

Diurnal Dynamics of Stand Transpiration and Stomatal Conductance in Rubber (*Hevea brasiliensis* Muell. Arg.)

Sumit Kunjet^{1,*}, Philippe Thaler^{2,3}, Frederic Gay^{2,3}, Boonthida Kositsup⁴, Pisamai Chuntuma⁵, Kumut Sangkhasila⁶ and Poonpipope Kasemsap^{7,*}

ABSTRACT

Transpiration at the leaf and stand level is mainly controlled by climatic conditions. The diurnal dynamics of stand transpiration and stomatal conductance were analyzed in rubber trees. The experiment was conducted using 13 yr-old rubber trees from clone RRIM 600 under natural conditions at the Chachoengsao Rubber Research Center during January to December 2007, with sampling in the dry season, the rainy season and early in the dry season. At the stand level, the stand transpiration was monitored using sap flow measurement and estimated evapotranspiration from meteorological data. At the leaf level, the stomatal conductance was measured using a portable photosynthesis system on the leaves exposed to the sun. The leaf water potential was measured using a pressure chamber and the soil water content was measured by the gravimetric method. Climatic measurements were recorded using a weather station above the canopy. The plant water status was correlated with the climatic conditions and soil water content. The diurnal dynamics of stand transpiration and stomatal conductance were mainly controlled by the vapor pressure deficit and net radiation. The stomatal conductance was more sensitive to climatic variations than stand transpiration. There were different time lags between the stomatal conductance and stand transpiration throughout the year. The relationship between the climatic factors and transpiration varied throughout the year.

Keywords: *Hevea brasiliensis*, leaf water potential, soil water content, stand transpiration, stomatal conductance

INTRODUCTION

Transpiration is the process of water loss from a plant through the stomata that are connected to the conduit tissue (Taiz and Zeiger, 2006). Many techniques are used to measure transpiration in plants such as stomatal conductance

(Motzer *et al.*, 2005), estimated transpiration from sap flow measurement (Hatton *et al.*, 1995; Granier *et al.*, 1996; Smith and Allen, 1996), and the water balance technique has been used to measure evapotranspiration (ETo) and its components such as soil water budget, sap flow, eddy covariance, and catchment water balance

¹ Tropical Agriculture Program, Faculty of Agriculture, Kasetsart University, Bangkok, 10900, Thailand.

² CIRAD, UMR Eco&Sols, 34060 Montpellier, France.

³ Center of Thai-French Cooperation in Higher Education and Research, Kasetsart University, Bangkok 10900, Thailand.

⁴ Department of Botany, Faculty of Science, Chulalongkorn University, Bangkok 10330, Thailand.

⁵ Chachoengsao Rubber Research Center, Sanam Chai Ket District, Chachoeugsao 24160, Thailand.

⁶ Department of Soil, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand.

⁷ Department of Horticulture, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand.

* Corresponding authors, e-mail : skunjet@yahoo.com, agrppk@ku.ac.th

(Wilson *et al.*, 2001), bowen ratio (Denmead *et al.*, 1993), The phenology coefficient was proposed to improve evapotranspiration estimate of rubber plantations from the reference evapotranspiration (ETo) (Guardiola-Claramonte *et al.*, 2010). ETo can be used to predict the rate of transpiration in many plants (Pereira *et al.*, 2006). Moreover, transpiration at the stand level can be assessed by sap flow measurements. This approach has been used to estimate the transpiration in a *Pinus* species (Ford *et al.*, 2004) and in rubber trees (Isarangkool Na Ayutthaya, 2010). There is usually a positive relationship between ETo and stand transpiration (Granier, 1987). Measurement of stomatal conductance is difficult under natural conditions because of the large size of the trees and differences in the leaf age and position (Ansley *et al.*, 1992).

Stomatal regulation of transpiration and a stomatal response to environmental conditions have been observed in several species (Meinzer *et al.*, 1997; Cruziat *et al.*, 2002). Stomatal closure occurred to maintain a minimum leaf water potential above the cavitation threshold (Sperry and Tyree, 1988; Cochard *et al.*, 1996; Oren *et al.*, 1999; Sperry *et al.*, 2002). Stomatal closure in the afternoon enhanced tissue rehydration which increased the leaf water potential (Davies and Kozowski, 1997). Transpiration directly relates to radiation and the vapor pressure deficit (VPD). At a low VPD, stomatal conductance increases rapidly due to increasing radiation (Will and Teskey, 1999; Pieruschka *et al.*, 2010). Stomatal closure occurs as the VPD increases (Sperry and Tyree, 1988). Therefore, transpiration may decrease despite a high VPD (Meinzer *et al.*, 1997; Roupsard *et al.*, 2006). Moreover, stomatal conductance decreased despite a high evaporative demand and a soil water deficit (Granier *et al.*, 2000; Meinzer, 2003). Consequently, tree and stand transpiration rates often increase during the rainy season and decline in the dry season, due to drying soils (Wullschleger *et al.*, 2001; Roupsard *et al.*, 2006; Isarangkool Na Ayutthaya, 2010).

Sangsing *et al.* (2004) studied the stomatal conductance in young rubber trees during water stress. Isarangkool Na Ayutthaya (2010) estimated the stand transpiration in mature rubber trees from sap flow measurements. With the lack of measurement of stomatal conductance and stand transpiration in rubber trees at the same time, the stomatal conductance has been correlated with radiation whereas stand transpiration estimated from sap flow measurements has responded to the VPD (Phillips *et al.*, 1999). The objective of the current study was to analyze the diurnal dynamics of the stand transpiration and stomatal conductance in rubber trees. In addition, the stomatal conductance and stand transpiration throughout the day were also measured to assess the time lag between the stomatal conductance and stand transpiration in response to radiation and the VPD. Understanding stand transpiration and stomatal conductance is important as they are the dominant factors in the water relations of plants because of the water loss from the plant to the atmosphere through the stomata. This study will provide information on the sensitivity of stand transpiration and stomatal conductance in rubber to variations in climatic variables throughout the year.

MATERIALS AND METHODS

Location, climate and stand

The experiment was conducted in a rubber plantation approximately 6.2 ha in size, which was part of the Chachoengsao Rubber Research Center (CRRC 13.41° N, 101.04° E), located 200 km east of Bangkok and 69 m above sea level. The site consisted of 13 yr-old rubber trees from clone RRIM 600, which is the main clone planted in Thailand. The plant spacing was 7.5 × 2.5 m and 9 × 2.5 m. The trees had been tapped for 6 yr for latex. The average girth of the trees at 1.80 m from the ground was 61.4 cm and the average height was about 19.2 m. The climate is tropical and humid with an average annual

rainfall of 1,288 mm.year⁻¹; rainfall usually starts in March with its peak during June to August with monthly averages from 115 to 385 mm based on data recorded at the CRRC weather station. The soil is a clayey, skeletal, kaolinitic, typic Paleustults (Kabin Buri series) with mean contents of sand, silt, clay, and organic matter being 49%, 16%, 35% and 1.08%, respectively and the profile is less than 1m deep before reaching a hard-packed, rocky bedrock consisting mainly of iron oxide rocks and stone (Silpi, 2006). Measurements in this study were monitored during three periods throughout the year—6 April (the dry season), 31 August (the rainy season) and 18 November (the early dry season) in 2007.

Climatic measurements

A weather station was located on a 25 m tower inside the plot. Data were recorded half hourly on air temperature (Ta), relative humidity (RH), rainfall, net radiation (Rn), global radiation (Rg) and wind speed (WS). The reference evapotranspiration (ETo, measured in millimeters per day) was calculated using the Penman-Monteith equation and FAO recommendations (Allen *et al.*, 1989).

Soil water content

The soil water content was determined by a gravimetric method. In brief, soil samples were collected in cans at 20, 40, and 60 cm depth from three locations in the plot. Sampling was done monthly from January to December 2007. Fresh samples were weighed and dried in a hot air oven for 24 hr at 105 °C. The dry samples were then reweighed and the difference in the weights was used to estimate the mass of water removed.

Sap flow measurement

The sap flow was measured in the stem of seven trees during the experiment using the heat dissipation method adapted from Granier (1985, 1987). Two home-made probe sets were

installed in rubber trees under field conditions to study the spatial variations of the sap flux density in the rubber tree stem. For each set of probes, two sections (each approximately 4 cm²) of bark were removed with a chisel, one above the other and separated by about 10 cm. Two probes per tree (one on the north face and the other on the south face), were located about 50 cm above the tapping panel. After the latex had dried, holes were drilled into the exposed xylem, and aluminum tubes were inserted straight into the holes. The probes were then inserted into the aluminum tubes. Prior to insertion, the probes were coated with silicone grease to ensure there was good thermal contact and to ease the removal of the probes and also to protect the probes from rain. These probes were connected to a data logger (21X; Campbell Scientific; Leicester, UK) which was put in an insulated box for protection from moisture and direct sunlight. Seven trees were selected for long-term monitoring of the sap flow and stand transpiration from January to December 2007. The trunk girths at 1.5 m above the ground ranged from 62.5 to 65.5 cm and the sapwood areas were about 250 cm². The sap flux density was calculated using Equation 1 (Granier, 1985):

$$J_s = \alpha K^\beta \quad (1)$$

where J_s is the sap flux density (measured in liters per square decimeter per hour), K is the sap flow index and α and β are calibration coefficients for the heat-dissipative probes ($\alpha = 312 \times 10^{-6}$ m³.m⁻².s⁻¹ or 11.24 L.dm⁻².hr⁻¹ and $\beta = 1.231$). These data were obtained by calibration in the laboratory and fitted to a power function. The sap flow index (K) was calculated using Equation 2:

$$K = \frac{\Delta T_0 - \Delta T_i}{\Delta T_i} \quad (2)$$

where ΔT_0 is the daily maximum temperature (°C) and ΔT_i is the current temperature difference (°C) between the two sensors of the probe.

Assuming the trunk sap flow in a tree is equal to whole tree transpiration, then the stand transpiration was calculated using Equation 3:

$$T = J_{S_{\text{mean}}} \times A_{\text{mean}} \times N \quad (3)$$

where T is the stand transpiration of the rubber tree layer of the stand level in millimeters per hour, $J_{S_{\text{mean}}}$ is the mean sap flux density in liters per square decimeter per hour, A_{mean} is the mean sapwood area per tree in square decimeters, and N is number of trees per hectare.

Leaf water potential

The leaf water potential was measured with a Scholander-type pressure chamber (plant water status console, Soilmoisture Equipment Corp.; Santa Barbara, CA, USA). Ten sunlit, fully expanded mature leaves were sampled from the upper layer of canopy of two rubber trees. Regular measurements of the leaf water potential were performed rapidly after cutting, and measured throughout the day (0800 to 1700 hours), from January to December 2007.

Stomatal conductance

The stomatal conductance was measured with a portable photosynthesis system (model Li-Cor 6400; Li-Cor Inc., Lincoln, NE, USA). The diurnal stomatal conductance at hourly intervals was measured between 0800 and 1700 hours. The stomatal conductance was measured on a sunlit leaf and each measurement was done at a photosynthetically active photon flux value of $1,500 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

Leaf area index ratio

The leaf area index (LAI) ratio was estimated from a hemispherical photograph. The camera was set at height of 1 m above the ground at 20 positions along with a litter trap every week. The photos were taken using a digital camera (COOLPIX995, 3.2 mega pixels; Nikon Corp.; Tokyo, Japan) with a fisheye converter (FC-E8;

Nikon Corp.; Tokyo, Japan). Gap fractions from the images were calculated using the Gap Light Analyzer software (Frazer *et al.*, 1999). The LAI ratio was calculated using Equation 4:

$$\text{LAI Ratio} = \frac{\text{LAI}_i}{\text{LAI}_{\text{max}}} \quad (4)$$

where LAI_i is the LAI from the fisheye lens measured every week and LAI_{max} is the maximum LAI from the fisheye lens measured over the year.

Statistical analyses

All statistical analyses were performed with the XLSTAT software (version 2003; Addinsoft, Paris, France). The mean and standard error were computed for all measurements, and the significance of a treatment effect was evaluated at the ($P < 0.05$) level. Curve fits and estimates were compared using the root mean square error.

RESULTS

Variation in climatic conditions

Following the rainfall events in March, the soil water content first increased slightly in the upper part of the soil. Later, it remained high throughout the rainy season (16–20%) and then declined slowly after the rainfall had ceased at the end of the year during the dry season (Figure 1). The cumulative rainfall of 1,085 mm was 15.76% below the long-term average for 10 yr in this area (Silpi, 2006). The diurnal variation of net radiation (R_n) and the VPD are shown in Figure 2. R_n increased rapidly around 1000 hours each day, reached a maximum around midday and then decreased sharply in the afternoon. There was a significant difference in R_n among the seasons. The maximum values of R_n in April and August were 680 and $700 \text{ W} \cdot \text{m}^{-2}$, respectively, and it was lowest in November ($420 \text{ W} \cdot \text{m}^{-2}$). There were no significant differences among the R_n values from April to August (680 – $700 \text{ W} \cdot \text{m}^{-2}$). The vapor pressure deficit (VPD) increased in the morning

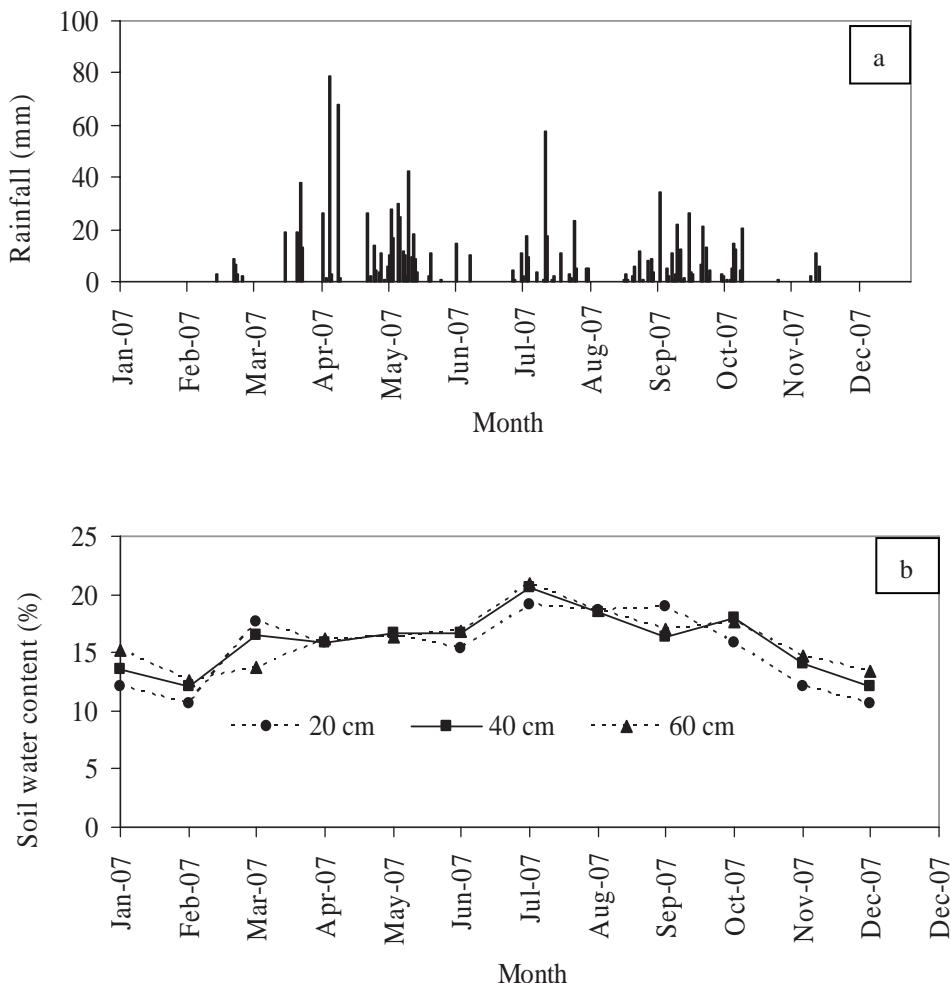


Figure 1 Seasonal variation from January to December 2007: (a) Rainfall (columns), and (b) Soil water content at different soil depths of 20, 40 and 60 cm

and then decreased in the late afternoon. There was a significant difference in the VPD among seasons. The maximum VPD occurred in April (2.8 kPa), and was lower in August (1.8 kPa) and November (2.2 kPa). The maximum VPD occurred later than the peak for Rn.

Plant water status variation

Figure 3 shows that the diurnal variations of leaf water potential (ψ_{Leaf}) which declined throughout the morning and minimum values occurred around midday, with a recovery in the afternoon. The leaf water potential varied

throughout the year. There was a highly significant difference in ψ_{Leaf} among seasons ($P < 0.01$) and it was highest in April (-0.42 MPa), lower in August (-0.65) and lowest in November (-0.86).

Seasonal variation of leaf area index ratio

The LAI ratio was correlated with the soil water content at 20 cm depth. When the soil water content in the top layer of the soil increased rapidly after a rainfall event, the LAI ratio also increased strongly during the refoliation period (Figures 1 and 4). The LAI ratio was constant in the rainy season with fully expanded leaves after which it

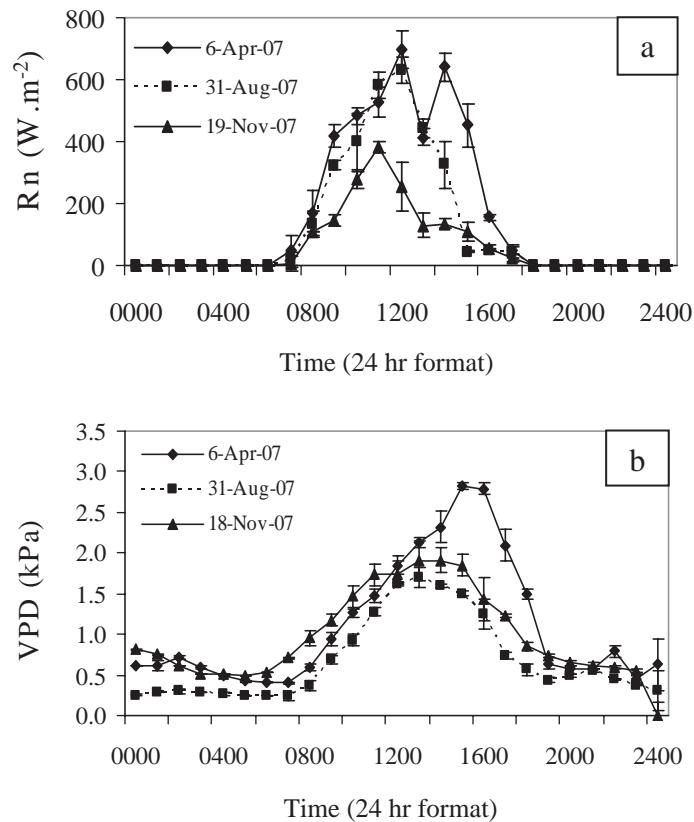


Figure 2 Diurnal variations of (a) Net radiation (R_n), and (b) Vapor pressure deficit (VPD) on 6 April at end of dry season, 31 August in rainy season and 18 November early in dry season. Vertical bars indicate SE. Both R_n and VPD were significantly different among seasons ($P < 0.05$).

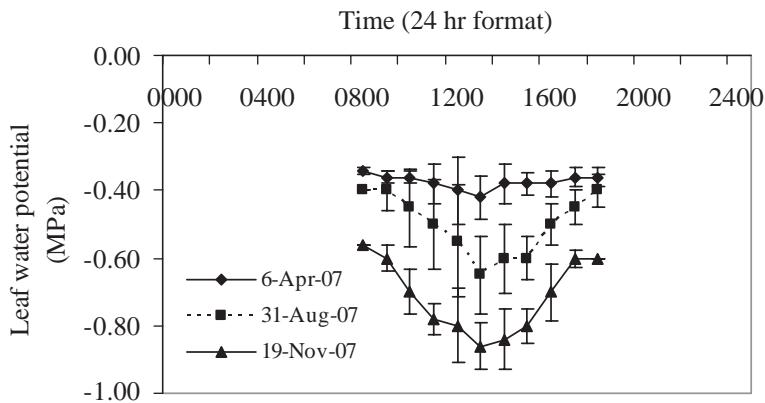


Figure 3 Diurnal variations of daytime leaf water potential as measured with a pressure chamber on 6 April at end of dry season, on 31 August in the rainy season and on 18 November early in dry season. Vertical bars indicate SE. Leaf water potential was highly significantly ($P < 0.01$) different among seasons.

decreased early in the dry season in November (Figure 4).

Diurnal dynamics of ETo, stand transpiration and stomatal conductance

Figure 5 shows the diurnal pattern of evapotranspiration (ETo), stand transpiration and stomatal conductance for 3 d of intensive measurements on 6 April 2007, 31 August 2007 and 18 November 2007. ETo increased rapidly in the morning and peaked around noon and then decreased in the afternoon. Both the maximum and average ETo values were not significantly different among seasons. The maximum ETo tended to be higher in April and August (0.62 mm.hr^{-1}) than in November (0.43 mm.hr^{-1}) (Figure 5a). The stand transpiration (T) increased in the morning as the radiation and the VPD increased. T generally reached its maximum around midday and then it declined in the afternoon when there were low light levels and a high VPD. Both the maximum and average stand transpiration were significantly different among seasons. The stand transpiration was highest in April (0.45 mm.hr^{-1}), intermediate in August (0.4 mm.hr^{-1}), and lowest in November (0.3 mm.hr^{-1}) (Figure 5b). Similarly, the stomatal conductance (g_s) increased rapidly in the morning as a result of stomatal opening under conditions

of high radiation, moderate air temperature and a low VPD. The maximum g_s occurred around 1000 hours before the peak in the stand transpiration occurred. After that g_s declined more steeply as the stand transpiration continued to increase until around midday. Both the maximum and average stomatal conductance were significantly different among seasons. The maximum g_s value occurred in August ($461 \text{ mmol.m}^{-2}.\text{s}^{-1}$), was lower in April ($274 \text{ mmol.m}^{-2}.\text{s}^{-1}$) and was lowest in November ($216 \text{ mmol.m}^{-2}.\text{s}^{-1}$) (Figure 5c). There were different time lags between the stomatal conductance and stand transpiration; the stomatal conductance was more sensitive to climatic variables than the stand transpiration.

Relationships between stand transpiration and evapotranspiration, radiation or vapor pressure deficit

The relationships between the stand transpiration and ETo, Rn or VPD showed a pattern of hysteresis. The diurnal stand transpiration (T) was positively correlated with the diurnal evapotranspiration (ETo) (Figure 6). A strong relationship between the stand transpiration (T) and the net radiation (Rn) was demonstrated in rubber trees (Figure 7). In addition, the results showed a relationship between T and VPD for

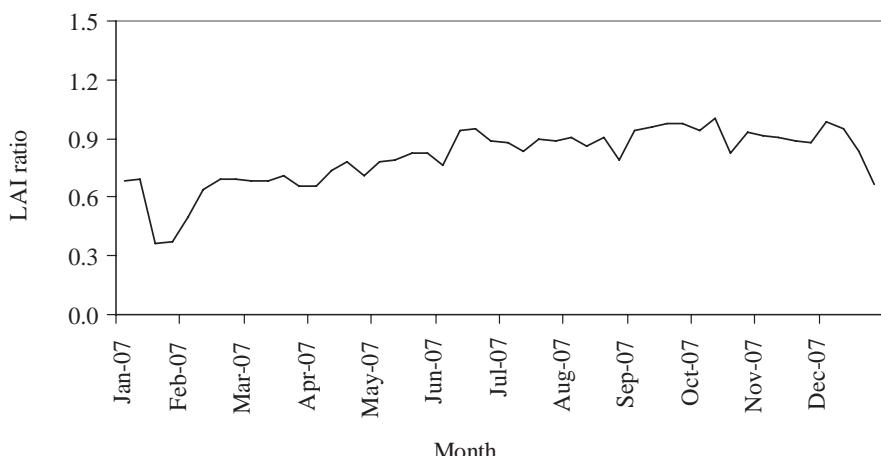


Figure 4 Seasonal variation of the leaf area index (LAI) ratio from January to December 2007.

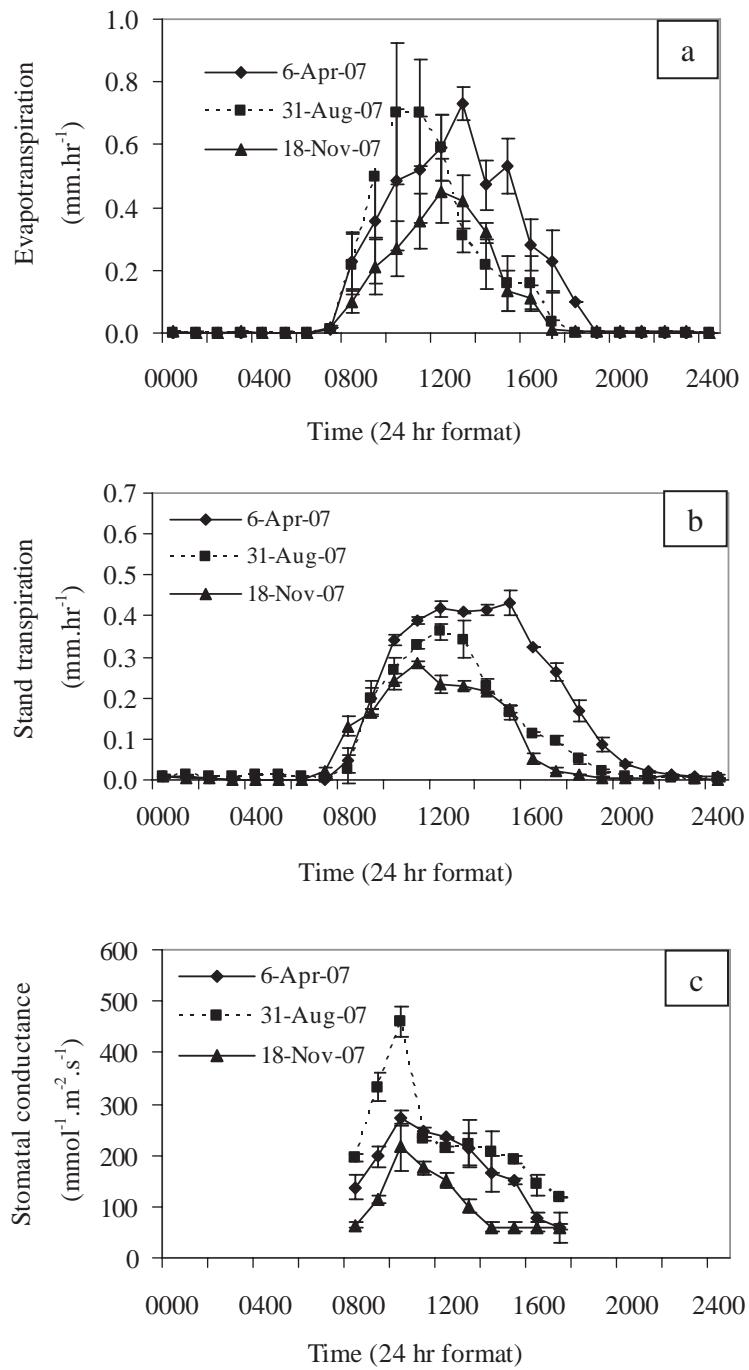


Figure 5 Diurnal variations of: (a) Evapotranspiration (not significantly different among seasons, $P > 0.05$); (b) Stand transpiration (significantly different among seasons $P < 0.05$); and (c) Stomatal conductance (significantly different among seasons $P < 0.01$) on 6 April 2007 at end of dry season, 31 August 2007 in rainy season and 18 November 2007 early in dry season. Vertical bars indicate SE.

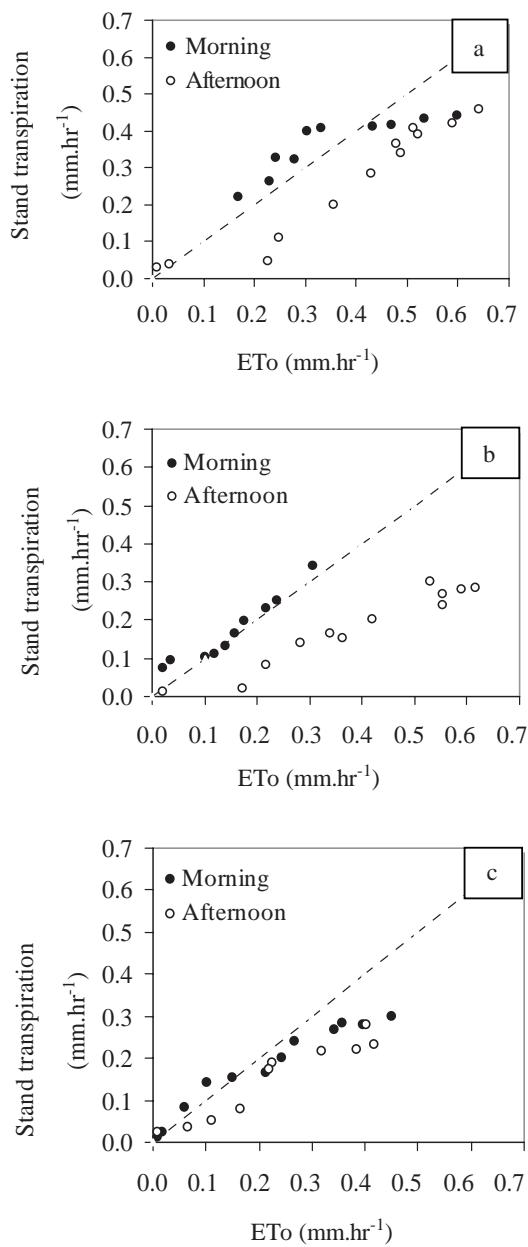


Figure 6 Relationship between stand transpiration (T) and evapotranspiration (ETo) on: (a) 6 April 2007 (in the morning, correlation coefficient (R^2) = 0.94, in the afternoon, R^2 = 0.79); (b) 31 August 2007 (in the morning, R^2 = 0.96, in the afternoon, R^2 = 0.79); and (c) 18 November 2007 (in the morning, R^2 = 0.96, in the afternoon, R^2 = 0.80). The dotted line shows the 1:1 ratio line.

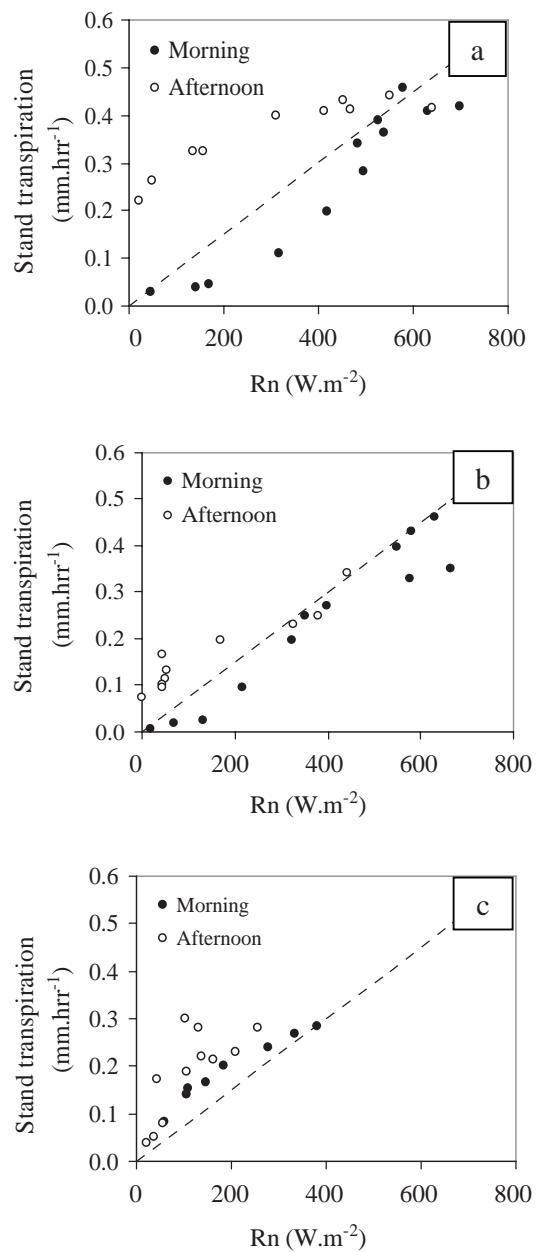


Figure 7 Diurnal relationship between stand transpiration (T) and net radiation (Rn) on: (a) 6 April 2007 (in the morning, correlation coefficient (R^2) = 0.93, in the afternoon, R^2 = 0.62); (b) 31 August 2007 (in the morning, R^2 = 0.91, in the afternoon, R^2 = 0.88); and (c) 18 November 2007 (in the morning, R^2 = 0.87, in the afternoon, R^2 = 0.65). The dotted line is the 1:1 ratio line.

the three measurement days (Figure 8). Generally, VPD could explain approximately 87% variations in stand transpiration ($R^2 = 0.64\text{--}0.97$), while R_n explained about 81% ($R^2 = 0.62\text{--}0.93$). The relationships between T and ETo , radiation or VPD in the morning were greater than in the afternoon. Moreover, they were low in the dry season.

Relationship between stomatal conductance and radiation or vapor pressure deficit

The stomatal conductance was related to the net radiation for the three days sampled—6 April 2007 ($R^2 = 0.53$), 31 August 2007 ($R^2 = 0.90$) and 18 November 2007 ($R^2 = 0.70$) (Figure 9). The stomatal conductance increased as the radiation increased in the morning. Moreover, the stomatal conductance was related to the VPD on 6 April ($R^2 = 0.59$) and 31 August ($R^2 = 0.65$) (Figure 10). The stomatal conductance declined in response to the increasing VPD in the afternoon. The slope of the relationship between the g_s and VPD reflected the sensitivity of the stomata to the VPD. The higher stomatal sensitivity to the VPD occurred in the rainy season while there was a lower stomatal sensitivity in the dry season. Stomatal closure occurred when the VPD reached 2.2 kPa in the rainy season. However, the stomata closed when the VPD was more than 2.5 kPa in the dry season.

DISCUSSION

Plant water status is a dynamic property and changes in response to the water availability in the soil and to climatic variations. The leaf water potential is a thermodynamic expression, which is a reliable indicator of plant water status (Kramer and Kozlowski, 1979). The value of the leaf water potential responds to environmental variables such as the soil water content, radiation and VPD (Nadezhina, 1999). The leaf water potential decreased as the soil water stress and VPD increased. The leaf water potential is regulated by the stomatal conductance in many

species (Fordyce *et al.*, 1997; Myers *et al.*, 1997). The minimum leaf water potential corresponds to the maximum transpiration. Sangsing (2004) reported a strong relationship between stomatal conductance and leaf water potential in the young rubber tree clones of RRIM 600 and RRIT 251. The tree regulates the stomatal apertures to avoid an excessive loss of water and stomatal closure occurred to maintain the water potential above a critical threshold, thus protecting against xylem cavitation (Tyree and Sperry, 1989; Sperry, 2000; Cochard *et al.*, 2002; David *et al.*, 2004). Under drought stress, the water deficit causes a decrease in the leaf water potential and stomatal conductance. This leads to a reduction of transpiration in the rubber trees.

Diurnal stand transpiration (T), evapotranspiration (ETo) and leaf stomatal conductance (g_s) showed similar patterns (Figure 4). Variations in T and g_s occurred throughout the day and season (Montieh, 1995; Addington *et al.*, 2004). There were different time lags between the stand transpiration and stomatal conductance throughout the year. The results indicated that the maximum g_s occurred around 1000 hours following high radiation and low VPD in the morning. The maximum T appeared around midday whereas g_s continued to decrease with increasing VPD. The results implied that T and g_s decreased in the afternoon and in the dry season. There was evidence of stomatal control of transpiration. Stomatal closure occurred to limit the transpiration despite the high VPD and low soil water content (Meinzer, 1993; Franks, 2004). Thereby, water loss through transpiration was regulated by the stomata and driven by evaporative demand (Jackson *et al.*, 2000). The variation in the stand transpiration throughout the year may vary according to the LAI ratio. The stand transpiration in the dry season was higher than those in the rainy season and early in the dry season according to increasing VPD and radiation. In addition, leaf flushing occurred in February which further increased the stand transpiration.

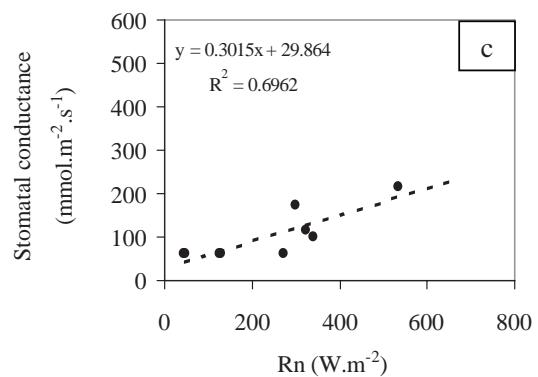
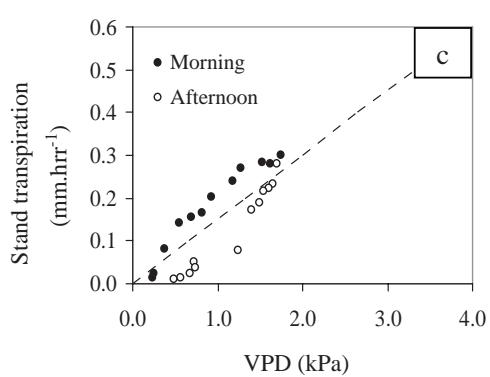
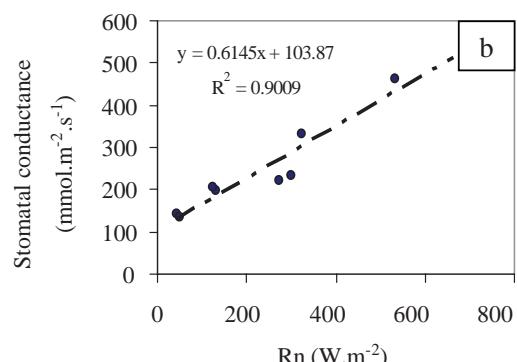
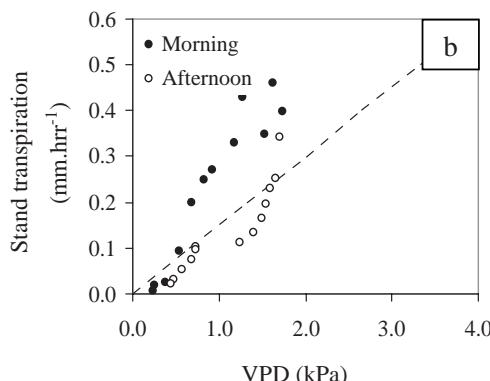
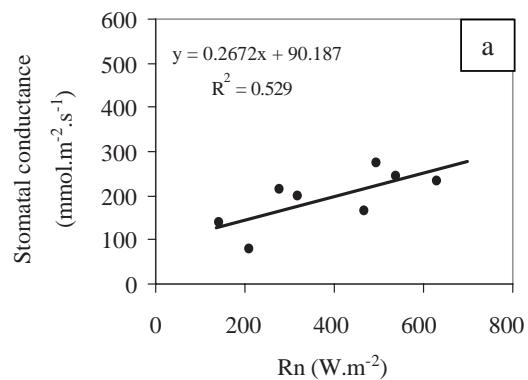
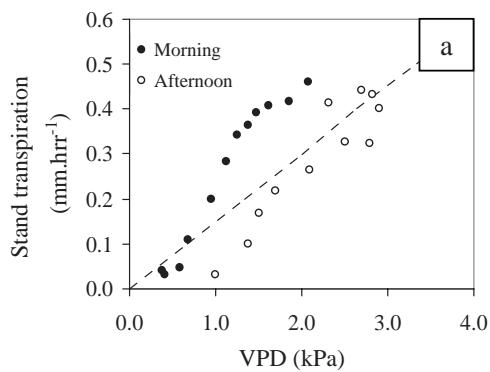


Figure 8 Diurnal stand transpiration and vapor pressure deficit (VPD) on: (a) 6 April 2007 (in the morning, correlation coefficient (R^2) = 0.96, in the afternoon, R^2 = 0.79); (b) 31 August 2007 (in the morning, R^2 = 0.94, in the afternoon, R^2 = 0.92); and (c) 18 November 2007 (in the morning, R^2 = 0.97, in the afternoon, R^2 = 0.64). The dotted line is the 1:1 ratio line.

Figure 9 Diurnal relationship between diurnal stomatal conductance and net radiation (R_n) on: (a) 6 April 2007 (correlation coefficient (R^2) = 0.53); (b) 31 August 2007 (R^2 = 0.90); and (c) 18 November 2007 (R^2 = 0.70). The line indicates the curve regression between diurnal stomatal conductance and R_n .

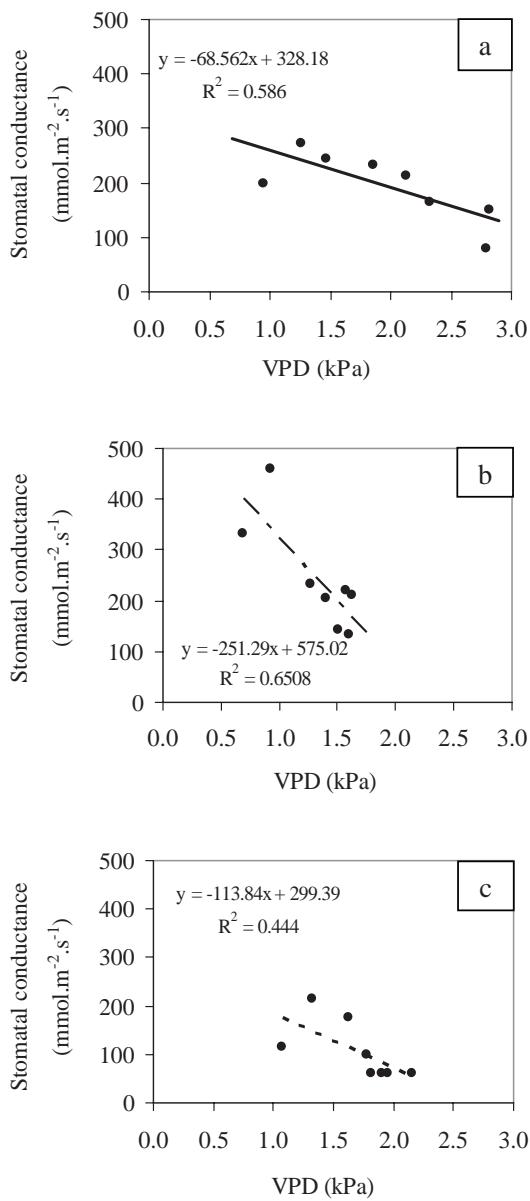


Figure 10 Diurnal relationship between stomatal conductance and vapor pressure deficit (VPD) On: (a) 6 April 2007 (correlation coefficient (R^2) = 0.59); (b) 31 August 2007 (R^2 = 0.65); and (c) 18 November 2007 (R^2 = 0.44). The dotted line indicates the curve regression between stomatal conductance and VPD on the three days.

After leaf flushing in rubber trees, the hydraulic conductance of the leaves increased due to the development of new xylem conduits for the new leaves (Isarangkool Na Ayutthaya, 2010). Stand transpiration was high during full canopy and close to the optimum soil water availability. When the vegetation completely shades the ground, it can be assumed that the transpiration surface is equivalent to the ground area (Pereira *et al.*, 2006). Furthermore, stomatal conductance was highest in the rainy season during the period of stable full canopy due to the low VPD and high soil water content. In contrast, the stand transpiration and stomatal conductance were lowest in November, early in the dry season, during the defoliation period. Leaf senescence and shedding decreased the hydraulic conductance of the whole tree. The results may have been caused by xylem cavitation that reduces the xylem hydraulic conductivity and impairs the water transport to the leaves (Taiz and Zeiger, 2006). Stomatal closure occurs during a period of soil drought to prevent the water potential decreasing below the critical threshold (Frank *et al.*, 2004). The transpiration rate decreased with an increasing soil water deficit (Roupsard *et al.*, 2006).

The current study found a strong linear relationship between the stand transpiration and reference evapotranspiration (ETo) (Figure 6) as was also reported by Poyatos *et al.* (2005) who found that the daily stand transpiration had a strong linear relation to ETo.

Transpiration was mainly controlled by radiation and VPD. There was a strong relationship between the stand transpiration and net radiation (Figure 7). If Rn is low, transpiration may decrease (Meinzer *et al.*, 1997). Stand transpiration was strongly related to the VPD (Figure 8). This may suggest that both radiation and VPD control the magnitude of the daily water uptake. It was found that stand transpiration increased with an increasing VPD and it decreased at a high VPD (O'Grady *et al.*, 1999; Granier *et al.*, 1996; Wullschleger *et al.*, 2001). The relationships

between the stand transpiration, ETo, radiation and VPD in the morning were greater than in the afternoon because increasing the daily Rn leads to an increase in the transpiration. Therefore, the stand transpiration and ETo increased rapidly in the morning with increasing Rn and VPD. However, the transpiration generally declined despite the high VPD while the soil evaporation continued with the high VPD in the afternoon.

Stomatal conductance was related to radiation and VPD (Figure 9 and 10). These results showed that stomatal activity is sensitive to radiation. The radiation-induced stomatal opening occurred shortly after sunrise when the radiation increased and the VPD was low (Will and Teskey, 1999). Therefore, increasing the radiation load on the leaf increased the stomatal conductance (Pieruschka *et al.*, 2010). This may have been due to the sensitivity of the stomata to radiation. However, there was a relatively strong relationship between the stomatal conductance and the VPD. The stomatal conductance decreased in the afternoon with the diminishing sunlight and a high VPD that induced stomatal closure (Motzer *et al.*, 2005). The shape of the graphical relationship between the stomatal conductance and VPD may be revealed as a result of the stomatal closure response to the increasing VPD, supporting a mechanism to maintain tree transpiration (Montieth, 1995; Pataki *et al.*, 1998; David *et al.*, 2004). It has been commonly observed that a greater sensitivity is associated with higher maximum g_s at low VPD under well-watered conditions, while conversely, the lower stomatal sensitivity to VPD occurred at low rainfall and high VPD (Oren *et al.*, 1999; Cunningham, 2004). Then, rubber trees showed high stomatal sensitivity to the VPD in the rainy season and low stomatal sensitivity to the VPD in the dry season.

CONCLUSION

The study found that environmental conditions produce important interacting controls on the plant water status in rubber trees. The plant

water status was correlated with the climatic conditions and soil water content. The diurnal dynamics of the stand transpiration (T) and stomatal conductance (g_s) were mainly controlled by the radiation and VPD. There were different time lags between T and g_s throughout the year. In addition, the stomatal conductance was more sensitive to climatic changes. The relationship between the climatic factors and transpiration varied throughout the year. Thus, it is not possible to predict transpiration from climatic data only.

ACKNOWLEDGEMENTS

The study was funded by the Thai-French Committee for Training, by CIRAD and by Burapha University and Kasetsart University. The authors thank the French Embassy in Bangkok and the Commission on Higher Education for supporting the bilateral fellowship and the Chachoengsao Rubber Research Center (CRRC) for allowing access to the rubber plantation and some equipment used in this research. The authors are also grateful to the French CIRAD researchers and the Thai partners from Kasetsart University and the CRRC.

LITERATURE CITED

Addington, R.N., R.J. Mitchell, R. Oren and L.A. Donovan. 2004. Stomatal sensitivity to vapor pressure deficit and its relationship to hydraulic conductance in *Pinus palustris*. **Tree Physiol.** 24: 561–569.

Allen, R.G., M.E. Jensen, J.L. Wright and R.G. Burman. 1989. Operational estimates of evapotranspiration. **Agron. J.** 81: 650–662.

Ansley, R.S., P.W. Jacoby, C.H. Meadors and B.K. Lawrence. 1992. Soil and leaf water relations of differentially moisture-stressed honey mesquite (*Prosopis glandulosa* Torr). **J. Arid Environ.** 22: 147–159.

Cochard, H., N. Breda and A. Granier. 1996. Whole tree hydraulic conductance and water

loss regulation in *Quercus* during drought: Evidence for stomatal control of embolism. **Ann. For. Sci.** 53: 197–206.

Cochard, H., L. Coll, X.L. Roux and T. Ameglio. 2002. Unraveling the effects of plant hydraulics on stomatal closure during water stress in walnut. **Plant Physiol.** 128: 282–290.

Cruziat, P., H. Cochard and T. Ameglio. 2002. Hydraulic architecture of trees: Main concepts and results. **Ann. For. Sci.** 59: 723–752.

Cunningham, S.C. 2004. Stomatal sensitivity to vapour pressure deficit of temperate and tropical evergreen rainforest trees of Australia. **Trees** 18: 399–407.

David, T.S., M.I. Ferreira, S. Cohen, J.S Pereira and J. David. 2004. Constraints on transpiration from an evergreen oak tree in southern Portugal. **Agric. For. Meteorol.** 122: 193–205.

Davies, W.J. and T.T. Kozowski. 1997. Variations among woody plants in stomatal conductance and photosynthesis during and after drought. **Plant and Soil** 46: 435–444.

Denmead, O.T., F.X. Dunin, S.C. Wong and F.A.N. Greenwood. 1993. Measuring water use efficiency of Eucalypt trees with chambers and micrometeorological techniques. **J. Hydrol.** 150: 649–664.

Ford, C.R., C. Goranson, R.J. Mitchell, R.E. Will and R.O. Teskey. 2004. Diurnal and seasonal variability in the radial distribution of sap flow. Predicting total stem flow in *Pinus taeda* trees. **Tree Physiol.** 24: 951–960.

Fordyce, I.R., G.A. Duff and D. Eamus. 1997. The water relations of *Allosynearpia ternata* at contrasting sites in the monsoonal tropics of northern Australia. **Aust. J. Bot.** 45: 259–274.

Franks, P.J. 2004. Stomatal control and hydraulic conductance, with species reference to tall trees. **Tree Physiol.** 24: 865–878.

Frazer, G.W., C.D. Canham and K.P. Letzman. 1999. **Gap Light Analyser (GLA), Version 2.0 : Imaging Software to Extract Canopy Structure and Gap: Light Transmission Indices from True-Colour Fisheye Photographs, User Manual and Program Documentation.** Simon Frazer University, Burnaby, British Columbia and Institute of Ecosystem Studies, Millbrook, NY, USA.

Granier, A. 1985. Une nouvelle méthode pour la mesure des flux de séve dans le tronc des arbres. **Ann. Sci. For.** 42: 193–200. [in French]

_____. 1987. Evaluation of transpiration in Douglas fir stand by means of sap flow measurement. **Tree Physiol.** 3: 309–323.

Granier, A., P. Biron and D. Lemoine. 2000. Water balance, transpiration and canopy conductance in two beech stands. **Agric. For. Meteorol.** 100: 291–308.

Granier, A., P. Biron, N. Breda, J.Y. Pontailler and B. Saugier. 1996. Transpiration of trees and forest stands: Short and long-term monitoring using sap flow methods. **Global Change Biol.** 2: 256–274.

Guardiola-Claramonte, M., P.A. Troch, A.D. Ziegler, T.W. Giambelluca, M. Durcik, J.B. Vogler and M.A. Nullet. 2010. Hydrologic effects of the expansion of rubber (*Hevea brasiliensis*) in a tropical catchment. **Ecohydrol.** 3: 306–314.

Hatton, T.J., S.J. Moore and P.H. Reece. 1995. Estimating stand transpiration in a *Eucalyptus populnea* woodland with the heat pulse method: Measurement errors and sampling strategies. **Tree Physiol.** 15: 219–227.

Isarangkool Na Ayutthaya, S. 2010. **Change of Whole-Tree Transpiration of Mature *Hevea brasiliensis* under Soil and Atmospheric Droughts: Analysis in Intermittent and Seasonal Droughts under the Framework of the Hydraulic Limitation Hypothesis.** PhD Thesis, Université Blaise Pascal. Clermont Ferrand, France.

Jackson, R.B., J.S. Sperry and T.E. Dawson. 2000. Root water uptake and transport: Using physiological process in global predictions.

Trends Plant Sci. 5(11): 482–488.

Kramer, P. and T.T. Kozlowski. 1979. **Physiology of Woody Plants**. Academic Press. New York, NY, USA. 462 pp.

Meinzer, F.C. 1993. Stomatal control of transpiration. **Trends Ecol. Evol.** 8: 289–294.

_____. 2003. Functional convergence in plant responses to the environment. **Oecologia** 134: 1–11.

Meinzer, F.C., T.M. Hinckley and R. Ceulemans. 1997. Apparent responses of stomata to transpiration and humidity in a hybrid poplar canopy. **Plant Cell Environ.** 20: 1301–1308.

Monteith, J.L. 1995. A reinterpretation of stomatal responses to humidity. **Plant Cell Environ.** 18: 357–364.

Motzer, T., N. Munz, M. Kuppers, D. Schmitt and D. Anhuf. 2005. Stomatal conductance, transpiration and sap flow of tropical montane rainforest trees in the southern Ecuadorian Andes. **Tree Physiol.** 25: 1283–1293.

Myers, B.A., G.A. Duff, D. Eamus, I.R. Fordyce, A. O'Grady and R.J. Williams. 1997. Seasonal variation in water relations of trees of differing leaf phenology in a wet-dry tropical savanna near Darwin, northern Australia. **Aust. J. Bot.** 45: 225–240.

Nadezhina, N. 1999. Sap flow index as an indicator of plant water status. **Tree Physiol.** 19: 885–891.

O'Grady, A.P., D. Eamus and L.B. Hutley. 1999. Transpiration increases during the dry season: Patterns of tree water use in eucalyptus open-forests of northern Australia. **Tree Physiol.** 19: 591–597.

Oren, R., J.S. Sperry, G. Katul, D.E. Pataki, B.E. Ewers, N. Philips and K.V.R. Schafer. 1999. Survey and synthesis of intra-and inter-specific variation in stomatal sensitivity to vapor pressure deficit. **Plant Cell Environ.** 22: 1515–1526.

Pataki, D.E., R. Oren and N. Philips. 1998. Responses of sap flow and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. **J. Exp. Bot.** 49: 871–878.

Pereira, A.R., S. Green and N.A. Vilb-Nova. 2006. Penman-Monteith reference evapotranspiration adaptation to estimate irrigated tree transpiration. **Agric. Water Manage.** 83: 153–161.

Phillips, N., R. Oren and R. Zimmemann. 1999. Temporal patterns of water flux in trees and lianas in a Panamanian moist forest. **Trees** 14: 116–123.

Pieruschka, R., G. Huber and J.A. Berry. 2010. Control of transpiration by radiation. **PNAS**. 107(30): 13372–13377.

Poyatos, R., P. Liorens and F. Gallart. 2005. Transpiration of montane *Pinus sylvestris* L. and *Quercus pubescens* Willd. Forest stands measured with sap flow sensors in NE Spain. **Hydrology and Earth System Science** 9: 493–505.

Roupsard, O., J.M. Bonnefond, M. Irvine, P. Berbigier, Y. Nouvellon, J. Dauzat, S. Taga, O. Hamel, C. Jourdan, L. Saint-André, I. Mialet-Serra, J.P. Labouisse, D. Epron, R. Joffe, S. Bracnnier, A. Rouzière, M. Navarro, J.P. Bouille. 2006. Partitioning energy and evapo-transpiration above and below a tropical palm canopy. **Agric. For. Meteorol.** 139: 252–268.

Sangsing, K. 2004. **Carbon Acquisition and Plant Water Status in Response to Water Stress of Rubber (*Hevea brasiliensis* Muell. Arg.)**. PhD. thesis. Kasetsart University, Bangkok, Thailand.

Sangsing, K., P. Kasemsap, S. Thanisawanyangkura, K. Sangsila, E. Gohet, P. Thaler and H. Chochard. 2004. Xylem embolism and stomatal regulation in two rubber clones (*Hevea brasiliensis* Muell. Arg.). **Trees** 18: 109–114.

Silpi, P. 2006. **Carbon partitioning in *Hevea brasiliensis* Muell. Arg.): Dynamics among functional sinks (latex regeneration, respiration, growth, and reserves) at trunk scale.** PhD. thesis. Kasetsart University, Bangkok, Thailand.

Smith, D.M. and S.J. Allen. 1996. Measurement of sap flow in plant stems. **J. Exp. Bot.** 47: 1833–1844.

Sperry, J.S. 2000. Hydraulic constraints on gas exchange. **Agric. For. Meteorol.** 104: 13–23.

Sperry, J.S. and M.T. Tyree. 1988. Mechanism of water stress-induced xylem embolism. **Plant Physiol.** 88: 581–587.

Sperry, J.S., U.G. Hacke, R. Oven and J.P. Comstock. 2002. Water deficits and hydraulic limits to leaf water supply. **Plant Cell Environ.** 25: 251–263.

Taiz, L. and E. Zeiger. 2006. **Plant Physiology.** 4th ed. Sinaner Associates, Inc. Sunderland, MA, USA. 702 pp.

Tyree, M.T. and J.S. Sperry. 1989. Vulnerability of xylem to cavitation and embolism. **Ann. Rev. Plant Mol. Bio.** 40: 19–38.

Will, R.E. and R.O. Teskey. 1999. Influence of rate of change in stomatal conductance to fluctuating irradiance on estimates of daily water use by *Pinus taeda* leaves. **Tree Physiol.** 19: 761–765.

Wilson, K.B., P.J. Hanson, P.J. Mulholland, D.D. Baldocchi and S.D. Wullschleger. 2001. A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance. **Agric. For. Meteorol.** 106: 153–168.

Wullschleger, S.D., K.B. Wilson and P.J. Hanson. 2001. Environmental control of whole plant transportation, canopy conductance and estimates of the decoupling coefficient for large red maple trees. **Agric. For. Meteorol.** 104: 157–168.