

Interannual variation in transpiration onset and its predictive indicator for a tropical deciduous forest in northern Thailand based on 8-year sap-flow records

Natsuko Yoshifuji,¹ Hikaru Komatsu,^{2,3*} Tomo'omi Kumagai,² Nobuaki Tanaka,⁴ Chatchai Tantasirin⁵ and Masakazu Suzuki⁶

¹ Graduate School of Agriculture, Kyoto University, Sakyo-ku, Kyoto, Japan

² Kasuya Research Forest, Kyushu University, Sasaguri, Fukuoka, Japan

³ School of Forestry and Resource Conservation, National Taiwan University, Taipei 106, Taiwan

⁴ University Forest in Aichi, Graduate School of Agriculture and Life Sciences, The University of Tokyo, Seto, Aichi, Japan

⁵ Faculty of Forestry, Kasetsart University, Bangkok, Thailand

⁶ Graduate School of Agricultural and Life Sciences, The University of Tokyo, Tokyo, Japan

ABSTRACT

In deciduous forests, leaf-out and leaf-fall determine the durations of canopy transpiration and photosynthesis and affect interannual variations in energy, water, and carbon exchanges. Despite numerous studies on the interannual variation in vegetation phenology and its modelling for boreal and temperate deciduous forests, few studies have examined these topics for tropical deciduous forests. We quantified the extent of interannual variation in the transpiration onset dates in a teak plantation in northern Thailand, one of the major deciduous forests in Thailand, on the basis of 8 years of sap-flow measurements and developed an empirical model to predict their interannual variation through correlation analysis with environmental variables. Interannual variation in the transpiration onset date at this site spanned 41 days over the 8-year observation period. The transpiration onset date corresponded to the date when the leaf area index reached 0.2–0.4. Interannual variation in the transpiration onset date was reproduced by the date when relative extractable water in the soil layer of 0–0.6 m depth became greater than 0.2 with a root mean square error of 10 days. The interannual variation in the transpiration onset dates for the studied tropical deciduous forest site was greater than that of deciduous forests in temperate and boreal regions, implying the considerable potential effect on annual energy, water, and carbon exchanges between vegetation and the atmosphere. Our results also suggest that the use of soil moisture would allow predictions of interannual variations in the transpiration onset and the leaf-out for deciduous forests in tropical regions. Copyright © 2011 John Wiley & Sons, Ltd.

KEY WORDS transpiration onset; interannual variation; tropical deciduous forest; phenology; sap flow

Received 25 February 2011; Accepted 27 February 2011

INTRODUCTION

Examinations of energy, water, and carbon exchanges between vegetation and the atmosphere are considered critical in various research fields such as meteorology, ecology, and hydrology (Granier *et al.*, 1999; Pitman, 2003; Komatsu *et al.*, 2008). In deciduous forests, vegetation phenology such as leaf-out and leaf-fall dates determine durations of canopy transpiration and photosynthesis and affect interannual variations in energy, water, and carbon exchanges (White *et al.*, 1999; Black *et al.*, 2000; Aubinet *et al.*, 2002; Carrara *et al.*, 2003; Barr *et al.*, 2004; Saigusa *et al.*, 2005). For example, Aubinet *et al.* (2002) suggests that one day earlier leaf initiation could induce a 3–5 g Cm⁻² day⁻¹ increase in carbon sequestration in the spring by the beech in a mixed forest in Belgium.

Among various terrestrial ecosystems, tropical forests account for a large portion of terrestrial net carbon

sequestration (Malhi and Grace, 2000) and are an important latent energy source of the global and regional climate (Lean and Warrilow, 1989; Kanae *et al.*, 2001). As deciduous and dry forests account for 43% of the total tropical forest area (Food and Agriculture Organization, 2001), it is important to clarify the interannual variation in leaf-out and leaf-fall in tropical deciduous forests in examining the interannual variation in the water and carbon exchange of tropical forests.

Numerous studies have examined interannual variations in leaf-out and leaf-fall and resulting changes in water and carbon exchanges in temperate and boreal deciduous forests (Black *et al.*, 2000; Wilson and Baldocchi, 2000; Barr *et al.*, 2006). Prediction models of the interannual variation in leaf-out and the consequent onset of carbon assimilation have also been developed for temperate and boreal forests (Baldocchi *et al.*, 2005; Linkosalo *et al.*, 2006). However, only a few studies have investigated these topics for tropical deciduous forests. Despite several studies examining the leaf phenology of tropical deciduous tree species at an individual tree scale (Reich and Borchert, 1982; Borchert, 1994; Elliot *et al.*,

* Correspondence to: Hikaru Komatsu, School of Forestry and Resource Conservation, National Taiwan University, 1, Sec. 4, Roosevelt Road, Taipei 106, Taiwan. E-mail: kmthkr@gmail.com

2006), studies at stand or larger scales based on long-term observation data are still rare.

Our previous study (Yoshifuji *et al.*, 2006) examined interannual variations in onset and cessation of tree transpiration in a tropical deciduous forest in northern Thailand, based on 3-year sap-flow data. We reported that both the onset and cessation of tree transpiration varied more than 30 days and that rainfall and soil water content varied markedly among the 3 years, implying that these factors correspond to the onset and cessation dates of tree transpiration. Our previous study was seminal in reporting interannual variations in onset and cessation dates of transpiration for a tropical deciduous forest. However, the study was preliminary, because it was based on only a 3-year record and, therefore, did not develop a model to predict dates of the onset and cessation of transpiration because of the insufficient length of the data period (i.e. 3 years).

In this study, we focus on the date of transpiration onset. After quantifying its interannual variation based on 8-year sap-flow records, we examine whether soil water content is an indicator of the transpiration onset employing correlation analysis. We also examine the relationship between transpiration onset and leaf-out. The results show the validity of using soil water content as a key controlling factor in phenology models for tropical deciduous forests.

MATERIALS AND METHODS

Site and measurements

Measurements were conducted in an even-aged teak (*Tectona grandis* Linn. f.) stand planted in 1968 in Mae Moh plantation, Lampang province, northern Thailand (18°25'N, 99°43'E, 380 m above sea level). Teak occurs naturally on the Indochina peninsula and in India and is now planted widely throughout the tropics because of its commercial value (Pandey and Brown, 2000; Tanaka *et al.*, 2008). Teak plantations are prevalent in Thailand (Krishnapillay, 2000), especially in northern areas and are completely leafless in the late dry season. The soils in the Mae Moh plantation were classified as Loamy Paleustults (Thai classification).

There was a 26-m tall research tower at the study site and a new 40-m tall scaffold tower was constructed approximately 100 m from it in June 2004. Meteorological variables above the canopy were measured on the 26-m tall tower from June 2000 to March 2006 and on the new scaffold tower from July 2005. Details of sensor installation and measurements of meteorological variables on the 26-m tall tower were described in Yoshifuji *et al.* (2006).

The details of the measurements on the new scaffold tower are as follows. The incident solar radiation above the canopy (S_0) was measured with a pyranometer (CMP21, Kipp & Zonen, Delft, The Netherlands) at a height of 41 m. Air temperature (T_a) and relative humidity (h) above the canopy were measured with

a naturally ventilated psychrometer (HMP45A, Vaisala, Helsinki, Finland) at a height of 39 m. S_0 , T_a , and h were measured every 5 s and their 10-min averages were recorded with data loggers (CR23X and CR1000, Campbell Scientific, Logan, UT, USA). Rainfall was measured at an open site approximately 500 m from the tower as detailed in Yoshifuji *et al.* (2006). Volumetric soil water content (θ ; $\text{m}^3 \text{m}^{-3}$) was measured about 5 m from the 26-m tall tower at depths of 0.1, 0.2, 0.4, and 0.6 m with time domain reflectometers (TDR; CS-615, Campbell Scientific) at 60-min and 10-min intervals from 2000 to July 2005 and from August 2005 to present, respectively. Data were recorded with a data logger (CR10X or CR1000, Campbell Scientific).

Solar radiation below the canopy (S_b) was measured on the forest floor at a height of approximately 0.5 m, 30 m from the 26-m tall tower, with a pyranometer (MS401, EKO, Tokyo, Japan, September 2000–August 2008; CMP21, Kipp & Zonen, August 2008–present), referred to as the main pyranometer hereafter. To examine the spatial variation in S_b , six additional pyranometers (IKS-37, Koito, Kanagawa, Japan; self-made solar radiation sensors with photodiodes) were installed in August 2005 on the forest floor at a height of approximately 1.0 m in a $200 \times 130 \text{ m}^2$ plot located about 350 m from both towers. The $200 \times 130 \text{ m}^2$ plot was divided into four subplots ($100 \times 65 \text{ m}^2$ each), and one or two sensors were installed around the centre of each subplot. All these data were collected every 5 s and the average 10-min value was recorded with a data logger (CR10X).

Sap flow measurements were performed for five *T. grandis* trees within 10 m of the 26-m tall tower. They were selected among trees for which the height and diameter at breast height (DBH) were representative of the dominant classes at the site. Tree density, tree height, and DBH at the site were measured in two $50 \times 30 \text{ m}^2$ plots, one of which includes the 26-m tall tower and the other the new scaffold tower. The mean tree density of both plots, including some tree species other than *T. grandis*, was $343 \text{ trees ha}^{-1}$. The mean tree height and DBH of *T. grandis* in 2006 were 21.2 m and 23.1 cm, respectively. The minimum and maximum heights of sampled trees in 2006 were 18.1 and 19.9 m, respectively, and the minimum and maximum DBHs were 19.1 and 22.9 cm, respectively.

For the five trees, the heat pulse velocity (HPV; cm h^{-1}) was measured using heat pulse sensors (HP-1, Hayashi Denko, Tokyo, Japan). Six sensors were installed into the outer xylem of tree stems at a height of 1.3 to 1.5 m. Details of sensors and their installation were in Yoshifuji *et al.* (2006). Three sensors were installed on two sample trees in May 2000, and the other three sensors were installed on the remaining three trees in November 2001. Sensors were reinstalled several times during the measurement period. Data were recorded every 20 min on a data logger (CR10X). The calculation of HPV follows Closs (1958). HPV tends to underestimate actual sap flux when sap flux is large (Swanson and Whitfield, 1981). This means that HPV does not always

correlate linearly with transpiration; nevertheless, HPV can show the relative variation in transpiration.

Leaf litter was collected by four litter-fall traps with a diameter of 80 cm set 5–15 m from the pyranometer (CMP21) every 2 weeks from September 2000 to September 2005, and the dry weight was measured. Collecting litter with small traps may result in considerable error in the litter-fall amount per area because leaves of teak trees were quite large, often as large as $35 \times 50 \text{ cm}^2$. We thus compared the dry weight of litter-fall per area measured using litter traps with 80 cm diameter and that measured using litter traps with 150 cm diameter at the site. The latter was 80% of the former, indicating the overestimation of the dry weight of litter-fall per area when using the litter traps with 80 cm diameter. Thus, the dry weights obtained using litter traps with 80 cm diameter were corrected by multiplying by 0.8.

Methods of analysis

We first quantified interannual variations of the date of transpiration onset on the basis of sap-flow data. We also examined the relationship between transpiration onset and leaf area index (LAI). Here, the time series of the LAI was based on continuous data of above- and below-canopy solar radiation and the periodic LAI data derived from litter-fall measurement. We then investigated whether soil water content could be an indicator to predict the transpiration onset dates using the correlation coefficient (R) and root mean square errors (RMSE) determined from the differences between the observed transpiration onset dates and the estimates based on the soil water content.

The date of transpiration onset was defined as the day when the daytime (06:00–18:00 h local time) mean HPV became greater than the maximum nighttime (00:00–05:40 h local time) HPV. Thus, the date of transpiration onset was the day when the diurnal trend in HPV was first observed. Figure 1 shows the time series of HPV measured by one of six sensors in the beginning of the rainy season in 2007 [from day of year (DOY) 125 to 139] as an example to illustrate the validity of this definition. The onset date for this sensor in 2007 was determined to be DOY 128. While the HPV did not have diurnal variations before the onset date determined,

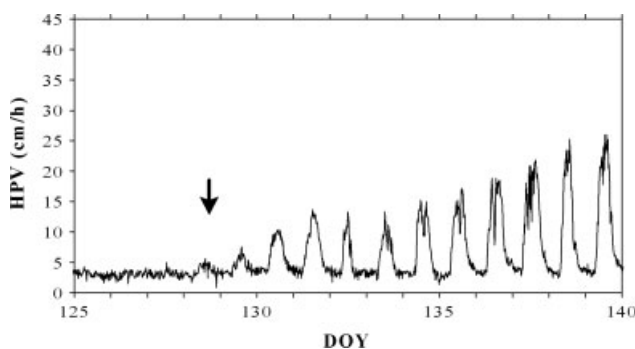


Figure 1. Time series of the HPV measured by one of the six sensors (solid line) from DOY 125 to 139 (May 5–19) in 2007. The vertical arrow shows the date of transpiration onset determined by the sensor.

clear diurnal variation was observed and increased in magnitude after the onset date. The date of transpiration onset was determined for each sensor and their averaged date of transpiration onset was calculated.

The daytime (06:00–18:00 h local time) mean HPV (V_d) was calculated for each sensor as an index for the seasonal variation in transpiration. In long-term continuous measurements, HPV tends to decrease gradually because of a decline in water transport ability around the implanted sensors, which might be caused by the deposition of resin in the xylem vessels around the sensors or cavitation (Smith and Allen, 1996) and/or by changes in the insertion depth because of circumferential tree growth. To remove the influence of this phenomenon, we calculated the relative mean daytime HPV (V) as

$$V = \frac{V_d - V_{d_{\min}}}{V_{d_{\max}} - V_{d_{\min}}} \quad (1)$$

where $V_{d_{\min}}$ is the minimum V_d over the entire observation period and $V_{d_{\max}}$ is the maximum V_d during each phenological year; i.e. from the day of $V_{d_{\min}}$ to that day the next year.

There are several popular methods for *in situ* measurement of the LAI: using a plant canopy analyzer (e.g. LAI-2000, LI-COR, Nebraska, USA), fish-eye image analysis, litter-fall collection, and visual checking. However, manual measurement employing these methods provides only sporadic data. Continuous monitoring of radiative transmittance ($R_t = S_b/S_0$) is often used to determine the temporal variation in LAI (Maass *et al.*, 1995; Holst *et al.*, 2004; Wang *et al.*, 2004). We thus produced continuous LAI data from the continuous monitoring of R_t and periodic LAI data derived from litter-fall collection data.

According to Beer's Law, R_t relates to LAI as (Holst *et al.*, 2004)

$$\text{PAI} = \text{LAI} + b = -\frac{1}{k} \ln(R_t) \quad (2)$$

where PAI is the plant area index, b is an empirical constant representing the contribution of stem and twigs to radiation extinction, and k is the extinction coefficient. k varies with the zenith angle and cloudiness (Baldocchi *et al.*, 1984; Holst *et al.*, 2004). To reduce this effect, we took the 15-day moving average of daily R_t ($R_{t_{\text{d,ave}}}$), which was calculated by averaging R_t values measured during the period with the zenith angle being greater than 75° , as an input into Equation (2). On the other hand, the periodic LAI data were calculated for dates on which litter-fall measurements were made 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. The teak canopy was completely dormant (i.e. LAI = 0) on the day of the maximum R_t . Thus, the LAI for each day on which litter-fall measurements were made was calculated by multiplying the total dry weight of the litter lost from the teak canopy during the period between this day and the day of the maximum R_t with the specific leaf area. Here, the specific leaf area was determined as $121.3 \text{ cm}^2 \text{ g}^{-1}$ from measurements of 40

sample leaves obtained at the site. [Note that previous studies reported a vertical profile in specific leaf area within the forest canopy (Kenzo *et al.*, 2006) but that we did not consider this profile in calculating LAI.] *k* and *b* were then determined as 0.37 and 1.43, respectively, from linear regression of the relationship between $-\ln(R_{td_ave})$ and the LAI (Figure 2).

We used R_{td_ave} data recorded with the main pyranometer installed on the forest floor as the input into Equation (2). R_{td_ave} values were also derived using the

other six pyranometers. We confirmed that the change in R_{td_ave} due to leaf appearance calculated using the main pyranometer synchronized with changes determined using the other six pyranometers (see Discussion Section).

Soil water content of the stand was represented by the relative extractable water in the 0–0.6 m soil layer (Θ) following Kumagai *et al.* (2004):

$$\Theta = \frac{\theta_{0-60} - \theta_{0-60_min}}{\theta_{0-60_max} - \theta_{0-60_min}} \quad (3)$$

where θ_{0-60} , θ_{0-60_max} , and θ_{0-60_min} are the weighted averages of θ in the 0–0.6 m soil layer and the maximum and minimum values over the entire observation period, respectively. Θ ranges from 0 (corresponding to the driest soil conditions during the entire observation period) to 1 (corresponding to the wettest soil conditions). We found many fine roots in the 0–0.4 m soil layer but less around the 0.6 m soil layer when we installed the soil moisture sensors, implying that our soil moisture measurement covers the soil layer in which most fine roots exist.

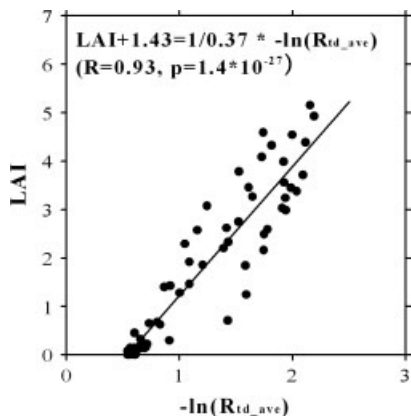


Figure 2. Comparison between $-\ln(R_{td_ave})$ and the LAI calculated from the litter collection data in the leaf-fall season from 2000–2001 to 2004–2005. The regression line, determined using the least-squares method, is written as $LAI + 1.43 = 1/0.37 \times -\ln(R_{td_ave})$. The linear regression line and equation, correlation coefficient (*R*), and *p*-value are also shown.

RESULTS

General climate

The mean annual rainfall and air temperature of the study site from 2001 to 2007 were 1389 mm and 25.5 °C, respectively. Rainfall has clear seasonality because of the influence of the Asian monsoon (Figure 3a). The dry

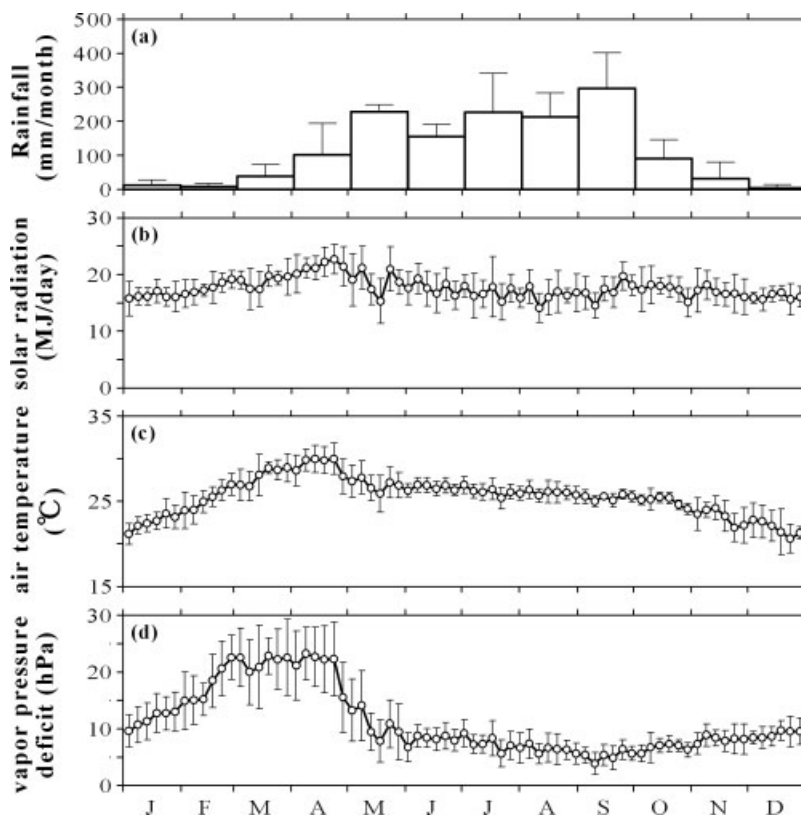


Figure 3. (a) Mean monthly rainfall (mm), (b) 5-day mean solar radiation (MJ day^{-1}), (c) 5-day mean air temperature ($^{\circ}\text{C}$), and (d) 5-day mean vapour pressure deficit (hPa) from June 2000 to July 2008 at the Mae Moh plantation. Vertical bars show the standard deviation.

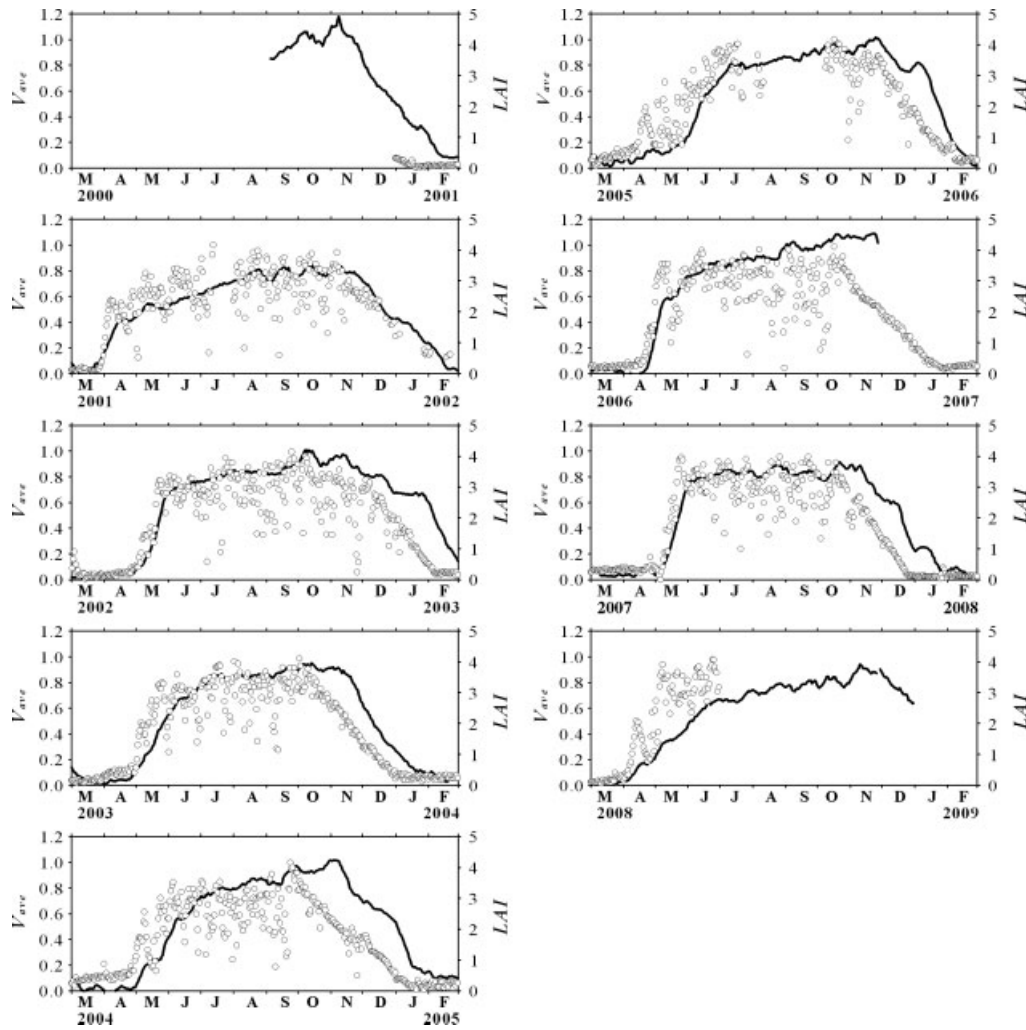


Figure 4. Seasonal variations in the relative mean daytime HPV averaged over all sample trees (V_{ave} ; open circles) and the LAI (solid lines) from 2000 to 2008. There is a considerable lack of data for V_{ave} in the periods of 14 July 2001–31 July 2001, 6 January 2002–1 March 2002, and 12 August 2005–8 October 2005, and for the LAI in the period 28 November 2006–9 March 2007.

season was generally from October to March, during which time the mean monthly rainfall was less than 100 mm; however, the timings of the beginning and end of the rainy season differed from year to year. S_0 , T_a , and vapour pressure deficit (D) also had clear seasonal variation (Figure 3b–d). D increased gradually at the beginning of the dry season and was highest during the late dry season, before declining at the beginning of the rainy season, throughout which it remained low.

Interannual variation in transpiration onset and leaf-out

Figure 4 shows seasonal variations in V_s averaged over all sample trees (V_{ave}) and the LAI for the entire observation period. Both V_{ave} and the LAI were large in the rainy season but were around 0 in the late dry season, indicating that *T. grandis* had a leafy canopy and a high level of transpiration in the rainy season but that *T. grandis* was leafless and the transpiration had stopped in the late dry season. The beginning of the increase in the LAI corresponded to the beginning of the increase in V_{ave} each year, although their timings differed from year to year; i.e. the onset of transpiration accompanied the

beginning of leaf-out, and the timings of transpiration onset and leaf-out varied synchronously from year to year. The timings of the decline in V_{ave} and the LAI also differed among the years, indicating that the timings of the cessation of transpiration and the leaf-fall also varied. The earlier decline in V_{ave} than in the LAI suggests that transpiration declined and stopped prior to the completion of leaf-fall.

Figure 5 shows the date of transpiration onset averaged over all sample trees during the period 2001–2008. The

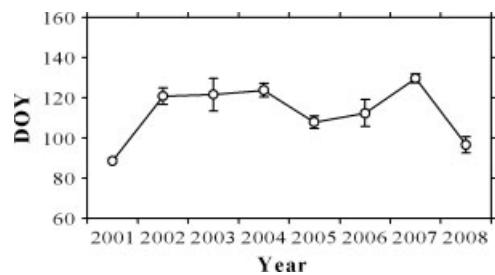


Figure 5. The date of transpiration onset averaged over all sample trees (solid line with open circles) with standard deviation (vertical bars) during the period 2001–2008.

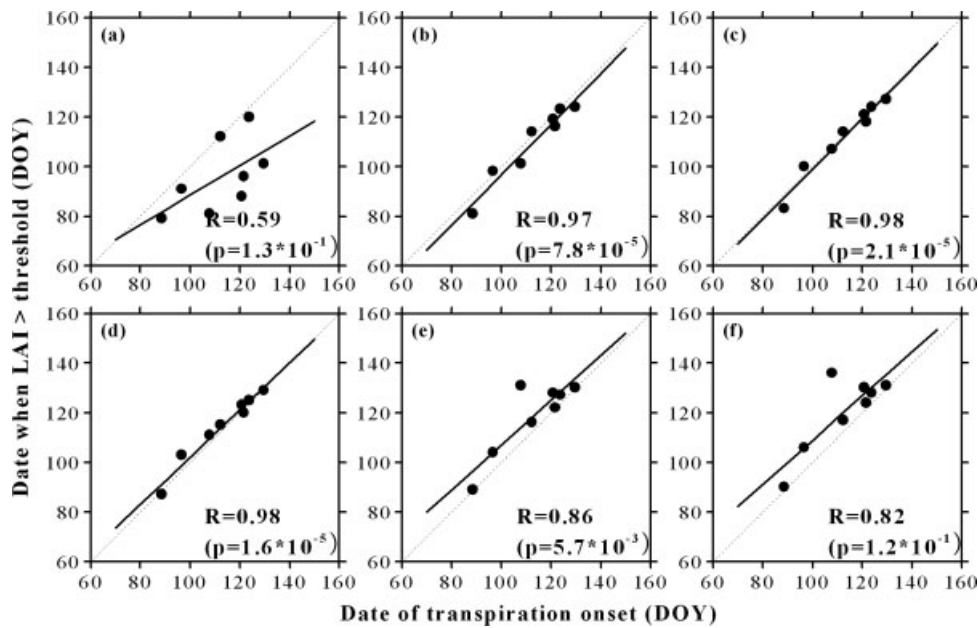


Figure 6. Relationship of the dates of transpiration onset averaged over all sample trees with the dates when LAI became greater than the threshold; (a) 0.1, (b) 0.2, (c) 0.3, (d) 0.4, (e) 0.5, and (f) 0.6. Regression lines (solid lines) were determined using the least-squares method. Correlation coefficients (R) and p -values are also shown. Broken lines indicate a 1 : 1 relationship.

earliest and the latest mean onset dates were DOY 88 and 129 for 2001 and 2007, respectively. Thus, the maximum interannual variation was 41 days. The mean date of the transpiration onset over 8 years was DOY 112, and the standard deviation was 14 days.

Figure 6 shows the relationship between the date of transpiration onset averaged over all sample trees and the initial date of the longest period in which the LAI was greater than 0.1, 0.2, 0.3, 0.4, 0.5, and 0.6 in each year. R and RMSE were higher and lower, respectively, when the threshold for the LAI was 0.2–0.4. Their values were 0.97–0.98 ($p < 0.0001$) and 2.9–4.7 days, respectively. This means that the transpiration onset always corresponded to the beginning of leaf-out, and that the beginning of leaf-out also varied among the years in synchronization with the transpiration onset.

Relationship between the transpiration onset and soil moisture

Figure 7 shows time series of Θ and cumulative rainfall since January 1 for the period from March to July in the years 2001–2008. Dates of transpiration onset averaged over all sample trees are also shown. The timings and courses of the increases in Θ and cumulative rainfall differed among the years. The transpiration onset dates also varied among the years, and the interannual variation seemed to correspond to that of Θ . In 2001, Θ increased markedly in the beginning of March owing to unexpectedly heavy rainfall events in the late dry season. The increase in Θ was followed, with a time lag, by an earlier transpiration onset than in other years. The transpiration onset was early in 2008, 2005, and 2006 next to in 2001, accompanying the distinct increase in Θ observed in April. In 2002, 2003, and 2004, Θ and cumulative rainfall increased gradually, and transpiration

onset was observed at the beginning of their increases. In 2007, Θ was low until the end of April because there was almost no rainfall, and then increased abruptly. The transpiration onset in 2007 followed this abrupt Θ increase with a time lag and was the latest among the 8 years. These results suggest that the interannual variation in the date of transpiration onset corresponded to interannual variation in the timing of the increase in Θ due to variations in the interannual rainfall.

Figure 8 shows the transpiration onset dates averaged over all sample trees and the initial dates when Θ became greater than 0.1, 0.2, 0.3, and 0.4. The data were plotted close to the 1 : 1 line when the Θ threshold was set at 0.2, and R and RMSE were highest and lowest, respectively. R and RMSE are examined for a Θ threshold from 0.1 to 0.5 in Figure 9. It is again shown that the threshold set at 0.2 results in the highest R and lowest RMSE values. R was 0.94 ($p = 0.0016$) and RMSE was 10 days when the threshold was set at 0.2, indicating that the use of this threshold enabled prediction of the transpiration onset date with a 10-day error. A similar prediction is possible on the basis of rainfall data. The use of the date preceding 20-day cumulative rainfall exceeding 60 mm was found to allow prediction of the date of transpiration onset with $R = 0.98$ ($p = 0.00019$) and an RMSE of 8 days, after examining various lengths of cumulative rainfall and thresholds (data not shown).

DISCUSSION

Spatial representativeness of R_{td_ave} calculated using the main pyranometer

In this study, we used R_{td_ave} calculated from S_b data of the main pyranometer for the LAI estimates. Figure 10 shows seasonal variations in R_{td_ave} values calculated

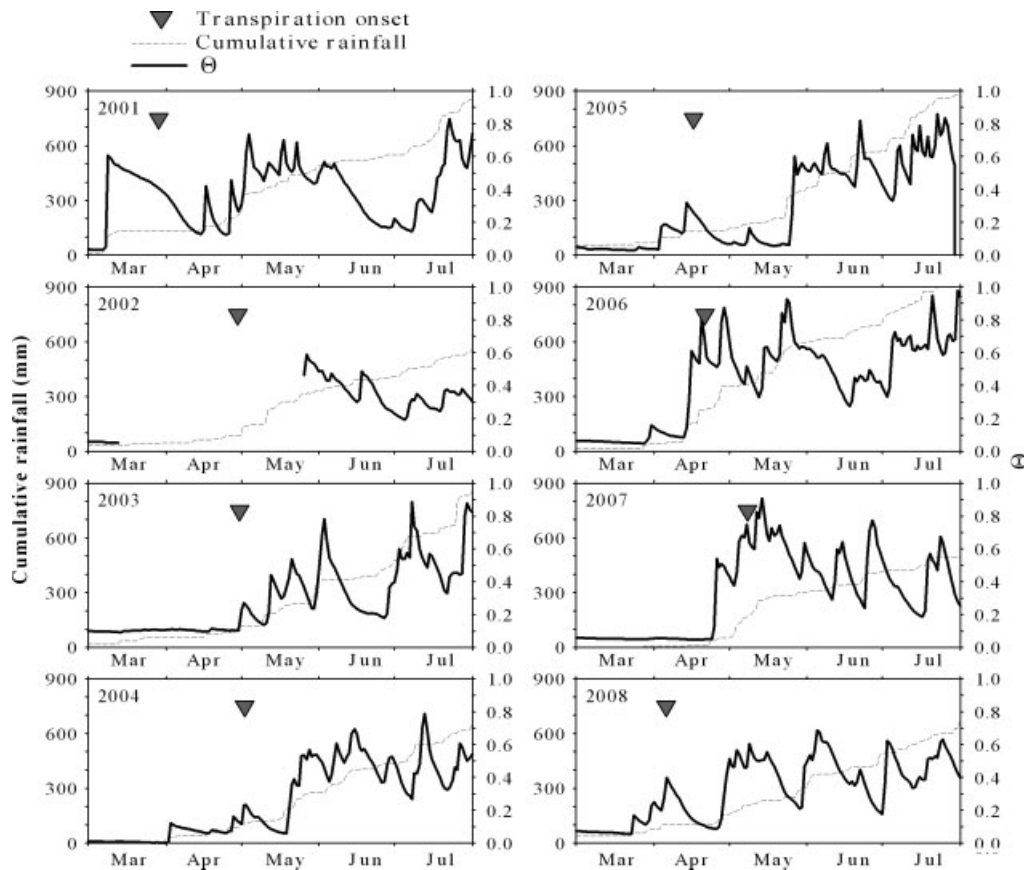


Figure 7. Time series of cumulative rainfall (thin broken line, left axis) and relative extractable water (Θ , thick solid line, right axis) from March to July in the period 2001–2008. Cumulative rainfall was calculated from 1st January for each year. Triangles show the dates of transpiration onset averaged over all sample trees for each year.

from S_b data of the main pyranometer and six additional radiation sensors. The vertical axis is reversed because R_{td_ave} is inversely related to the LAI, Equation (2). The timings of the initial decrease in R_{td_ave} (rise of the lines in the figure) in the leaf-out season were similar, although the absolute R_{td_ave} values for leafless seasons differed. Hence, the timings of the initial increase in LAI in the leaf-out season are quite synchronous at the study site. Indeed, our results presented in Figure 6 did not change when using the mean R_{td_ave} values for the seven sensors (data not shown).

Availability of meteorological variables as a predictive indicator of the transpiration onset

We found that a Θ threshold of 0.2 works well as an indicator for predicting transpiration onset dates even though it is a simple indicator (Figure 9). This result is reasonable in that transpiration onset occurs during the transitional period from dry to rainy seasons. In addition to Θ , other meteorological variables (S_0 , T_a , and D) also change in the transitional period (Figure 3). Thus, it might be possible that these variables are indicators of the date of transpiration onset. This possibility is examined here.

The following presents the results of investigating D , which best predicts the date of the transpiration onset among meteorological variables (S_0 , T_a , and D). We tested two indices: (i) the initial date when the mean daily

D of the previous 15 days (D_{ave}) became smaller than the threshold after it reached the maximum in that year following the cessation of transpiration and (ii) the initial date when the accumulation of consecutive decreases in D_{ave} reached the threshold after D_{ave} reached the maximum in that year following the cessation of transpiration. We changed the threshold value and calculated R and RMSE for the relationship between the transpiration onset date and the date selected by the indices (Figure 11). The highest R of 0.78 ($p = 0.022$) was obtained when using the latter index with the threshold of D_{ave} decrement being 4.0 hPa, and the RMSE was 27.5 days. Still, the model predictability (evaluated with R and RMSE) obtained here was lower than that observed when using Θ . Similarly, when using S_0 or T_a as an indicator, we observed lower predictability of the transpiration onset date than when using Θ . Here, we did not use LAI data for predicting the date of transpiration onset, because the ultimate goal of modelling phenology is to predict it using environmental data, not vegetation data (Baldocchi *et al.*, 2005).

Comparison with other studies

The date of transpiration onset at the study site based on 8-year observation data varied a maximum of 41 days, with a standard deviation of 14 days. The extent of this interannual variation was larger than variations in the

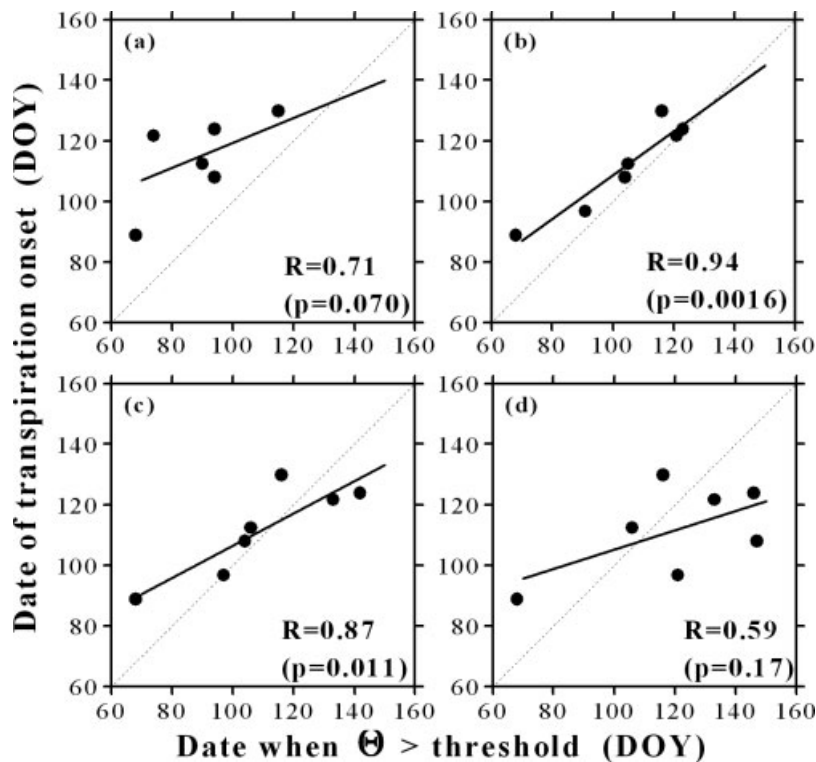


Figure 8. Relationships between the date of transpiration onset averaged over all sample trees and the initial date when daily mean relative extractable water (Θ) became greater than (a) 0-1, (b) 0-2, (c) 0-3, and (d) 0-4. Regression lines (solid lines) were determined using the least-squares method. Correlation coefficients (R) and p -values are also shown. Broken lines indicate a 1 : 1 relationship.

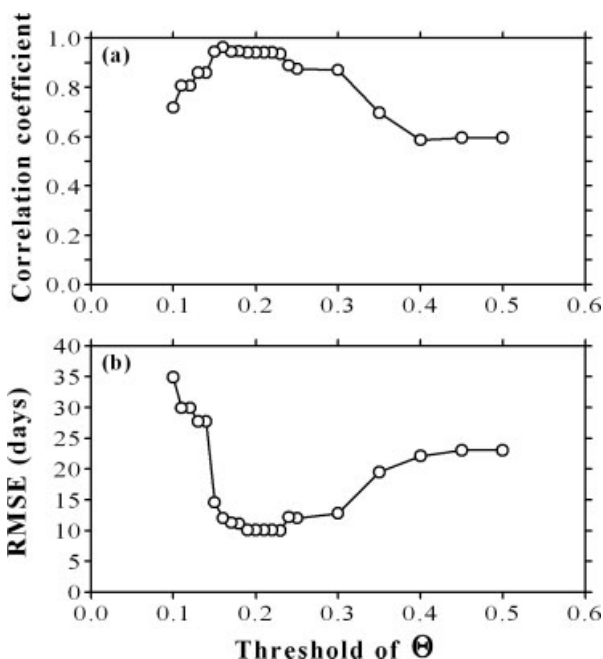


Figure 9. Relationships of the threshold of relative extractable water (Θ) with (a) the correlation coefficients and (b) the RMSE in estimating transpiration onset dates.

date of leaf-out and the onset of carbon uptake reported previously for deciduous forests in boreal and temperate regions (Table I). This greater variation suggests greater potential effects on interannual variations in annual energy, water, and carbon exchanges between deciduous forests and the atmosphere in tropical regions than in

temperate and boreal regions. Evaluating this effect may be critical because tropical forests play a significant role in global and regional climate formation (Lean and Warrilow, 1989; Kanae *et al.*, 2001) and in the global carbon budget (Mellilo *et al.*, 1993; Malhi and Grace, 2000).

Our previous study (Yoshifuji *et al.*, 2006), which was based on 3-year data, has already noted that the extent of the interannual variation in the transpiration onset date is greater for the tropical deciduous forest than for temperate deciduous forests. The present study further confirms this observation on the basis of 8-year data. The present study also provides the new insight that the interannual variation in the transpiration onset date can be reproduced using an index representing the soil water content or antecedent rainfall.

This insight contrasts with the scheme of phenology models developed for temperate and boreal regions. The key controlling variables in these models are air and/or soil temperature, with there being additional effects of light and rainfall in some cases (White *et al.*, 1997; Baldocchi *et al.*, 2005; Linkosalo *et al.*, 2006; Piao *et al.*, 2006). Our results are consistent with the results for more sparse vegetation in the dry tropics obtained by Jolly and Running (2004). They reported that the timing of leaf flush in the Kalahari could be predicted by rainfall and potential evapotranspiration, suggesting that soil moisture and plant water relations determined the timing of leaf flush. Do *et al.* (2005) conducted regression-prediction analysis of the canopy fullness and environmental variables based on 5-year observation

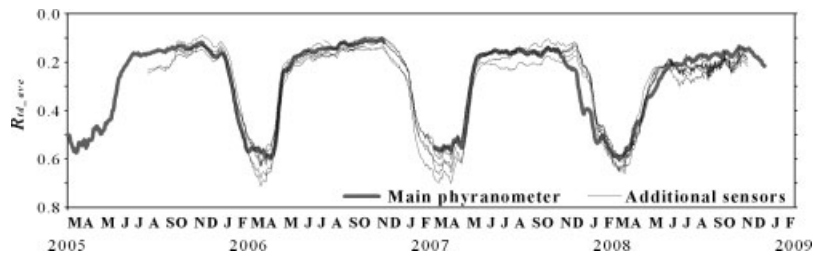


Figure 10. Time series of the 15-day moving average of daily radiative transmittance ($R_{td,ave}$) calculated from the data of the main pyranometer (thick line) and the six additional radiation sensors (thin lines). The vertical axis is reversed because $R_{td,ave}$ is inversely related to LAI.

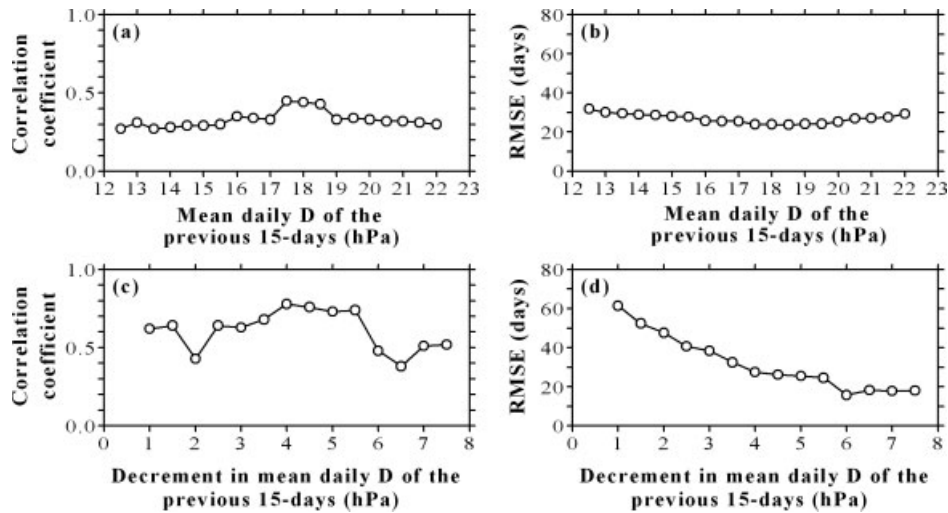


Figure 11. Correlation coefficients (a and c) and RMSEs (days; b and d) between the transpiration onset dates and the dates when the mean daily vapour pressure deficit of the previous 15 days (D_{ave} , hPa) became smaller than the threshold after it reached the maximum in that year following the cessation of transpiration (a and b), and the initial date when the accumulation of consecutive decreases in D_{ave} reached the threshold after D_{ave} reached the maximum in that year following the cessation of transpiration (c and d), plotted against the thresholds.

data in a sparse woody community in the grazing land ecosystem in the northern Sahelian zone, and reported that the course of canopy fullness in the leaf-out season and the timings of the leaf-flush peak were predicted well by the vapour pressure deficit or global radiation, but not by rainfall or upper-soil moisture. The results of Do *et al.* (2005) are inconsistent with our results that the interannual variation in transpiration onset and the beginning of leaf-out can be estimated by the soil moisture. Differences in tree species and/or deep soil water availability might be a reason for this inconsistency because a considerable increase in canopy fullness was observed by Do *et al.* (2005) before the first rains while the peak of the increase in the LAI was after the rain at our study site.

CONCLUSIONS

We quantified the range of the interannual variation in the transpiration onset dates in a teak plantation in northern Thailand on the basis of 8-year observation data. The beginning of leaf-out varied among the years synchronously with the transpiration onset, as demonstrated by the transpiration onset date corresponding to the date

at which the LAI exceeded 0.2–0.4. The long-term observation data enabled us to examine the predicting indicators of the interannual variation in transpiration onset through correlation analysis. We revealed that the simple soil water index, the date when Θ became greater than 0.2, or an index representing antecedent rainfall can predict the transpiration onset.

The strong correlations between the transpiration onset date and the indices do not always reflect a process-based relationship; however, the correlations clearly show the usefulness of the indices in predicting the transpiration onset date empirically. The use of these indices will allow examination of changes in the transpiration onset date with the change in precipitation due to climate change. In addition, if we include this sub-model into the vegetation schemes of climate models, we can evaluate the extent of interannual variations in water and carbon exchanges in tropical deciduous forests due to climate change through phenological fluctuation. Global-scale phenology models often adopt water availability as a controlling variable for tropical forests employing soil moisture and/or D (e.g., Botta *et al.*, 2000; Jolly *et al.*, 2005). Our results support the scheme of such models. However, there are still few investigations of interannual variations in the transpiration onset for tropical deciduous forests. This makes it difficult to evaluate the accuracy of the prediction of the interannual variation

Table I. Maximum differences in the dates of leaf-out or onset of carbon uptake in deciduous forests in boreal and temperate regions.

Site	Species	Phenological event	Maximum difference (number of sample year)	Source
<i>Boreal deciduous forest</i>				
Saskatchewan, Canada	Aspen, hazelnut	Leaf emergence	4 weeks (9)	Barr <i>et al.</i> (2004)
Tomakomai, Japan	Larch	Leaf-out	2 weeks (3)	Hirata <i>et al.</i> (2007)
<i>Temperate deciduous forest</i>				
Manitoba, Canada	Black spruce	Leaf emergence, onset of carbon uptake	6–10 days (5)	Goulden <i>et al.</i> (1996)
Oak Ridge, USA	Oak, maple, hickory	Leaf emergence	2 weeks (3)	Wilson and Baldocchi (2000)
Hesse, France	Beech	Onset of carbon uptake	6 days (3)	Granier <i>et al.</i> (2002)
Soro, Denmark	Beech	Onset of carbon uptake	3 days (3)	Granier <i>et al.</i> (2002)
Takayama, Japan	Birch, oak	Leaf-out	20 days (6)	Saigusa <i>et al.</i> (2002)

in phenology and consequent changes in water and carbon exchanges in tropical deciduous forests derived by these global-scale phenology models and climate models. Thus, we recommend similar studies to ours be carried out for various types of tropical deciduous forests.

ACKNOWLEDGEMENTS

This work was supported by CREST (Core Research for Evolution Science and Technology) of JST (Japan Science and Technology Agency), GEWEX (Global Energy and Water Cycle Experiment) Asian Monsoon Experiment-Tropics (GAME-T), and a short-term intensive research support program of the Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University. We are grateful to Katsunori Tanaka (Frontier Research Center for Global Change, Japan Agency for Marine–Earth Science and Technology) for cooperation with field measurements and suggestions. We would like to thank Suwan Pakrat, Srinuan Tunjai, and graduate students of Kasetsart University for their assistance in the field. We would also like to acknowledge Masatoshi Aoki, Samakee Boonyawat, and the Thai Forest Industry Organization for their support during this project. We greatly appreciate the insightful comments and suggestions made by the editor and the reviewers that helped us to improve the article. Finally, we express sincere thanks to Makoto Tani and Yoshiko Kosugi (Kyoto University) for their dedicated help for communications among co-authors.

REFERENCES

- Aubinet M, Heinesch B, Longdoz B. 2002. Estimation of the carbon sequestration by a heterogeneous forest: night flux correlations, heterogeneity of the site and inter-annual variability. *Global Change Biology* **8**: 1053–1071.
- Baldocchi DD, Matt DR, Hutchison BA, McMillen RT. 1984. Solar radiation within an oak-hickory forest: an evaluation of the extinction coefficients for several radiation components during fully-leaved and leaf-less periods. *Agricultural and Forest Meteorology* **32**: 307–322.
- Baldocchi DD, Black TA, Curtis PS, Falge E, Fuentes JD, Granier A, Gu L, Knohl A, Pilegaard K, Schmid HP, Valentini R, Wilson K, Wofsy S, Xu L, Yamamoto S. 2005. Predicting the onset of net carbon uptake by deciduous forests with soil temperature and climate data: a synthesis of FLUXNET data. *International Journal of Biometeorology* **49**: 377–387. DOI: 10.1007/s00484-005-0256-4.
- Barr AG, Black TA, Hogg EH, Kljun N, Morgenstern K, Nestic Z. 2004. Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. *Agricultural and Forest Meteorology* **126**: 237–255. DOI: 10.1016/j.agrformet.2004.06.011.
- Barr AG, Black TA, Hogg EH, Griffis TJ, Morgenstern K, Kljun N, Theede A, Nestic Z. 2006. Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003. *Global Change Biology* **12**: 1–16. DOI: 10.1111/j.1365-2486.2006.01220.x.
- Borchert R. 1994. Water status and development of tropical trees during seasonal drought. *Trees* **8**: 115–125.
- Botta A, Viovy N, Ciais P, Friedlingstein P, Monfray P. 2000. A global prognostic scheme of leaf onset using satellite data. *Global Change Biology* **6**: 709–725.
- Black TA, Chen WJ, Barr AG, Arain MA, Chen Z, Nestic Z, Hogg EH, Neumann HH, Yang PC. 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophysical Research Letters* **27**: 1271–1274.
- Carrara A, Kowalski AS, Neiryck J, Janssens IA, Yuste JC, Ceulemans R. 2003. Net ecosystem CO₂ exchange of mixed forest in Belgium over 5 years. *Agricultural and Forest Meteorology* **119**: 209–227. DOI: 10.1016/S0168-1923(03)00120-5.
- Closs RL. 1958. The heat pulse method for measuring rate of sap flow in a plant stem. *New Zealand Journal of Science* **1**: 281–288.
- Do FC, Goudiaby VA, Gimenez O, Diagne AL, Diouf M, Rocheteau A, Akpo LE. 2005. Environmental influence on canopy phenology in the dry tropics. *Forest Ecology and Management* **215**: 319–328. DOI: 10.1016/j.foreco.2005.05.022.
- Elliott S, Baker PJ, Borchert R. 2006. Leaf flushing during the dry season: the paradox of Asian monsoon forests. *Global Ecology and Biogeography* **15**: 248–257. DOI: 10.1111/j.1466-822x.2006.00213.x.
- Food and Agriculture Organization. 2001. *Global Forest Resources Assessment 2000—Main Report*. FAO Forestry Paper 140. Food and Agriculture Organization: Rome.
- Goulden ML, Munger JW, Fan SM, Daube BC, Wofsy SC. 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. *Science* **271**: 1576–1578.
- Granier A, Bréda N, Biron P, Villette S. 1999. A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands. *Ecological Modelling* **116**: 269–283.
- Granier A, Pilegaard K, Jensen NO. 2002. Similar net ecosystem exchange of beech stands located in France and Denmark. *Agricultural and Forest Meteorology* **114**: 75–82. DOI: 10.1016/j.agrformet.2007.07.005.
- Hirata R, Hirano T, Saigusa N, Fujinuma Y, Inukai K, Kitamori Y, Takahashi Y, Yamamoto S. 2007. Seasonal and interannual variations in carbon dioxide exchange of a temperate larch forest. *Agricultural and Forest Meteorology* **147**: 110–124.
- Holst T, Hauser S, Kirchgäßner A, Matzarakis A, Mayer H, Shindler D. 2004. Measuring and modeling plant area index in beech stands. *International Journal of Biometeorology* **48**: 192–201.
- Jolly WM, Running SW. 2004. Effects of precipitation and soil water potential on drought deciduous phenology in the Kalahari. *Global*

- Change Biology* **10**: 303–308. DOI: 10.1046/j.1529–8817.2003.00701.x.
- Jolly WM, Nemani R, Running SW. 2005. A generalized, bioclimatic index to predict foliar phenology in response to climate. *Global Change Biology* **11**: 619–632. DOI: 10.1111/j.1365–2486.2005.00930.x.
- Kanae S, Oki T, Musiak K. 2001. Impact of deforestation on regional precipitation over the Indochina Peninsula. *Journal of Hydrometeorology* **2**: 51–70.
- Kenzo T, Ichie T, Watanabe Y, Yoneda R, Ninomiya I, Koike T. 2006. Changes in photosynthesis and leaf characteristics with tree height in five dipterocarp species in a tropical rain forest. *Tree Physiology* **26**: 865–873.
- Komatsu H, Kume T, Otsuki K. 2008. The effect of converting a native broad-leaved forest to a coniferous plantation forest on annual water yield: a paired-catchment study in northern Japan. *Forest Ecology and Management* **255**: 880–886. DOI: 10.1016/j.foreco.2007.10.010.
- Krishnapillay B. 2000. Silviculture and management of teak plantations. *Unasylva* **201**: 14–21.
- Kumagai T, Katul GG, Saitoh TM, Sato Y, Manfroi OJ, Morooka T, Ichie T, Kuraji K, Suzuki M, Porporato A. 2004. Water cycling in a Bornean tropical rain forest under current and projected precipitation scenarios. *Water Resource Research* **40**: W01104. DOI: 10.1029/2003WR002226.
- Lean J, Warrilow DA. 1989. Simulation of the regional climate impact of Amazon deforestation. *Nature* **342**: 411–413.
- Linkosalo T, Häkkinen R, Hänninen H. 2006. Models of the spring phenology of boreal and temperate trees: is there something missing? *Tree Physiology* **26**: 1165–1172.
- Maass JM, Vose JM, Swank WT, Martínex-Yrizar A. 1995. Seasonal changes of leaf area index (LAI) in a tropical deciduous forest in west Mexico. *Forest Ecology and Management* **74**: 171–180.
- Malhi Y, Grace J. 2000. Tropical forests and atmospheric carbon dioxide. *Trends in Ecology and Evolutions* **15**: 332–337.
- Melillo JM, McGuire AD, Kicklighter DW, Moore B III, Vorosmarty CJ, Schloss AL. 1993. Global climate change and terrestrial net primary production. *Nature* **363**: 234–240.
- Pandey D, Brown C. 2000. Teak: a global overview. *Unasylva* **201**: 3–13.
- Piao S, Fang J, Zhou L, Ciais P, Zhu B. 2006. Variations in satellite-derived phenology in China's temperate vegetation. *Global Change Biology* **12**: 672–685. DOI: 10.1111/j.1365–2486.2006.01123.x.
- Pitman AJ. 2003. The evolution of, and revolution in, land surface schemes designed for climate models. *International Journal of Climatology* **23**: 479–510. DOI: 10.1002/joc.893.
- Reich PB, Borchert R. 1982. Phenology and ecophysiology of the tropical tree, *Tabebuia neochrysantha* (BIGNONIACEAE). *Ecology* **63**: 294–299.
- Saigusa N, Yamamoto S, Murayama S, Kondo H, Nishimura N. 2002. Gross primary production and net ecosystem exchange of a cool-temperate deciduous forest estimated by the eddy covariance method. *Agricultural and Forest Meteorology* **112**: 203–215.
- Saigusa N, Yamamoto S, Murayama S, Kondo H. 2005. Inter-annual variability of carbon budget components in an AsiaFlux forest site estimated by long-term flux measurements. *Agricultural and Forest Meteorology* **134**: 4–16. DOI: 10.1016/j.agrformet.2005.08.016.
- Smith DM, Allen SJ. 1996. Measurement of sap flow in plant stems. *Journal of Experimental Botany* **47**: 1833–1844.
- Swanson RH, Whitfield DWA. 1981. A numerical analysis of heat pulse velocity theory and practice. *Journal of Experimental Botany* **32**: 221–239.
- Tanaka N, Kume T, Yoshifuji N, Tanaka K, Takizawa H, Shiraki K, Tantasirin C, Tangtham N, Suzuki M. 2008. A review of evapotranspiration estimates from tropical forests in Thailand and adjacent regions. *Agricultural and Forest Meteorology* **148**: 807–819. DOI: 10.1016/j.agrformet.2008.01.011.
- Wang Q, Tenhunen J, Granier A, Reichstein M, Bouriaud O, Nguyen D, Breda N. 2004. Long-term variation in leaf area index and light extinction in a *Fagus sylvatica* stand as estimated from global radiation profiles. *Theoretical and Applied Climatology* **79**: 225–238.
- White MA, Thornton PE, Running SW. 1997. A continental phenology model for monitoring vegetation responses to interannual climatic variability. *Global Biogeochemical Cycles* **11**: 217–234.
- White MA, Running SW, Thornton PE. 1999. The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *International Journal of Biometeorology* **42**: 139–145.
- Wilson KB, Baldocchi DD. 2000. Seasonal and interannual variability of energy fluxes over a broadleaved temperate deciduous forest in North America. *Agricultural and Forest Meteorology* **100**: 1–18.
- Yoshifuji N, Kumagai T, Tanaka K, Tanaka N, Komatsu H, Suzuki M, Tantasirin C. 2006. Inter-annual variation in growing season length of a tropical seasonal forest in northern Thailand. *Forest Ecology and Management* **229**: 333–339. DOI: 10.1016/j.foreco.2006.04.013.