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Forest Ecology and Management 229 (2006) 333-339

Forest Ecology and Management

www.elsevier.com/locate/foreco

Inter-annual variation in growing season length of a tropical seasonal forest in northern Thailand

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Received 1 July 2005; received in revised form 5 April 2006; accepted 10 April 2006

Abstract

Tropical seasonal forests play an important role in global cycling of carbon, water and energy in terms of inter-annual variation in the growing season. We investigated year-to-year variations in the canopy duration and transpiration period as measures of growing season length using time series data of radiative transmittance and sap flux in a teak plantation in Thailand over a 3-year period. In 2001, leaf-out and tree transpiration commenced earlier than in 2002 and 2003 following exceptionally heavy rainfall in the late dry season, strongly suggesting that enhanced soil moisture advanced the timing of leaf unfolding and commencement of tree transpiration. The commencement of leaf-fall and decline in tree transpiration at the beginning of 2003 were late in coming in correlation with a prolonged rainy season. Declines in tree transpiration were directly controlled by soil moisture conditions at the beginning of the dry season, with time lags between the timing of leaf-fall and decline in tree transpiration. These results revealed that soil moisture conditions are a major determinant of large inter-annual variation in the growing season at this site. The variation in canopy duration and transpiration period in this study, from 2001 to 2004, spanned about 40 and 60 days, respectively. This was much larger than the inter-annual variations previously reported in temperate deciduous forests, implying a profound potential impact on surface energy balance and canopy-atmosphere water and carbon exchange on an annual time scale.

Keywords: Growing season; Inter-annual variability; Tropical deciduous forest; Phenology; Sap flux measurement

1. Introduction

Tropical forests play a significant role in the global carbon budget (Melillo et al., 1993; Malhi and Grace, 2000) and are also an important latent energy source, having a strong influence on both global and regional climates (Lean and Warrilow, 1989; Kanae et al., 2001). Tropical moist deciduous forests and tropical dry forests represent 43% of the total tropical forest area, which is comparable to that of tropical rainforests (Food and Agriculture Organization, 2001). Furthermore, the total area of tropical deciduous forests is estimated to be larger than that of temperate deciduous forests (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 and Baldocchi, 2000). 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). The impact of inter-annual climatic anomalies on the annual energy and carbon cycle through modification of leaf phenology, the timing of leaf-out and leaf-fall and the consequent length of the growing season, is likely to be critical especially in tropical forests because of the large annual energy fluxes. However, the potential impact in tropical deciduous forests has received

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^{0378-1127/\$ –} see front matter \odot 2006 Elsevier B.V. All rights reserved. doi:10.1016/j.foreco.2006.04.013

much less attention than that in temperate and boreal deciduous forests (Goulden et al., 1996; White et al., 1999; Black et al., 2000; Wilson and Baldocchi, 2000; Barr et al., 2004).

Furthermore, our understanding of inter-annual variation in growing season length in tropical deciduous forests based on field observation data is limited. Many studies have investigated the leaf phenology of tropical trees at an individual tree scale, especially phenological patterns and synchronousness among species and habitats, and examined phenological mechanisms and cues (e.g., Borchert, 1994a,b, 1999; Reich, 1995). At the stand scale, Maass et al. (1995) examined inter-annual seasonal variation in the leaf area index (LAI) of a tropical deciduous forest for two years, and reported that year-to-year differences in the minimum LAI are probably attributed to atypical rainfall in the dry season, which retards leaf abscission. However, no study has examined the impact of inter-annual variation in leaf phenology on energy, water, and carbon exchanges within a tropical deciduous forest canopy.

The goal of this study, therefore, was to investigate interannual variation in the length of the growing season in a tropical deciduous forest in Southeast Asia with respect to the hydrometeorological impact. The length of the growing season has a two-fold effect on energy and water fluxes in a forest ecosystem, i.e., through canopy duration and transpiration period. Canopy duration represents the physical presence of leaves in the forest canopy, while transpiration period corresponds to active canopy-atmosphere water exchange and photosynthesis, which can cease even in the presence of a foliated canopy. We determined the lengths of the canopy duration and transpiration period in a teak plantation in Thailand using field measurements obtained over a 3-year period to reveal the extent of inter-annual variation. We also examined how year-to-year variations in the lengths of the canopy duration and transpiration period respond to inter-annual variations in environmental factors. The outcomes show the predictive applicability of the canopy duration and transpiration period of tropical deciduous forests in global climate and carbon balance models (e.g., White et al., 1997).

2. Materials and methods

2.1. Site description

The experiments were carried out in an even-aged 37-yearold teak (*Tectona grandis* Linn. f.) standing in Mae Moh plantation, Lampang province, northern Thailand (18°25' N, 99°43' E, 380 m above sea level). Teak plantations are widely established throughout the tropics due to their market value. In Thailand, as a result of the significant decrease in forest area up until the 1980s, forest rehabilitation and plantation have been promoted, resulting in establishment of teak plantations by the Forest Industry Organization (FIO) mainly in northern regions. Mae Moh plantation was established by the FIO around 1968. The study site had a mean annual temperature of 25.8 °C and mean annual precipitation of 1284 mm for the period 2000– 2004. The climate of this area is influenced by Asian monsoons, which produce highly seasonal variation in precipitation. There is a clear dry season from November to April, in which mean monthly rainfall was below 100 mm between 2000 and 2004. The dry season can be separated into two: the cool dry season, which occurs first and presents a relatively low air temperature followed by the hot dry season, which presents a high air temperature and vapor pressure deficit (VPD). The soil in Mae Moh plantation is classified as Loamy Paleustults (Thai classification). The study site was located on an area of flat land where the stand structure is almost homogenous. Tree density around the study site was 360 trees ha⁻¹ and the mean tree height and diameter at breast height (DBH) were 17.2 m and 19.5 cm, respectively. The understory vegetation around the study site is sometimes cut back and, in the dry season, often burned.

2.2. Meteorological and soil moisture measurements

Incident solar radiation above the canopy (S_0) was measured with a silicon pyranometer (LI200X, Li-Cor, Lincoln, NE, USA) at a height of 22 m using a research tower situated in the study site. Incident solar radiation below the canopy (S_b) was also measured with a pyranometer (MS401, EKO, Tokyo, Japan) on the forest floor at a height of about 0.5 m, 30 m away from the tower. Both radiation data were measured every 5 s and their 10 min averages were recorded with a data logger (CR10X, Campbell Scientific, Logan, UT, USA). The radiative transmittance through the canopy was calculated as the ratio of S_b to S_0 (described later).

Air temperature and relative humidity above the canopy were measured at a height of 26 m with an aspirated psychrometer (HMP45D, Vaisala, Helsinki, Finland) installed on the tower and recorded every 10 min with a data logger (SQ1250, Grant Instruments, Cambridge, UK). Rainfall was measured every day with a self-made storage-type rain gauge in an open site about 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 storage-type rain gauge, and the time of tip was recorded to give the time distribution of rainfall.

Volumetric soil water content (θ ; m³ m⁻³) was measured near the tower at depths of 0.1, 0.2, 0.4, and 0.6 m at 60-min intervals (CR10X, Campbell Scientific). A time domain reflectometer (TDR; CS-615, Campbell Scientific) was used to measure the time series of θ . The relative extractable water in a 0–0.6 m soil layer (Θ) was computed as described in Kumagai et al. (2004); Θ ranges from 0 to 1, corresponding to the driest and wettest conditions of the soil during the entire observation period, respectively.

2.3. Transpiration measured using the heat pulse method

Heat pulse velocity (HPV; cm h^{-1}) was measured as an index of tree transpiration using heat pulse sensors (HP-1, Hayashi Denko, Tokyo, Japan) consisting of three vertically aligned probes: a heater probe and upstream and downstream thermistor probes (2.0 mm in diameter, 50 mm in length). The heat pulse sensors were inserted into the outer xylem of tree stems at a height of about 1.5 m with 5 or 6 and 10 mm between

the heater probe and upstream and downstream thermistor probes, respectively. A heat-pulse tracer was released for a duration of 1.5 s every 20 min. The temperature difference between the two thermistor probes was measured every 0.25 s, and the time at which it returned to 0 following the heat pulse was recorded on a data logger (CR10X, Campbell Scientific). HPV was calculated as described in Closs (1958).

Five *T. grandis* trees near the tower were selected for the HPV measurements. The height and DBH of these sample trees belonged to the dominant classes around the study site: their minimum and maximum heights were 17.3 and 19.0 m, respectively, and their minimum and maximum DBH were 18.0 and 22.1 cm, respectively. Three sensors were installed in two trees in May 2000 then reinstalled in different positions once or twice until February 2004. Sensors were installed in the remaining three trees in November 2001. HPV data from February 2001 to February 2004 were used in this study.

2.4. Determination of canopy duration and transpiration period

Transmittance of incident radiation through the canopy is often used to monitor temporal variation in LAI (Maass et al., 1995; Holst et al., 2004, Wang et al., 2004). Based on the Beer-Lambert equation, radiative transmittance $(R_t = S_b/S_0)$, which exponentially decreases with increasing LAI, is estimated as an index of LAI. The extinction coefficient dominates R_t but is not constant year-round, depending on the zenith angle, cloudiness, and LAI (Baldocchi et al., 1984; Holst et al., 2004). Considerable spatial variation in $S_{\rm b}$ on the forest floor could be caused mainly due to the locality of direct radiation, which is affected by the canopy openness just above the pyranometer; an even-aged plantation is commonly characterized by small spatial variation in canopy openness. To reduce the impacts of the zenith angle and direct radiation on the representativeness of R_t in this site, we calculated daily $R_t(R_{td})$ by averaging the R_t when the zenith angle was over 75° each day. The relative daily radiative transmittance (ϕ) is then calculated using R_{td} as:

$$\phi = \frac{R_{\text{td_avg}} - R_{\text{td_min}}}{R_{\text{td_max}} - R_{\text{td_min}}} \tag{1}$$

where R_{td_avg} , R_{td_min} and R_{td_max} are the 15-day-moving average of R_{td} and the minimum and maximum values over the entire observation period, respectively. Since ϕ ranges from 0 to 1 and is inversely correlated with changes in LAI, we used $1 - \phi$ as an index of the changes in LAI. The beginning of leafout and completion of leaf-fall were assumed to be the dates when $1 - \phi$ became higher and lower than 0.2, respectively. This threshold (0.2) was determined after several attempts considering the correspondence between the $1 - \phi$ changes and leaf-out and leaf-fall. Thus, canopy duration was defined as the period from the date of leaf unfolding to the completion of leaf-fall. The commencement of leaf-fall was defined as the initial date in the period when $\phi_i - \phi_{i+1} > 0$ continued for more than 15 days, where i = 1, 2, 3, ..., n denotes the day of the year.

For each day, the mean daytime HPV $(V_d; \text{ cm h}^{-1})$ was computed by averaging the measurements obtained between 06:00 and 18:00 h, while the maximum nighttime HPV (V_{n_max}) was defined as the maximum value obtained between 00:00–06:00 and 18:00–24:00 h on the same day. The dates of commencement and cessation of tree transpiration were determined for each sample tree as the dates when the V_d became higher and lower than the V_{n_max} , respectively. Thus, the transpiration period of each observation year was defined as the period from the onset to end of tree transpiration, which were obtained by averaging the dates of both events for all sample trees.

In long-term continuous measurements, HPV values tend 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 by cavitation (Smith and Allen, 1996). To remove the influence of this phenomenon in the present study, we calculated the relative V_d (V) of each sample tree as:

$$V = \frac{V_{\rm d} - V_{\rm d_min}}{V_{\rm d_max} - V_{\rm d_min}} \tag{2}$$

where $V_{d_{min}}$ is the minimum value of V_d over the entire observation period and $V_{d_{max}}$ is the maximum value of V_d during each observation period, i.e., 2001–2002, 2002–2003 and 2003–2004 (described later).

3. Results

3.1. Inter-annual variation in the rainfall regime

Daily rainfall, incident solar radiation, air temperature, and VPD from February 2001 to February 2004 are shown in Fig. 1. The rainy season commenced from the end of April to the beginning of May each year, corresponding with abrupt decreases in both air temperature and VPD. Heavy rainfall events with 117 mm of rain in 6 days were also observed during the hot dry season of 2001, but not during the dry seasons of 2002 and 2003. It is notable that despite the timing of commencement, the end of the rainy season appreciably differed each year. In 2001, rainfall events disappeared around the end of October; however, in 2002, rainfall was noted in November and December. In 2003, rainfall events disappeared around the middle of October.

According to the commencement and end of the rainy seasons, three specific periods were defined, I, II and III (March 2001–February 2002, March 2002–February 2003 and March 2003–February 2004, respectively), for analyses of the environmental control of growing season length.

3.2. Seasonal and inter-annual variations in LAI

Fig. 2 shows seasonal changes in $1 - \phi$, corresponding to seasonal changes in LAI, against rainfall and Θ for periods I–III. In general, LAI increased at the end of the hot dry season or beginning of the rainy season, and decreased in the dry season. Thus, corresponding to the variation in rainfall regimes for periods I–III (see Fig. 1), the timing of leaf-out and leaf-fall were considerably different between periods.



Fig. 1. Year long climate data for Mae Moh teak plantation between February 2001 and February 2004. From the top, this figure shows the daily rainfall, the daily total solar radiation, daily mean air temperature, and the daily mean vapor pressure deficit. The upper horizontal bar roughly indicates the rainy, cool dry, and hot dry seasons.

In periods II and III, increases in $1 - \phi$ showed that leaf-out started at the beginning of May with commencement of the rainy season (Fig. 2b and c). Note that this leaf unfolding corresponded to an increase in Θ (Fig. 2c). On the other hand, in period I, the increase in $1 - \phi$ appeared in March following a heavy rainfall event of 117 mm over 6 days at the beginning of the month. It is noteworthy that the leaf-out in period I occurred about one month earlier than in periods II and III, before commencement of the rainy season, corresponding to an increase in Θ in March (Fig. 2a). Furthermore, while there was a time lag between the peak of Θ in March 2001 and leaf-out in period I (Fig. 2a), leaf flush accompanied a gradual increase in Θ in period III (Fig. 2c). It is therefore possible that there is an optimal Θ or other environmental or physiological factors influencing leaf-out.

The timing of the beginning and end of leaf-fall were also appreciably different between periods; in period II, the start and end of the drastic decline in $1 - \phi$ were observed one month or more later than in periods I and III, indicating the later commencement and end of leaf-fall (Fig. 2). The canonical difference between periods I and III was related to Θ , which maintained a high soil moisture content in the latter part of period II due to the occurrence of rainfall in November and December. Corresponding to the consequent slow reduction in Θ , the plateau of high $1 - \phi$ values was prolonged in period II (Fig. 2b). In addition, the decline in $1 - \phi$ in period III was earlier than in periods I and II, corresponding to the earlier disappearance of rainfall events and earlier reduction in Θ in this period (Fig. 2c).

3.3. Seasonal and inter-annual variations in tree transpiration

Fig. 3 compares the seasonal variations in V as an index of tree transpiration with those of LAI described by $1 - \phi$. Tree transpiration activity accompanied leaf unfolding; however, a decline was observed even though $1 - \phi$ remained high and tree transpiration stopped before the completion of leaf-fall. In other words, canopy-atmosphere gas exchange ceased during the canopy duration.

Given this earlier decline in tree transpiration, it is instructive to investigate what factors, in addition to LAI, regulate transpiration activity during declining periods within the canopy duration. Thus, we investigated the effects of meteorological factors on tree transpiration from the late rainy season to commencement of leaf-fall (i.e., 13 September to 5 December 2001; 4 November 2002 to 26 January 2003; and 13 September to 20 November 2003) as shown in Fig. 4; here, the late rainy season was defined as the latest date when Θ increased over 0.9 for each observation year. In this figure, the



Fig. 2. Seasonal variations in $1 - \phi$ (bold line, ϕ : relative daily radiative transmittance), daily rainfall (bars), and daily mean relative extractable water (Θ , thin line) in period I (from March 2001 to February 2002) (a), period II (from March 2002 to February 2003) (b), and period III (from March 2003 to February 2004) (c). The dates of commencement of leaf-out (closed diamonds) and leaf-fall (closed triangles) and the end of leaf-fall (open diamonds) are indicated in the $1 - \phi$ plot.

relationship between the V averaged over all sample trees and Θ on no precipitation days was determined over the range of the mean daytime VPD. Here, the V values measured when the daily mean S_0 was below 300 W m⁻² were discriminated because low incident radiation reduces the tree transpiration rate regardless of Θ and VPD. Fig. 4 reveals that the decline in tree transpiration before leaf-fall was controlled directly by reductions in Θ , while there was no clear relationship between V and VPD distributed within a wide range of Θ . The relationship between V and Θ was not so clear in 2001 because of the earlier commencement of leaf-fall after the reduction in transpiration in 2001 compared to that in 2002 and 2003.

3.4. Inter-annual variation in canopy duration and transpiration period

The canopy durations and transpiration periods for I–III are compared in Fig. 5. The year-to-year variations in the lengths of canopy duration and transpiration period were synchronized and spanned about 40 and 60 days, respectively, implying a profound potential impact on surface energy balance and canopy-atmosphere water and carbon exchange on an annual time scale. Since the timing of leaf-out marked the commencement of tree transpiration, the difference between the canopy duration and transpiration period resulted from the



Fig. 3. Seasonal variations in the relative mean daytime heat pulse velocities (V) of all sample trees (dot plot) and $1 - \phi$ (line, ϕ : relative daily radiative transmittance) from February 2001 to February 2004.



Fig. 4. The relative mean daytime heat pulse velocities averaged over all sample trees (mean V) over the range of daily mean relative extractable water (Θ) on no precipitation days (a) from 13 September to 5 December 2001; (b) 4 November 2002 to 26 January 2003; and (c) from 13 September to 20 November 2003, in three classes of mean daytime vapor pressure deficit (VPD; h Pa): mean daytime VPD < 10 (closed diamonds), \geq 10 but <15 (open squares), and \geq 15 (crosses). Data from when daily mean solar radiation was below 300 W m⁻² were discriminated.



Fig. 5. The canopy duration (gray bar) and tree transpiration period (white bar) with individual differences over sample trees (horizontal bars) for period I (March 2001 to February 2002), period II (March 2002 to February 2003), and period III (March 2003 to February 2004). Numbers on the right of each bar represent the lengths in days.

time lag between the ends of leaf-fall and tree transpiration. This year-to-year time lag varied from about 30 to 50 days during the study period.

4. Discussion

From the time series of radiative transmittance and HPV measured over a 3-year period, we revealed large inter-annual variation in canopy duration and transpiration period in a tropical deciduous forest in northern Thailand and examined how these year-to-year variations are regulated by environmental factors. The exceptional heavy rainfall in the late dry season in 2001 and earlier commencements of leaf-out and tree transpiration in 2001 compared to 2002 and 2003 (Fig. 2) strongly suggest that enhanced soil moisture advances the timing of leaf unfolding and commencement of transpiration. In addition, commencement of leaf-fall and the decline in tree transpiration at the beginning of 2003 were late in coming in correlation with the prolonged rainy season (Figs. 2 and 3). Declines in tree transpiration were directly controlled by soil moisture conditions at the beginning of the dry season, with time lags between the timing of leaf-fall and decline in tree transpiration (Fig. 4). Soil moisture is therefore a major determinant of large year-to-year variations in the canopy duration and transpiration period in Mae Moh teak plantation, with variations spanning about 40 and 60 days, respectively (Fig. 5).

Tropical deciduous trees have evolved to acclimate to the seasonal dry period by minimizing their water use. Under augmented soil moisture conditions, leaf-out and leaf-fall of some tropical deciduous tree species are early and delayed, respectively, as demonstrated by irrigation experiments in a wet savanna in northern Australia (Myers et al., 1998) and tropical semi-deciduous forest in Costa Rica (Borchert and Rivera, 2002). Borchert and Rivera (2002) also reported leaf flushing in all leafless trees except dormant stem succulents as a result of an exceptional rainfall event in the dry season. More detailed investigation also revealed that the phenology of tropical dry forest trees is strongly correlated with changes in tree water status, which are determined mainly by the balance between transpiration and water uptake as well as the stem water storage capacity (Borchert, 1994a, 1999). Thus, in tropical deciduous forests, soil moisture can be a key factor in leaf flushing and abscission.

It is also important to note that the decline in tree transpiration was inconsistent with the timing of leaf-fall. The lack of transpiration during the canopy duration means that the leaves in the forest canopy are not active in photosynthesis and latent heat exchange; however, this period may be effective in maintaining the albedo and roughness of the vegetated surfaces. Sakai et al. (1997) also showed that, in a mixed deciduous forest in the northeastern United States (Harvard Forest), the initial increase in LAI in spring was accompanied by a decrease in canopy resistance, while the canopy resistance began to increase and transpiration and photosynthesis became less effective about one month before the commencement of leaf-fall. An important consequence of the difference between the period of leaf physiological processes and physical presence of leaves is that the net annual carbon exchange of the ecosystem will be correlated not with the canopy duration but with the carbon uptake period (e.g., White and Nemani, 2003).

The year-to-year variation in the length of the growing season, i.e., the canopy duration and transpiration period, observed here was much larger than previously reported in temperate deciduous forests, which at most was 20 days (Goulden et al., 1996; Wilson and Baldocchi, 2000; Granier et al., 2002; Saigusa et al., 2002). While radiant energy in spring

and fall is relatively small in temperate and boreal deciduous forests, high radiant energy is available throughout the year in tropical regions. This implies that tropical deciduous forests are among the most sensitive biome to changes in growing season length in terms of carbon and hydrological cycling. Tanaka et al. (2003) projected that in a hill evergreen forest in an Asian monsoon region in northern Thailand the maximum daily transpiration in dry and rainy seasons were 4 and 2 mm, respectively. It is interesting to note that, assuming the fluctuation in the transpiration period is 60 days with 2 mm transpiration per day, a 120 mm transpiration deference would arise among years, leading to concomitant high impact on primary productivity. Further research is now required on the effect of modification of growing season length in tropical deciduous forests on global and regional carbon and hydrological cycling, for example, using global climate and carbon balance models. Our results are important in that they enhance the descriptive application of the phenological sub-model. It is also necessary to determine the spatial and temporal frequency of large inter-annual variation in growing season length over tropical monsoon regions.

Acknowledgements

This work was supported by CREST (Core Research for Evolutional Science and Technology) of JST (Japan Science and Technology Agency) and GEWEX (Global Energy and Water Cycle Experiment) Asian Monsoon Experiment-Tropics (GAME-T). We are grateful to Jakkit Chaiyanet (Kasetsart University, Thailand) and Mika Kawamoto (Japan International Research Center for Agricultural Sciences) for their assistance during this project. We would also like to thank Tomonori Kume (The University of Tokyo) and Hideki Takizawa (Nihon University) for their useful critique, and Masatoshi Aoki, Samakkee Boonyawat, and the Thai Forest Industry Organization for their support during this project.

References

- Baldocchi, D.D., Matt, D.R., Hutchison, B.A., McMillen, R.T., 1984. Solar radiation within an oak-hickory forest: an evaluation of the extinction coefficients for several radiation components during fully-leafed and leafless periods. Agric. For. Meteorol. 32, 307–322.
- Barr, A.G., Black, T.A., Hogg, E.H., Kljun, N., Morgenstern, K., Nesic, Z., 2004. Inter-annual variability in the leaf area index of a boreal aspenhazelnut forest in relation to net ecosystem production. Agric. For. Meteorol. 126, 237–255.
- Black, T.A., Chen, W.J., Barr, A.G., Arain, M.A., Chen, Z., Nesic, Z., Hogg, E.H., Neumann, H.H., Yang, P.C., 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. Geophys. Res. Lett. 27, 1271–1274.
- Borchert, R., 1994a. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75, 1437–1449.
- Borchert, R., 1994b. Water status and development of tropical trees during seasonal drought. Trees 8, 115–125.
- Borchert, R., 1999. Climatic periodicity, phenology, and cambium activity in tropical dry forest trees. IAWA J. 20, 239–247.
- Borchert, R., Rivera, G., 2002. Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. Biotropica 34, 27–39.
- Closs, R.H., 1958. The heat pulse method for measuring rate of sap flow in a plant stem. NZ J. Sci. 1, 281–288.

- Food and Agriculture Organization, 2001. Global Forest Resources Assessment 2000—main report. FAO Forestry Paper 140, Rome.
- Goulden, M.L., Munger, J.W., Fan, S.-M., Daube, B.C., Wofsy, S.C., 1996. Exchange of carbon dioxide by a deciduous forest: response to interannual climate variability. Science 271, 1576–1578.
- Granier, A., Pilegaard, K., Jensen, N.O., 2002. Similar net ecosystem exchange of beech stands located in France and Denmark. Agric. For. Meteorol. 114, 75–82.
- Holst, T., Hauser, S., Kirchgäβner, A., Matzarakis, A., Mayer, H., Schindler, D., 2004. Measuring and modelling plant area index in beech stands. Int. J. Biometeorol. 48, 192–201.
- Kanae, S., Oki, T., Musiake, K., 2001. Impact of deforestation on regional precipitation over the Indochina Peninsula. J. Hydromet. 2, 51–70.
- Kumagai, T., Katul, G.G., Saitoh, T.M., Sato, Y., Manfroi, O.J., 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 Resour. Res. 40, doi:10.1029/2003WR002226 W01104.
- Lean, J., Warrilow, D.A., 1989. Simulation of the regional climate impact of Amazon deforestation. Nature 342, 411–413.
- Maass, J.M., Vose, J.M., Swank, W.T., Martínez-Yrízar, A., 1995. Seasonal changes of leaf area index (LAI) in a tropical deciduous forest in west Mexico. For. Ecol. Manage. 74, 171–180.
- Malhi, Y., Grace, J., 2000. Tropical forests and atmospheric carbon dioxide. Trends. Ecol. Evol. 15, 332–337.
- Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore III, B., Vorosmarty, C.J., Schloss, A.L., 1993. Global climate change and terrestrial net primary production. Nature 363, 234–240.
- Moore, K.E., Fitzjarrald, D.R., Sakai, R.K., 1996. Seasonal variation in radiative and turbulent exchange at a deciduous forest in Central Massachusetts. J. Appl. Meteorol. 35, 122–134.
- Myers, B.A., Williams, R.J., Fordyce, I., Duff, G.A., Eamus, D., 1998. Does irrigation affect leaf phenology in deciduous and evergreen trees of the savannas of northern Australia? Aust. J. Ecol. 23, 329–339.
- Reich, P.B., 1995. Phenology of tropical forests: patterns, causes, and consequences. Can. J. Bot. 73, 164–174.
- 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. Agric. For. Meteorol. 112, 203–215.
- Sakai, R.K., Fitzjarrald, D.R., Moore, K.E., 1997. Detecting leaf area and surface resistance during transition seasons. Agric. For. Meteorol. 84, 273–284.
- Schmid, H.P., Grimmond, C.S.B., Cropley, F., Offerle, B., Su, H.-B., 2000. Measurements of CO_2 and energy fluxes over a mixed hardwood forest in the mid-western United States. Agric. For. Meteorol. 103, 357–374.
- Smith, D.M., Allen, S.J., 1996. Measurement of sap flow in plant stems. J. Exp. Bot. 47, 1833–1844.
- Tanaka, K., Takizawa, H., Tanaka, N., Kosaka, I., Yoshifuji, N., Tantasirin, C., Piman, S., Suzuki, M., Tangtham, N., 2003. Transpiration peak over a hill evergreen forest in northern Thailand in the late dry season: assessing the seasonal changes in evapotranspiration using a multilayer model. J. Geophys. Res. 108 (D17), 4533, doi:10.1029/2002JD003028.
- Wang, Q., Tenhunen, J., Granier, A., Reichstein, M., Bouriaud, O., Nguyen, D., Breda, N., 2004. Long-term variations in leaf area index and light extinction in a *Fagus sylvatica* stand as estimated from global radiation profiles. Theor. Appl. Climatol. 79, 225–238.
- White, M.A., Nemani, R.R., 2003. Canopy duration has little influence on annual carbon storage in the deciduous broad leaf forest. Global Change Biol. 9, 967–972.
- White, M.A., Running, S.W., Thornton, P.E., 1999. The impact of growingseason length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. Int. J. Biometeorol. 42, 139–145.
- White, M.A., Thornton, P.E., Running, S.W., 1997. A continental phenology model for monitoring vegetation responses to interannual climatic variability. Global Biogeochem. Cycles 11, 217–234.
- Wilson, K.B., Baldocchi, D.D., 2000. Seasonal and interannual variability of energy fluxes over a broadleaved temperate deciduous forest in North America. Agric. For. Meteorol. 100, 1–18.