# Effects of Drought and Tapping for Latex Production on Water Relations of *Hevea brasiliensis* Trees

Sumit Kunjet<sup>1</sup>, Philippe Thaler<sup>2</sup>, Frederic Gay<sup>2</sup>, Pisamai Chuntuma<sup>3</sup>, Kumut Sangkhasila<sup>4</sup> and Poonpipope Kasemsap<sup>5,\*</sup>

# ABSTRACT

The impact of drought conditions on the water relations of rubber trees is important because the trees could shed leaves while they are being continuously tapped. The aim of this work was to study the effect of soil drought and the tapping of latex on the water relations of rubber trees. This study distinguished between untapped trees and trees affected by tapping activity. The experiment was conducted on 14–15 year-old rubber trees from the clone, RRIM 600, at the Chachoengsao Rubber Research Center (CRRC). Climatic measurement, soil water content, predawn and midday leaf water potential, stand transpiration and percentage loss of hydraulic conductivity (PLC) were measured from January 2009 to January 2010, especially in the dry season. Under drought conditions, during the rainy season, stand transpiration and predawn leaf water potential decreased in response to soil drought in August. The midday leaf water potential and PLC did not change following soil water stress. In the dry season, the plant water status was related to climatic variables and soil drought. The results indicated that drought induces a reduction in the plant water status of rubber trees. Tapping activity did not have a marked influence on the water balance of the rubber trees. However, tapping reduced the sap flux density and stomatal conductance; thus, attention must be paid to tapping in the dry season, particularly in dry areas.

Keywords: drought, tapping, latex production, water relations, Hevea brasiliensis

# **INTRODUCTION**

The rubber tree is one of the major economic crops in Southeast Asia, valued for its latex production and timber. The sale price of latex is high and thus, rubber plantations have been expanded to drought-prone areas that provide suboptimal growing conditions in northern and northeastern regions, where there is a long dry season and growth and latex production is limited by water availability and climatic conditions (Roa *et. al.*, 1990; Manmuen *et al.*, 1993; Sivanadyan *et al.* 1995; Chandrashekar *et al.*, 1996). Climate change due to global warming is likely to increase the stress caused by such environmental variables if there are more frequent periods of drought in Southeast Asia. Drought may affect the water relations in rubber trees because the trees could

<sup>&</sup>lt;sup>1</sup> Tropical Agriculture Program, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand.

<sup>&</sup>lt;sup>2</sup> CIRAD Rubber Program, Kasetsart University, Bangkok 10900, Thailand.

<sup>&</sup>lt;sup>3</sup> Chachoengsao Rubber Research Center, Sanam Chai Ket District, Chachoengsao 24160, Thailand.

<sup>&</sup>lt;sup>4</sup> Department of Soil, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand.

<sup>&</sup>lt;sup>5</sup> Department of Horticulture, Faculty of Agriculture, Kasetsart University, Bangkok 10900, Thailand.

<sup>\*</sup> Corresponding author, e-mail: agrppk@ku.ac.th

shed their leaves while they are also being tapped. Consequently, knowledge about the water relations in rubber trees is necessary.

Soil drought conditions cause stress in plants and reduce growth. Soil drought occurs whenever the soil water status drops below a threshold that limits transpiration (Grady et al., 2008). Under drought conditions, the predawn and midday leaf water potential were closely related to leaf stomatal conductance and soil water content (Ansley et al., 1992). Kume et al. (2007) confirmed that the leaf water potential decreased, caused by stomatal closure resulting from drought stress. Stand transpiration was strongly limited when the soil water deficit increased (Poyatos et al., 2005). In addition, shoot hydraulic conductivity decreased in response to water stress (Sperry and Tyree, 1990), while the loss of hydraulic conductance induced stomatal closure and caused cavitation in the xylem (Sperry, 2000). The minimum leaf water potential in both young and mature rubber trees reached -1.95 MPa. Transpiration decreased during the period of leaf senescence and shedding in the dry season (Sangsing et al., 2004; Isarangkool Na Ayutthaya, 2010).

Tapping induces a deviation of resources (carbon and water) and strongly reduces growth due to the wounding stress. The latex contains about 60-70% water. Therefore, the water status in the plant and soil affects latex production (Pakianathan et al., 1989). Variations in rubber yield were associated with the soil water content and climatic factors (Roa et al., 1990). However, the impact of tapping on water relations could be related to growth reduction and may be caused by the physiological disorder of trunk phloem necrosis (TPN), particularly if the tapping calendar extends into the dry season (Nandris et al., 2006). Therefore, assessment of the water relations in rubber trees as they relate to climatic conditions and tapping activity is important in forecasting the productivity and sustainability of a rubber plantation. The aim of this research was to study the effect of soil drought and tapping activity for

latex production on the water relations of rubber trees.

#### MATERIALS AND METHODS

# Location, climate and stand

The experiment was conducted at a rubber plantation (about 6.2 ha), in part of the Chachoaengsao Rubber Research Center (CRRC) (13.41 °N 101.04 °E), located 200 km east from Bangkok and 69 m above sea level. It consisted of 14–15 year-old rubber trees of the clone RRIM 600, which is the main clone planted in Thailand. The spacings were 7.5 m  $\times$  2.5 m and 9 m  $\times$  2.5 m. The trees had been tapped for six years for latex yield. The average girth of the trees at 1.8 m above the ground was 61.4 cm. The average height was about 19.2 m. The climate in this area is tropical and humid with an annual rainfall of 1,288 mm.year<sup>-1</sup>. Rainfall usually starts in March and peaks during June to August, with an average of 115–385 mm.month<sup>-1</sup>. Tapping of the trees started at 1.5 m above ground level.

Tapping activity is performed by cutting the bark on one half of the trunk (tapping panel) with a sharp knife, and severing the maximum number of latex vessels. Cuts are controlled by regularly removing a thin shaving of bark from the sloping cut. The latex flows out, driven by turgor pressure, and soon dries out (George and Jacob, 2000). The tapping system used in this study was a half spiral cut, tapped every two days (S/2 d2). Treatments included six untapped trees (control) and six tapped trees. Tapping started in May 2009 and stopped in January 2010.

#### **Climatic measurements**

A weather station was located on a 25 m tower inside the plot and recorded half hourly values of air temperature  $(T_a)$ , relative humidity (RH), rainfall, net radiation  $(R_n)$  and wind speed (WS). The reference evapo-transpiration (ETo in mm.day<sup>-1</sup>) was calculated by the Penman-Monteith equation and recommendations from Food and

Agriculture Organization of the United Nations (2009).

#### Soil water content

The soil water content was determined by the gravimetric method. Soil samples at 20, 40 and 60 cm depth were taken from six parts of the rubber plantation. Sampling was done monthly from January 2009 to January 2010. Fresh samples were weighed and dried in a hot air oven for 24 hr at 105 °C. The dry samples were weighed to estimate the mass of water removed.

### Sap flow measurement

The sap flow was measured by the heat dissipation method adapted from Granier (1987), using home-made 20 mm-long radial probes. The set consisted of two sensor probes (needles). One probe was continuously heated (0.2 W)and the other probe was unheated to measure the temperature of sapwood tissue and used as a reference probe. The experimental devices were calibrated for the rubber field conditions. Accordingly, two probes sets per tree (one on the north facing side and the other on the south facing side), located above the tapping panel were used for monitoring. Pieces of bark about  $4 \text{ cm}^2$ in size were removed with a chisel, one above the other but separated by about 10 cm. After the latex coming from the bark chip removal sites had dried, holes were drilled about 2 cm into the sapwood and aluminum tubes 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 good thermal contact and easy removal of the probes. These probes were connected to a data logger (21X, Campbell Scientific, Leicester, UK). They were protected from rainfall and direct sunlight. Two tapped trees and two untapped trees were selected for long-term monitoring of the sap flow and stand transpiration from January 2009 to January 2010. The trunk girth at 1.5 m above the ground averaged 62.5-65.5 cm and the sapwood area averaged 250 cm<sup>2</sup>. The sap flux density  $(J_s)$  was calculated from Equation 1:

$$J_{s} = 312 \text{ x } 10^{-6} \text{ K}^{1.231}$$
(1)

where  $J_s$  is the sap flux density ( $J_s$ , liters per square decimeter per hour) and K is the sap flow index. The sap flow index was calculated using Equation 2:

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

where  $\Delta T_o$  is the daily maximum temperature difference and  $\Delta T_i$  is the current temperature difference between the two sensors of the probe (°C).

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

$$\mathbf{T} = \mathbf{J}_{s \text{ mean}} \times \mathbf{A}_{\text{mean}} \times \mathbf{N}$$
(3)

where T is the stand transpiration of the rubber tree at the stand level (millimeters per hour),  $J_{s mean}$  (liters per square decimeter per hour) is the mean of the sap flux density,  $A_{mean}$  is the mean of sapwood area and N is number of trees per hectare.

#### Leaf water potential

The leaf water potential was measured by a Scholander-type pressure chamber (plant water status console, Soil Moisture Equipment Corporation; Goleta, CA, USA). Two fully expanded mature leaves per tree were sampled from the outside canopy of six tapped and six untapped trees. Regular measurements of the leaf water potential were performed rapidly after cutting, and measured monthly around predawn (0430 to 0600 hours) and midday (1100 to 1300 hours) from March 2009 to January 2010.

#### Percentage loss of hydraulic conductivity

The percentage loss hydraulic conductivity (PLC) was measured from six tapped and six untapped trees which were the same trees that were measured for the sap flux density and leaf water potential from March 2009 to January 2010. The PLC was measured on the petioles with the technique described by Sperry et al. (1988). The petioles were cut about 2-3 cm under water to prevent air entry into the conduits and connected to the XYL'EM apparatus (Embolism Meter; Institut National de la Recherche Agronomique; Paris, France) (Cochard et al., 2001). Then they were wrapped with Teflon tape to prevent lateral leaks. The initial conductivity (Ki; millimoles per square meter per second per megaPascal) of each segment was measured with a hydrostatic pressure gradient of 3 kPa with deionized, degassed and filtered water. They were perfused at a pressure of 0.15 MPa for 5 min to dissolve and expel any air bubbles. After that, the hydraulic conductivity (Km; millimoles per square meter per second per megaPascal) of the segments was determined again. Then, the PLC was calculated using Equation 4:

$$PLC = \frac{100 (Km - Ki)}{Km}$$
(4)

#### Stomatal conductance

The stomatal conductance was measured with an AP4 Porometer (Delta-T Devices Ltd.; Cambridge, England). The measurement was obtained from the leaflets randomly chosen on each tree from one tapped and one untapped tree near the tower being the same trees used to measure the sap flow and leaf water potential. The stomatal conductance was measured between 1130 and 1300 hours each day on leaves exposed to sunlight in the middle of the canopy from November 2009 to January 2010 during the dry season.

#### RESULTS

# Variations in climatic conditions and stand transpiration

Rainfall started in March and varied during the rainy season. Evapotranspiration (ETo) decreased slightly in the middle of the rainy season when the rainfall was delayed in August. Despite full canopy, stand transpiration showed a similar pattern to ETo. Stand transpiration was generally high in July which is in the middle of the rainy season (3.5–4.0 mm.d<sup>-1</sup>). However, stand transpiration dramatically decreased down to 1.2 mm.d<sup>-1</sup> in August when the rainfall decreased. In the dry season at the end of the year, stand transpiration and evapotranspiration declined strongly during the defoliation period (Figure 1a).

The soil water content varied throughout the year and increased in March after rainfall occurred, after which it slightly decreased during April to May and dramatically decreased in June. The soil water content slightly increased from July to October and declined significantly from beginning of November to its minimum value at the end of the year (Figure 1b).

#### Sap flux density

The diurnal sap flux density in the rainy season was high, with a relatively small difference in the sap flux density (Js) between tapped and untapped trees (Figure 2a). The diurnal sap flux density in the dry season decreased significantly from the rainy season. The maximum sap flux density in the tapped trees was significantly lower than in the untapped trees, especially on the tapping days.

#### Leaf water potential

The predawn leaf water potential  $(\psi_{predawn})$  was high and relatively stable in the rainy season; values ranged between -0.30 and -0.35 MPa. However, the value of  $\psi_{predawn}$  dropped markedly in August (-0.42 MPa) due to the soil water stress during the rainfall delay period. The predawn leaf water potential decreased significantly in the dry season. The minimum value of  $\psi_{predawn}$  reached -0.72 MPa, at the peak of the drought at the end of the year (Figure 3a). The midday leaf water potential ( $\psi_{midday}$ ) was high and remained rather constant during the rainy season (between -1.10 and -1.20 MPa) until October,



Figure 1 Daily variations of stand transpiration (Stand T) and evapotranspiration (ETo) from January 2009 to January 2010: (a) Rainfall (columns), daily evapotranspiration (dotted line) and daily stand transpiration (black line), and (b) Soil water content at 20 cm (closed circles with black line), 40 cm (closed squares with dotted line) and 60 cm (opened squares with dotted line). (Vertical errors bars = Mean±SE)



Figure 2 Diurnal course of sap flux density (Js) for tapped and untapped trees: (a) During rainy season and (b) During dry season. Arrows showed tapping days.

after which, it decreased significantly from -1.20 to -1.55 MPa in the dry season (Figure 3b). There was no significant difference (P > 0.05) in the predawn and midday leaf water potential between tapped and untapped trees.

# Percentage loss of hydraulic conductivity

The seasonal variation in the percentage loss of hydraulic conductivity (PLC) is shown in Figure 4. The PLC increased continuously from 26.5 to 45% early in the rainy season and remained rather constant between 45.6 and 47.5% in the rainy season, after which it increased significantly (P < 0.05) from 47.5 to 55.5% during the dry season at the end of the year, as the shedding of leaves started in response to soil drought. There was no significant difference (P > 0.05) in the PLC between tapped and untapped trees.

# **Stomatal conductance**

The stomatal conductance  $(g_s)$  reduced markedly in the dry season (Figure 5). The values of  $g_s$  decreased from 276 to 16.5 mmol m<sup>-2</sup> s<sup>-1</sup>. While there were no differences in the  $g_s$  values between tapped and untapped trees early in the dry season, the  $g_s$  values of tapped trees were significantly (P < 0.05) lower than in untapped trees during the defoliation period later in the dry season.

# DISCUSSION

The results suggested the regulation of plant water status following variation in the soil water content and climatic conditions. Moreover, tapping activity may affect the water relations in rubber trees. Despite the lack of soil



Figure 3 Seasonal variations of predawn and midday leaf water potential of both tapped and untapped trees from March 2009 to January 2010: (a) predawn leaf water potential and (b) midday leaf water potential. There was no significant difference (P > 0.05) between tapped and untapped trees. (Vertical errors bars = Mean±SE)

drought-stress conditions, stand transpiration did not always follow evapotranspiration which was consistent with the results reported by Isarangkool Na Ayutthaya (2010). The results indicated that some peaks of transpiration were reduced on rainy days, which could be attributed to transpiration stopping when the foliage was wet (Granier, 1987). The results of the current study showed that both evapotranspiration and stand transpiration declined in August when the rainfall stopped, due to soil drought during the rainy season. In the dry season, stand transpiration declined significantly (P < 0.05) during the defoliation period because the plant had to limit the loss of water from plant tissue by closing the stomata due to the soil water limitation (Jackson *et al.*, 2000). This suggests that soil water stress in the rainy season and at the onset of the dry season induced a decrease in stand transpiration in the rubber trees.

The maximum sap flux density decreased during the dry season. It was found that the sap flow of several tree species decreased under conditions of high vapor pressure deficit and soil water stress during the dry season (Granier



Figure 4 Seasonal variations of percentage loss of hydraulic conductivity (PLC) in both tapped and untapped trees from March 2009 to January 2010. There was no significant difference (P > 0.05) between tapped and untapped trees. (Vertical errors bars = Mean±SE)



Figure 5 The measurements of leaf stomatal conductance commenced after the rainfall stopped at the end of rainy season and continued until the defoliation period. Vertical error bars = Mean + SE (n =10). An asterisk (\*) indicates a significant difference (P < 0.05) between tapped and untapped trees, ns = Not significant.

*et al.*, 1992). The maximum sap flux density in tapped trees was lower than in the untapped trees, especially on the tapping day. Sap flow is expected to be fully compensated by the uptake of water by the roots and by water use in transpiration (Pataki *et al.*, 1998). The flow of water through the trunk of tapped trees was lower than in untapped trees, due to the water loss with the latex flow after tapping.

The predawn leaf water potential measures the plant water status and is assumed to be close to the value of the soil water potential around the root zone (Frank et al., 2007). The values dropped in August (-0.42 MPa) following soil drought during the rainy season. The predawn leaf water potential was reported to decrease in response to increasing soil water deficit (Grady et al., 2008). The midday leaf water potential corresponds with maximum transpiration (Tyree and Sperry, 1988). However, the midday leaf water potential was unaffected by a change in the soil water content in the rainy season. This pattern expressed isohydric behavior which maintains leaf water potential above a critical value (West et al., 2007). The midday leaf water potential declined progressively during water stress as the leaf water potential is regulated by the stomatal conductance. Stomatal closure appears to maintain the minimum leaf water potential above the critical threshold (Oren et al., 1999).

The percentage loss of hydraulic conductivity (PLC) remained rather constant in the rainy season, due to the high soil water content. The PLC tended to increase in the middle of the rainy season when the soil water content dropped in August. The PLC increased slightly at the beginning of the dry season. The increasing PLC induced stomatal closure because xylem embolism developed in the petioles when the water potential became lower than a critical value due to the soil water stress (Sperry and Tyree, 1988; Cochard *et al.*, 1996). The loss of hydraulic conductivity induced stomatal closure and caused cavitation in the xylem (Sperry, 2000).

The stomatal conductance  $(g_s)$  reduced markedly in the dry season. The reduction in plant water status induced stomatal closure at high vapor pressure deficit and soil drought to maintain the minimum leaf water potential above the cavitation threshold (Sperry and Tyree, 1988). There was no difference in g<sub>s</sub> values between tapped and untapped trees early in the dry season but the g<sub>s</sub> values of tapped trees was significantly lower than in untapped trees during the defoliation period in the dry season because the tapped trees lost water through latex production. Therefore, rubber trees exhibit a strong control over water losses by closing the stomata to prevent embolism in the xylem during the dry season (Cochard et al., 1996).

#### CONCLUSION

The results showed that soil drought during the rainy and the dry seasons had a strong effect on the plant water status of rubber trees. Rubber trees exhibit a well known drought-induced reduction in the plant water status. Moreover, drought stress is enhanced by tapping activity, which could consequently lead to TPN. Do *et al.* (2006) suggested that water stress is involved in the outbreak of TPN in rubber trees, caused by hydraulic failure, which affects the annual growth. The tapping activity had a low impact on the plant water status and water transport. However, during the dry season, tapping acts as a stress on the stomatal conductance and sap flux density, particularly in dry areas.

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### LITERATURE CITED

- 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.
- Chandrashekar, T.R., J.G. Marattukalam and M.A. Nazeer. 1996. Growth reaction of *Hevea brasiliensis* to heat and drought stress under dry subhumid climatic conditions. India J. Nat. Rub. Res. 9(1): 1–5.
- 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., D. Lemoine, T. Ameglio and A. Granier. 2001. Mechanism of xylem recovery from winter embolism in *Fagus sylvatica*. Tree Physiol. 21: 27–33.
- Do, F.C., A. Pierret, P. Couteron, G. Lesturgez, S. Isarangkool Na Ayutthaya, J. Junjittakarn, S. Gonkhamdee, J. L. Maeght, C. Hartmann, K. Pannengpetch and D. Nandris. 2006. Rubber tree trunk phloem necrosis (TPN) in northeast Thailand: 2, within-stand characterization of affected trees, pp. 157–170. *In* Vietnam Rubber Research Institute, (ed.). Proceedings of the International Natural Rubber Conference 2006, IRRDB Symposium. Ho Chi Minh City, Vietnam.
- Food and Agriculture Organization of the United Nations. 2009. The ETo Calculator: Evapotranspiration From a Reference.

Land and Water Division. Rome, Italy. 465 pp.

- Frank, P.J., D.L. Drake and R.H. Froend. 2007. Anisohydric but isohydrodynamic: seasonally constant plant water potential gradient explained by a stomatal control mechanism incorporating variable plant hydraulic conductance. **Plant Cell Env.** 30: 19–30.
- George, P.J. and C.K. Jacob. 2000. Natural Rubber Agromanagement and Crop Processing. Rubber Research Institute of India. Kottayam, India. 236 pp.
- Grady, A.P., D. Wonledge and M. Battaglia. 2008. Constraints on transpiration of *Eucalyptus* globulus in Southern Tasmania, Australia. Agr. For. Meteorol. 148: 453–465.
- Granier, A. 1987. Evaluation of transpiration in Douglas fir stand by means of sap flow measurement. **Tree Physiol.** 3: 309–3223.
- Granier, A., R. Huc and F. Colin. 1992. Transpiration and stomatal conductance of two rain forest species growing in French Guyana. Ann. For. Sci. 49: 17–24.
- Isarangkool Na Ayutthaya, S. 2010. Change of Whole-Tree Transpiration of Mature *Hevea* brasiliensis under Soil and Atmospheric Droughts: Analyze in Intermittent and Seasonal Droughts under the Framework of the Hydraulic Limitation Hypothesis. PhD. thesis. Université Blaise Pascal, 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.
- Kume, T., H. Takizawa, N. Yoshifuji, K. Tanaka, C. Tantasirin, N. Tanata and M. Suzuki. 2007. Impact of soil drought on sap flow and water status of evergreen trees in a tropical monsoon forest in northern Thailand. For. Eco. Manage. 238: 220–230.
- Manmuen, S., A. Chantuma and K. Teerawatanasak. 1993. Growth characteristic of rubber in the drought. Para. Pub. Bull. Thailand 1391: 12–30.

- Nandris, D., Moreau R., de Fay E., Masson A., Pellegrin F. and H. Chrestin. 2006. Etiological investigations on Trunk Phloem Necrosis of the rubber tree: Biotic or abiotic causal factors? pp. 85–92. *In* J. Jacob, R. Khrishnakumar and N.M. Mathew, (eds.). **Tapping Panel Dryness** of Rubber Trees. Rubber Research Institute of India. Kottayam. India.
- 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 Env. 22: 1515–1526.
- Pakianathan, S.W., G. Haridas and J. Auzac. 1989.
  Water Relations and Latex Flow. CRC Press, Inc. Boca Raton, FL, USA. 256 pp.
- 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.
- Poyatos, R., P. Liorens and F. Gallart. 2005. Transpiration of montane *Pinus sylvestris* L. and *Quercus pubescens*. Wild forest stands measured with sap flow sensors in NE Spain. Hydrol. and Earth Syst. Sci. 9: 493–505.
- Roa, G.G., P.S. Rao, R. Rajagopal, A.S. Denvakumar, K. Vijiayakumar and M.R. Sethuraj. 1990. Influence of soil, plant and meteorological factors on water relations and yield in *Hevea brasiliensis*. Int. J. Biometeo. 34: 175–180.

- Sangsing, K., P. Kasemsap, S. Thanisawanyangkura, K. Sangsila, E. Gohet, P. Thaler and H. Cochard. 2004. Xylem embolism and stomatal regulation in two rubber clones (*Hevea brasiliensis* Muell. Arg.). Tree 18: 109–114.
- 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. and M.T. Tyree. 1990. Water stress induced xylem embolism in three species of conifers. **Plant Cell Env.** 13: 427–436.
- Sivanadyan, K., H. Ghandimathi and G. Haridas. 1995. Rubber a Unique Crop: The Mature Hevea Stand as a Nutritionally Selfsustaining Ecosystem in Relation to Latex Yield. Rubber Research Institute of Malaysia, Malaysia. 320 pp.
- Tyree, M.T. and J.S. Sperry. 1988. Do woody plant operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? **Plant Physiol.** 88: 574–580.
- West, A.G., K.R. Hultine, T.L. Jackson and J.K. Ehleringer. 2007. Differential summer water use by *Pinus edulis* and *Juniperus osteosperma* reflects contrasting hydraulic characteristics. Tree Physiol. 27: 1711–1720.