the regulation of water status, plants can be categorized as isohydric or anisohydric (see McDowell et al., 2008). Isohydric plants regulate transpiration by stomatal closure to maintain constant ψ_L , thus avoiding drought-induced hydraulic failure. In contrast, anisohydric plants have less stomatal sensitivity and allow ψ_L to decrease with decreasing soil moisture. On an

intra-annual timescale, the teak trees showed sensitive stomatal regulation during the leaf-senescence season (i.e., under drought conditions), displaying isohydric behavior. However, anisohydric behavior during the leaf-out and mid-growing seasons may be more favored under moist environments in which little risk of hydraulic failure exists (see Kumagai and Porporato, 2012b). This combination of isohydric and anisohydric behaviors is an efficient way to manage water use. It is characteristic of these teak trees to take advantage of the wet season (i.e., under moist conditions) via productivity, but to avoid the risk of hydraulic failure in the dry season (i.e., under drought conditions).

The tropics of Southeast Asia can be generally classified into two regions based on the seasonal variation in precipitation (see Fig. 3 in Kumagai et al., 2005), with weak and strong seasonalities, corresponding to regions of tropical rain forest and tropical seasonal forest, respectively. While a clear difference between wet and dry seasons occurs in tropical seasonal forests, precipitation in tropical rain forests is abundant throughout the year (e.g., Kumagai et al., 2005; Yoshifuji et al., 2006). Furthermore, deciduous and evergreen forests are intermingled in tropical seasonal forest regions (e.g., Tanaka et al., 2008), which complicates research. Such seasonalities might affect hydrologic fluxes above and within vegetation via environmental changes, such as in air temperature and humidity. The g_s is among the most promising index for representing altered hydrologic fluxes and their environmental controls over vegetation surface. In this study, a simple 2-layer ET model was successfully used to separate latent heat fluxes from canopy trees and the vegetation floor, and to derive the canopy trees' g_s under the difficult condition of a tropical deciduous forest. However, this analysis assumed the studied canopy trees to be “monoculture”, and thus further studies should consider tropical deciduous forests with more complicated species composition.

Soil moisture dynamics, influenced by perturbations following precipitation, is the most important factor controlling hydrological, atmospheric, and ecological processes through the soil–plant–atmosphere continuum (see Kumagai et al., 2009). In this context, a linear relationship between soil moisture and g_{sref} could allow for a simple and straightforward treatment of the tropical seasonal forest canopy g_s , which is the important submodel needed for computing atmosphere–vegetation exchanges in global climate and vegetation dynamics models (see Sato et al., 2007). However, this relationship was only clearly obtained from this study site and is suspected to be site-specific. Because data regarding land surface processes in tropical deciduous forests are lacking, a need exists to collect data from a wider range of the tropics.

Although both occur in Southeast Asia, our study site in the tropical seasonal forest is clearly different from a tropical rain forest (e.g., Kumagai and Porporato, 2012a), which sporadically experiences short periods of drought, in terms of the strong control of wet and dry periods on forest biology, i.e., the duration between leaf-out and leaf-fall and the period of active canopy gas exchange. For example, the Amazonian tropical rain forest (e.g., Malhi et al., 1998) has some seasonal variation in precipitation, and Amazonian tropical semi-deciduous forests (e.g., Vourlitis et al., 2008) occupy a climatic transition zone between rain forest and savanna. An analysis of climatic trends of global tropical forests during the period 1960–1998 showed that rainfall has declined more significantly in Southeast Asia than in Amazonia, and that the El Niño–Southern Oscillation (ENSO) is the primary driver of drought in the former (Malhi and Wright, 2004). In addition, a close relationship was identified between the interannual variation in the onset of monsoons and ENSO on the Indochina Peninsula: the ENSO appears to be related to late monsoon onset, leading to a reduction in annual precipitation (Zhang et al., 2002). In addition, the projected growth of atmospheric greenhouse gases in this century will significantly impact global and regional temperatures, with concomitant

modifications to precipitation patterns (Intergovernmental Panel on Climate Change, 2013). Global climate models have shown more frequent El Niño-like conditions from human-induced greenhouse warming (e.g., Timmermann et al., 1999). Therefore, an urgent need exists to further examine current and future perturbations in the hydrological, atmospheric, and ecological processes in the tropical seasonal forests of Southeast Asia, resulting from seasonal and interannual (cf. ENSO-related) variations in precipitation in the TSF of SEA, using, e.g., the land–atmosphere exchange characteristics determined in this study.

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