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THESIS

PLANT WATER STATUS IN RESPONSE TO CLIMATE CHANGE AND TAPPING ACTIVITY OF MATURE RUBBER (*Hevea brasiliensis* Muell.Arg.)

SUMIT KUNJET

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Sumit Kunjet 2013: Plant Water Status in Response to Climate Change and Tapping Activity of Mature Rubber (*Hevea brasiliensis* Muell.Arg.). Doctor of Philosophy (Tropical Agriculture), Major Field: Tropical Agriculture, Faculty of Agriculture. Thesis Advisor: Associate Professor Poonpipope Kasemsap, Ph.D. 105 pages.

The variations of water status in response to climatic conditions and tapping activity of mature rubber trees clone RRIM 600 were investigated in the non-traditional planting area at Chachaengsao Rubber Research Center (CRRC) from January 2007 to January 2010. Sap flow was measured by heat dissipation method adapted from Granier (1985, 1987) using home-made radial probes which was developed by Roupsard *et al*. (2006) and then calibrated with the cut stems of rubber tree in the laboratory. Radial, axial and azimuthal variabilities of sap flow were evaluated using four to eight sets of probes. Radial variabilities were modeled to be functions of depth into the xylem. Seasonal dynamics of sap flow of 7 trees, ranging in sizes from 55 cm to 100 cm girth, were monitored using probes installed at north and south directions. Stand transpirations were estimated from sap flux density.

The results showed that stomatal conductance was more sensitive to climatic variations than stand transpiration. There was time lags between diurnal peaks of stomatal conductance and stand transpiration. In addition, the relationship between climatic factors and transpiration varied along the year. In general, seasonal variations of stand transpiration was related to LAI, VPD, and soil water content while diurnal variations of stand transpiration and stomatal conductance were related to VPD and net radiation. Finally, leaf water potential ($\psi_{predawn}$, ψ_{midday}), whole tree hydraulic conductance (gL) and percentage of loss of hydraulic conductivity (PLC) were not affected by tapping. This implied that tapping activity would not significantly change water balance of rubber trees. However, tapping activity reduced sap flux density and stomatal conductance in the dry season, particularly in the tapping day.

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Student’s signature Thesis Advisor’s signature

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LIST OF ABBREVIATIONS

SPAC	soil plant atmosphere continuum
Ta	air temperature
RH	relative humidity
VPD	vapor pressure deficit (kPa)
ETo	evapotranspiration (mm day^{-1})
Rg	global radiation
PAR	Photosynthetically active radiation
Ws	wind speed
Rn	net radiation
λE	latent heat
TDR	time domain reflectometry
REW	relative extractable water
PLC	percent loss of hydraulic conductivity (%)
gL	whole tree hydraulic conductance (ldm^{-2}h^{-1}MPa)
g_s	stomatal conductance
T	stand transpiration (mm day^{-1})
$\Psi_{predawn}$	predawn leaf water potential (MPa)
Ψ_{midday}	midday leaf water potential (MPa)
Js	sap flux density (Js, l dm^{-2}h^{-1})
K	sap flow index
ΔT_o	the maximum temperature between the two sensors of the probe
ΔT_i	the current temperature difference between the two sensors of the probe
HPFM,	high pressure flow meter
CTD	constant thermal dissipation method
TTD	transient thermal dissipation method
PVC	poly vinyl chlorine
$J_{s\text{-}reference}$	the reference sup flux density at 2 cm

LIST OF ABBREVIATIONS (Continued)

$J_{s\text{-young}}$	sap flux densities of young xylem
$J_{s\text{-old}}$	sap flux densities of old xylem
D	depth into the xylem
d_1 and d_2	empirical parameters
A	sapwood area (dm^2)
N	number of the tree per hectare
α	first coefficient of sap flux density calibration
β	second coefficient of sap flux density calibration
LAI_i	LAI fisheye every week
LAI_{max}	maximum LAI fisheye of the year
LAI	leaf area index
J_s max	the maximum sap flux density ($l\ dm^{-2}\ h^{-1}$)

PLANT WATER STATUS IN RESPONSE TO CLIMATE CHANGE AND TAPPING ACTIVITY OF MATURE RUBBER (*Hevea brasiliensis* Muell.Arg.)

INTRODUCTION

The rubber tree is one of Thai's major economic crop. The planting area covers more than 10 million hectares worldwide. About 90 % of rubber plantations established worldwide for latex production are in the Southeast Asia i.e. Thailand, Indonesia, and Malaysia. In Thailand, the main rubber planting areas are in the Southern and Eastern regions, but rubber plantations in these regions are now saturating the areas. Moreover, the lack of available land and competition with other crops such as oil palms, rubber plantations have been expanded to drought-prone areas that provide sub-optimal growing conditions of rubber trees in the Northern and North-Eastern regions, where soil, water availability and climatic conditions are limiting factors of growth and latex production (Roa, *et al*., 1990; Manmeun *et al*., 1993; Wichitchonchai and Manmuen, 1992; Sivanadyan *et al*., 1995; Chandrashekar *et al*., 1996). In these areas, the climate is too cold and too dry, causing reduced growth and yield production, increased immaturity period (Manmuen *et al*., 1993).

The research on water relations are important for study in ecophysiology of rubber plantation. Some researchers studied on the effects of water constraint on plant water status, girth increment and latex production (Sangsing, 2004; Silpi *et al*., 2006; Isarangkool Na Ayutthaya *et al*., 2007). There is a clearly correlation between diameter variations and changing in water availability. The radial growth rate in rubber tree decreased in the dry season when rainfall was limited. Significant radial growth occurred in the rainy season (May and early June) (Silpi *et al*., 2006). The study on water relations are reported on young rubber trees (Sangsing, 2004; Sangsing *et al*., 2004) and mature rubber trees in natural conditions (Isarangkool Na Ayutthaya *et al*., 2007; Kunjet *et al.*, 2007; Isarangkool Na Ayutthaya, 2010).

Hydraulic architecture is a main determinant of leaf water status and stomatal behavior. When plant hydraulic conductivity is limited, leaf water potential may be reduced to point of embolism occurrence. Therefore, stomatal closure and reducing transpiration occur to maintain leaf water potential above the threshold for preventing cavitation in the xylem (Sperry and Tyree, 1988; Sperry, 2000; Meinzer *et al*., 2001).

The reduction of the whole-tree hydraulic conductance induces decreasing minimum leaf water potential. Embolism of xylem occurs when decreasing xylem water potential reaches cavitation thresholds (Cruziat *et al*., 2002). Plant hydraulic property in rubber tree have been reported. (Sangsing *et al*., 2004; Isarangkool Na Ayutthaya, 2010).

Rubber can be tapped for latex production only when trunks have reached a minimum circumference of 50 cm at 1.5 m height above ground. Tapping activity involves cutting bark on the trunk, and hence severing latex vessels. The shaving bark was removed from the sloping cut. Then, the latex flows out, driven by turgor pressure, and soon dries out. (George and Jacob, 2000; Silpi *et al*., 2006). The latex contains on average 60 to 70 % of water, thus plant and soil water status are major factors of latex production (Pakianathan *et al*., 1989). General, tapping starts in May when the rainfall occurs and stops in January during defoliation period. Thus, taping activity may affect plant water status throughout the year, especially during the dry season in November to January, as soil and atmospheric droughts, and leaf senescence and shedding.

Previous studies on young rubber tree found transpiration, stomatal conductance and leaf water potential to decrease under water stress period. Hydraulic system in rubber tree is high vulnerability to cavitation which suggested that stomata were closed at onset of xylem cavitation in the petiole (Sangsing, 2004). Then, stomatal may play an important role in the control of xylem embolism. Isarangkool Na Ayutthaya (2010) obtained on mature rubber tree and used a transient thermal dissipation (TTD) method to assess tree transpiration. He found that the predawn leaf water potential was high and stable in the well-water period after that it decreased slightly and reached -0.83 MPa which related closely to soil water content in the drought conditions when leaf shedding started. Daily transpiration changed along the rainy season in response to low evapotranspiration (ETo) and rainfall events where tree transpiration does not follow to evaporative demand (David et al., 2004; Bovard *et al*; 2005; Isarangkool Na Ayutthaya, 2010). Moreover, transpiration decreased below a threshold whereas the minimum of daytime leaf water potential did not reduce and was stable under soil drought conditions. Under drought conditions, reduction in hydraulic conductivity may induce embolism in the xylem, so that leaf fall occur in this time. Whole-tree hydraulic conductance (gL) decreased during the period of leaf senescence and shedding (Isarangkool Na Ayutthaya, 2010).

Rubber plantation in this study is in the Eastern region of Thailand, occupying critical areas in term of soil water resources, with low rainfall and high evaporative demand in the dry season. The study on rubber trees in this area showed that rubber trees drop their leaves in December-January and completes their leaves-flushing within 2-3 weeks in February. Seasonal variations of sap flow and transpiration vary with leaf phenology and climatic conditions. Transpiration is low during defoliation period as reported in other species (Pataki *et al*., 1998). In refoliation period, which occurred just after defoliation completed, transpiration increased rapidly, although this was still in the dry season period (Kunjet *et al*., 2007). Daily variations of the stand transpiration were correlated closely to the variations of evapotranspiration (ETo).

This study we intend to estimate transpiration in mature rubber trees from sap flow measurement and to provide a first insight on changes in plant and soil water relations in response to environmental variables and tapping activity. To estimate tree transpiration with sap flow measurement, we used the constant thermal dissipation (CTD) method and applied the home-made probes developed by Roupsard *et al*. (2006). In this study, the XYLEM apparatus is used to measure the percentage of loss of hydraulic conductivity (PLC) in rubber tree. Understanding the water relations in a rubber tree plantation will provide information of plant and soil water status that should be relative with climatic variables and latex yield of rubber trees.

OBJECTIVES

1. The first objective was to adapt the sap flow probe from Granier method in rubber tree.

2. The second objective was to measure seasonal dynamics of sap flow, and stand transpiration for a long time.

3. The third objective was to analyse the diurnal dynamics of stand transpiration and stomatal conductance in rubber tree.

4. The fourth objective was to evaluate the effect of tapping activity on plant water relations in rubber trees.

LITERATURE REVIEW

1. Botany, rubber plantation, leaf phenology, growth and latex production

1.1 Rubber plantation

The rubber plantations in the worldwide covers more than 10 million hectares. There are about 80% of rubber plantations in Southeast Asia. In Thailand, rubber plantation covered 2.67 million hectares and latex production had 3.1 million tons in 2009 (RRIT, 2010). The suitable area for planting rubber trees should be less than 600 m above sea level, less slope, fertile and well-drain soil. The optimal temperature and annual rainfall are 28°C and 1,800-2,500 mm, respectively. According to lack of available planting area and spatial competition with other crops, rubber plantations have been grown to non-traditional zones where there are long dry season. In these areas, the climate is too cold and too dry, causing reduced growth and yield production, increased immaturity period (Roa, *et al*., 1990; Manmeun *et al*., 1993; Wichitchonchai and Manmuen, 1992; Chandrashekar *et al*., 1996). Soil water availability and climate are the important limiting factors of rubber plantation in this new prone planting area (Sivanadyan *et al*., 1995).

1.2 Botany of rubber tree

Hevea brasiliensis Muell. Arg., the well-known species is widely distributed over the planting areas. This species is the most important to grow in commercial as source of natural rubber (George and Jacob, 2000).

The rubber tree is a perennial tree which attains a height rarely exceed 25 m. The tree has a straight trunk with smooth light grey bark. Branches are usually developed to form an open leafy crown (George and Jacob, 2000). The leaves are trifoliate and spirally arranged. The color of laminate hang downwards are reddish or bronze (Webster and Baulkwill, 1989). The leaves are almost completely expanded and green color. The petioles are long, usually about 15 cm, with extra-flora nectarines at the point where there give rise to the leaflet. Stomata appear on the lower epidermis and epicuticular waxes are formed (George and Jacob, 2000). The partial or complete leaf shedding is followed for a short period within 2-3 weeks and return to pre-flushing within further weeks. Latex yields usually declined slightly at the onset of leaf fall event and more markedly reduced during refoliation period (Webster and Baulkwill, 1989). The trunk of mature rubber tree is a cylinder of wood, covered with smooth bark. The layer of vascular cambium generates xylem tissue on the inside and phloem tissue on the outside. The wood (xylem) consists mainly of fibers and vessels for the transport of water and nutrients taken up from the soil. The bark is outside the cambium tissue. The soft bark consists of latex vessels, sieve tubes, phloem rays and axial parenchyma. The former are concerned with the transport and storage of assimilates for the leaves and hold the containing of rubber latex. The hard bark also consists of sieve tubes and latex vessel which are discontinuous and nonfunctional (Webster and Baulkwill, 1989; George and Jacob, 2000). Latex vessels are distributed in the bark. The latex vessel characteristic is determined by number of rows, density of vessel per row, and diameter of latex vessel (Premakumari *et al*., 1985). As the tree grows, the latex vessel cylinders are produced by the cambium that are gradually pushed outwards and increase circumference of the trees (Webster and Baulkwill, 1989). The cross-sectional area of latex vessels per unit length of tapping cut in the trunk and the orientation of latex vessels contribute significantly to the annual ring (Premakumari *et al*., 1993). The number of latex vessel is the most important factor and is positively correlated with the latex yield. On tapping activity, a thin layer of bark is removed. Then the renewed bark is also regenerated later. From the new meristematic layer, the wound phellogen produced periderm and re-cutting is started again (George and Jacob, 2000). Under normal conditions of growth, the number of latex vessel rings in the renewed bark is usually greater than that found in the original initial bark.

1.3 Leaf phenology

Rubber tree is a brevi-deciduous tree. Rubber tree has replaced mostly evergreen vegetation in the rainy season and shows shedding and flushing of the leaves in the dry season. Removal of part of the leaves resulted in decreased transpiration (Kramer and Kozlowski, 1979). Moreover, the different stages of leaf phenology appear in response to particular changes of root phenology; root decay, or root growth in different soil layers according to soil water content (Becker *et al*., 1999; Brodribb *et al*., 2002; Domec *et al*., 2009). Leaf senescence and shedding should decrease the total leaf hydraulic conductance following drying soil. Root decay may decrease the soil to root conductance following drying soil. Conversely, after leaf flushing occurs, it should increase the hydraulic conductance in the leaves due to developed the new xylem conduits for the new leaves (Isarangkool Na Ayutthaya, 2010). Possibly, tree roots must directly access to the deep water table in deep soil when the upper soil was dry, allowing the development and maintenance of a deep root system in the dry season (Breman and Kessler, 1995). Moreover, water can remove from deep to shallow roots at night when soil surface is dry (Caldwell *et al*., 1998). It is an important strategy for tree survival in the dry conditions. Phenology variables were correlated with evapotranspiration (ETo) and water demand (Guardiola-Claramonte *et al*., 2010). When the rainfall occurred in March, the fine root density was obtained in the top soil layer (Gonkhamdee *et al.*, 2009). The rubber trees in the Eastern Thailand dropped their leaves in January and pre-flushing occurred completely within 2-3 weeks. The fully mature leaves appeared from March to November or December.

1.4 Growth of rubber tree

The limitation factors of growth is a consequence of water status that involved in tissue enlargement (cell division and cell expansion), and carbon balance between growth and latex production. (Daudet *et al*., 2004). Typical radial growth of rubber tree in the Eastern Thailand started with the onset of the rainy season and lasted until the on-set of the dry season. There is a clearly correlation between diameter variations and changes in the soil water availability. The trunk exhibited shrinkage in the middle of the dry season as the time of refoliation period, the trunk showed no radial growth until the rainfall occurred. The radial expansion appeared within one day after rainfall whereas the trunk shrinkage caused by dehydration (Silpi *et al*., 2006). Thus, rubber tree showed that drought-induced reduction in radial growth (Kozlowski, 1971). The immaturity period of the rubber tree under rain condition could be reduced from 10 years to 6 years by irrigation in the dry season (Vijayakumar *et al*., 1998). Carbon reserves is a structure material and the source of energy for metabolism. The new structures of the tree requires carbon. Moreover, wound responses and bark regeneration are carbon consuming process, they should be required carbon as sink functions (de Fay and Jacob, 1989). Then, after beginning of tapping, the radial growth rate of tapped tree was lower than untapped tree throughout the whole season, which can be explained on the basis of strong competition for carbon between two sink functions (Gohet, 1996; Silpi *et el*., 2006).

1.5 Latex production

Latex production is probably a defense system which the tree suffers a cut or any other wound, latex flows from the surrounding cells . The latex contains of water about 60-70%. Therefore, the water status in plant and soil control the latex production (Pakianathan *et al*., 1989). The variations in rubber yield were associated with soil moisture content and climatic factors (Roa *et al*., 1990). The highest flow rate of latex obtained during the rainy season and rubber yield decreased in the dry season (Chandrashekar *et al*., 1990). Tongsawang and Sdoodee (2008) found that the rubber tree under irrigation management may increase latex yield during the dry season. Yield of rubber showed significant negative correlation with maximum temperature, sunshine duration and vapor pressure deficit (Rao *et al*., 1998). Moreover, the latex yield of rubber tree as influenced by the type of clone and locations with varying fertility status (Akpan *et al*., 2007).

2. Water transport in Soil-Plant-Atmosphere-Continuum (SPAC)

Water movement through the soil-plant-atmosphere-continuum occurs in both liquid and vapor phases, driven largely by water potential gradient between the soil and the atmosphere (Boyer and Tuner, 1970). Amount of water flows along the soil-plant-atmosphere-continuum pathway that depends on driving force of water potential gradient and hydraulic conductivity. Water potential is the basis for assessment of plant water status. It is expressed in the thermodynamic or energy status within plant and soil (Jone, 2006). Water potential consists of several components such as gravitational, pressure, solution, and matric potentials. Water moves from higher water potential to where lower water potential (Micheal and Munus, 2002; Taiz and Zeiger, 2006). The flow of water through the plant in SPAC is controlled by the vapor pressure deficit of the atmosphere and soil water content (Steppe and Lemeur, 2004).

2.1 Water in air (water vapor)

2.1.1 Definition

Water vapor is the gas phase of water. Water vapor is continuously generated by evaporation from the soil and living plants. The evaporative demand is the driving force of tree transpiration which pulls water to flow along the soil-plant-atmosphere continuum (Granier *et.al*., 1996; Meinzer *et al*., 1999; Meinzer, 2003; David *et al*., 2004). The evaporative demand is the cumulative of the climatic variables on the rate of water evaporation (Larcher, 2001). Vapor pressure deficit (VPD) is an indicator of the amount of water vapor that the air mass can hold, it is the difference between the saturation and actual vapor pressure for a given time period. VPD depends mainly on air temperature (T_a) and relative humidity (RH) (FAO, 2009).

2.1.2 Esitmates evapotranspiration (ETo)

Evapotranspiration (ETo) is a key factor for the growth and product of plants, for the water balance of ecosystem and for watershed dynamic (Verdier, unplublished data). Potential evapotranspiration is the quantify of energy available for water evaporation from the soil and plant. Determination of evapotranspiration is important to apply for irrigation design, irrigation scheduling, water resource management, and hydrology. Moreover, evapotranspiration is an indicator for a wide variety of climatic conditions (Allen *et al*., 1989; Lemeur and Zhang, 1990; Jensen *et al*., 1990). Hence, ETo is a good indicator of the evaporative demand of the plantation calculated with temperature, relative humidity, wind and radiation. Moreover, The United Nations Food and Agriculture Organization (FAO) adapted the method to estimate reference crop evapotranspiration from meteorological data (Allen *et al*., 1989). Guardiola-Claramonte *et al*. (2010) reported that the water demand of rubber and consequently water loss to the atmosphere can be estimated through rubber tree evapotranspiration (ETo). ETo was limited during the wet season. Conversely, during the dry season the water requirement was mostly governed by environmental variables. The water requirement directly affected rubber phenology, vapor pressure deficit, temperature and photoperiodicity. Isarangkool Na Ayutthaya (2010) showed that daily transpiration changed along the rainy season, where the transpiration did not follow the increased ETo.

2.2 Soil water status

2.2.1 Definition

The state of water in soil is described either in terms of amount of the water or the energy associated with the force which hold the water in the soil. Water infiltrates the soil following precipitation, and gradually percolates to the ground water table (Larcher, 2001). The amount of water is defined by water content and the energy state of water is expressed on the water potential which is important for the availability to plants (Rundel and Jarrell, 1989). Water content indicates that how much water is stored in the soil. Soil water potential is estimated the state of water energy (Bilskie, 2001). Soil pores distribute in the soil that water can be hold for used by plant. The rate of water flow in soils depends on the pressure gradient through the soil, and hydraulic conductivity of the soil. Soil hydraulic conductivity is varied with the type of soil and water content. For example sandy soils with large spaces, have a high hydraulic conductivity, whereas clay soils, with small space have a low hydraulic conductivity. When the water content of the soil decreases, hydraulic conductivity reduces rapidly. When the air is filled into a soil channel, water movement through the soil is restricted to the peripheral channel of the soil (Taiz and Zeiger, 2006).

2.2.2 Soil water status measurement

Soil water content is measured with gravimetric method, neutron probe, time-domain reflectometry (TDR). However, soil water potential method is measured using tensiometer and thermocouple psychrometry (Bilskie, 2001).

2.3 Plant water status

2.3.1 Definition

The use of plant-based water status indicators are popular to study plant-water relations. Water movement from the root to the atmosphere is controlled by the conductance of water pathway. Water in the plant can be considered continuously hydraulic system, connecting the water in the soil with the water vapor in the atmosphere (Taiz and Zeiger, 1998). Plant water status is controlled by the relative rates of water loss and water uptake. Thus, plant water status is a dynamic property and would be changed with variations in the evaporative demand of the air and soil water content (Klepper, 1968).

2.3.2 The measurement of plant water status

The measurement of plant water status has been used for irrigation schedule and water use of the trees, which is directly related with climatic and soil conditions, as well as with crop productivity (Goldhemer *et al.,* 2003; Remosini and Massai, 2003). The measurement of plant water status is concerned with understanding the effects on the physiological process of plants. The approach can be used to evaluate plant water status such as leaf water potential (Clone *et al*., 2001) leaf stomatal conductance as an indirect index of water status (Hsiao, 1990). Sap flow methods can be used to estimate transpiration and tree water use (Smith and Allen, 1996). Whole tree hydraulic conductance is the coefficient of proportionality between the sap flow and the gradients of water potential in rubber tree (Isarangkool Na ayutthaya, 2010)

2.3.2.1 Sap flow measurement and tree transpiration

Sap flow indicates water use by tree as water transpired by the canopy. In addition, sap flow is expected to be fully compensated by uptake of water by root and flow of sap through the trunk (Pataki *et al*., 1998). Sap flow methods are suited to measure changes in the water relations, growth and water use efficiency of plant (Smith and Allen, 1996). Moreover, environmental variables that influence sap flow include radiation, vapor pressure deficit (VPD), soil water content, rainfall, air temperature, relative humidity, and wind speed (O'Brian *et al*., 2004). Granier *et al.* (1992) found that sap flow of several tree species decreased under conditions of high VPD. In addition, diurnal sap flow declined during the dry season and increased during the wet season (Lu *et al*., 2002; Ford *et al*., 2004).

Transpiration is the process of water loss from plant through the stomatal that are connected to the conduit tissue. Transpiration is the dominant factor in the water relations of plants because evaporation of water produces the energy gradient that causes movement of water through plants (Kramer and Kozlowski, 1979). Transpiration responds to changing atmosphere and soil water content (Bovard *et al*. 2005). Transpiration directly relates to vapor pressure deficit (VPD), radiation, evaporative demand, and soil water content (Poyatos *et al*., 2005). Myers *et al*. (1998) reported a strong positive correlation between daily transpiration and VPD in young *Eucalyptus grandis* stand. Transpiration decreased as VPD was high (O'Grady *et al*., 2008). Similarly, stomata generally closed as VPD increases (Addington *et al*., 2004). Some studies suggested that stomatal closure response to increasing VPD as feedback response to some aspect of transpiration and water loss from the leaf (Monteith, 1995; Meinzer *et al*., 1997). However, evergreen oak tree, transpiration rate remained approximately constant with high VPD (David *et al*., 2004). Global radiation (Rg) provides the energy required to support evaporation of the water from the plant to atmosphere. When Rg is absorbed in the leaf, it increases the dissipation of latent heat (λE). Tree transpiration is thus controlled by both Rg and VPD. If Rg is low, tree transpiration may decrease despite high VPD (Meinzer *et al*., 1997; Roupsard *et al.*, 2006) In contrast, transpiration become increasingly be dependent on the net radiation received and low VPD (Wullschleger *et al.*, 2000). At plot scale, the evaporative demand is estimated by the potential evapotranspiration (ETo), which depends mainly on VPD and Rg. There is usually a positive relationship between ETo and stand transpiration (Granier, 1987). Moreover, transpiration is strongly related to soil water content (Poyatos *et al*., 2005). Then, 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). In dry season the plants are necessary to limit the loss of water from plant tissue by closing their stomatal as the soil limitation. Thus, water loss through transpiration is regulated by stomatal and driven by evaporative demand (Jackson *et al*., 2000; Taiz and Zeiger, 2006). Thus, the closure of stomata is to reduce water loss and maintains leaf water potential above a critical cavitation threshold (Sperry, 2000; Cochard *et al*., 2002; David *et al*., 2004). Moreover, isohydric regulation of plant water status, stomatal control of transpiration occurs in woody plants to prevent water potential above the cavitation threshold level (Frank *et al*., 2007; West *et al*., 2007).

Tree transpiration can be measured at either the leaf-level measurement with porometer (McNaughton and Jarvis, 1991; Whitehead, 1998; Hogg *et al*., 2000) or the stand level with sap flow measurement (Hatton *et al*., 1995; Granier *et al*., 1996). Transpiration of an individual or the stand level can be assessed by sap flow measurements (Smith and Allen, 1996; Granier *et al*., 2000; Lu *et al*., 2004). Sap flow was measured by heat dissipation method adapted from Granier (1985, 1987), with two sensor probes (20 mm-long radial probes) per set. The upper probe of each pair is continuously heated at constant power, while the low probe is unheated to measure the temperature of sapwood tissue and serves as a reference probe. It has been used to estimate transpiration in *Pinus sp*. (Ford *et al*., 2004), rubber trees (Isarangkool Na ayutthaya *et al*., 2010). Hence, the sap flow measurements are continuous and enable the automatic recording of transpiration.

However, the calibration of the probes should be checked in laboratory with reference to the gravimetric method (Do and Rocheteau, 2002; Lu *et al*., 2004; Roupsard *et al*., 2006; Isarangkool Na Ayutthaya *et al*., 2010). This method can be used in research on sap flow density and estimated stand transpiration of rubber trees, the resulting related to environmental variations (Kunjet *et al*., 2007 ; Isarangkool Na Ayuthaya, 2010).

2.3.2.2 Leaf water potential measurement

Leaf water potential is the thermodynamic expression of plant water status (Nadezhdina, 1999). Predawn leaf water potential measures plant water status and assumed close to the value of soil water potential around the root zone (Chone *et al*., 2001; Frank, 2007). In addition, predawn leaf water potential can be used as indicator of water stress in rubber trees (Isarangkool Na Ayuthaya *et al*., 2007). For instance, Ansley *et al*. (1992) found a relationship between predawn leaf water potential and soil water content. Predawn leaf water potential was high value in the rainy season and after that it decreased in the dry season. Reduction in predawn leaf water potential was correlated with increasing soil water deficit during the drought (Alarcon *et al*., 2000; O’Grady *et al*., 2008). The value of leaf water potential responds to environmental variable such as radiation, VPD, Ta and RH (Nadezhdina, 1999). Midday leaf water potential corresponds to the maximum of transpiration (Tyree and Sperry, 1988; Lu *et al.*, 1996). However, midday leaf water potential remained rather constant throughout the rainy season, it varied strongly at the onset of drought period (David *et al*., 2004). Then, leaf water potential is regulated by stomatal conductance. Tree regulates stomatal closure to avoid excessive loss of water and stomata closed to maintain the minimum leaf water potential above a critical threshold, protecting the cavitation in the xylem (Tyree and Sperry, 1989).

Sangsing (2004) showed that a strong relationship between stomatal conductance and leaf water potential in young rubber tree clone RRIM 600 and RRIT 251. The stomatal closure was maximum when leaf water potential reach to -2.2 MPa. In mature rubber trees, Isarangkool Na Ayuthaya (2010) found that predawn leaf water potential varied range between -0.32 to -0.44 MPa in the well-watered period. It declined slightly and reached -0.83 MPa at the peak of drought. Midday leaf water potential declined progressively during water stress and was reached -1.95 MPa. However, midday leaf water potential did not appear to relate with soil drought during the rainy season. The minimum leaf water potential values ranged between -1.8 and -2.2 MPa for sunny days. This pattern expressed an isohydric behaviour which maintaines leaf water potential above a critical value (West *et al*., 2007).

Leaf water potential is measured with pressure chamber. The pressure chamber described by Scholander *et al*. (1995) is frequency used to measure water potential of plants. The method is necessary to increase the pressure around the leaf until sap in the xylem removes to the cut end of the leaf. The amount of the water potential of the leaf cell is described in unit of pressure, derived from energy per unit volume of water.

2.3.2.3 The hydraulic conductance measurement

Hydraulic architecture is the structure of water transport system. Water flow along the xylem conduit develops a large tension (a negative hydrostatic pressure) at the top of the tree, and this tension pulls water through the xylem (Tyree and Ewers, 1991; Taiz and Zeiger, 2006). Therefore, long distance of water transport from the soil through the plant may be vulnerable to cavitation. This process can lead to cavitation or embolism (Cochard *et al*., 2007).

Cavitation develops when air is refilled into a functional xylem conduit through the pit membrane (Zimmermann, 1983; Sperry and Tyree, 1988). Cavitation breaks the water transport in the water column (Tyree and Sperry, 1989). Embolism would block the water transport pathway (Taiz and Zeiger, 1998). Cavitation can occur during water stress. Cavitation reduced hydraulic conductivity of xylem conduit, which increases in resistance of water flow in the stem to leaves (Yang and Tyree, 1994; Meinzer *et al*., 2001). In addition, the hydraulic resistance associated with moving water through xylem conduits may affected on leaves of canopy trees during period of high evaporative demand, and low soil water content (Goldstein, 1998). However, high conductance is also associated with increased vulnerability to cavitation in the xylem and requirement for greater stomatal control of plant water status (Sperry, 2000).

The hydraulic characteristics of rubber trees are in the range of reports for tropical trees (Tyree and Ewers, 1991; Cruiziat *et al*., 2002). The hydraulic characteristics in rubber tree exhibited differences in vulnerability to embolism and xylem hydraulic resistance according to the different plant segmentations and clones (Sangsing, 2004). Sangsing *et al*. (2004) found that the rubber tree was high vulnerable to cavitation. There is a correlation between xylem vulnerability to cavitation and stomatal closure during water stress in the same clones. Then, stomatal closure occurred at onset of xylem cavitation in petiole (Sangsing *et al*., 2004). Isarangkool Na Ayuthaya (2010) found that decrease of tree transpiration was mainly due to the change of the whole tree hydraulic conductance (gL). The decrease of gL was strongly correlated to the decline of the “relative extractable water” (REW) and predawn leaf water potential in the dry season. Conversely, the saturating transpiration appeared in well-watered conditions that was stimulated by maximum gL. The decrease of tree transpiration due to the effect of the whole tree hydraulic conductance (gL) has been reported in many species (Cochard *et al*., 1996; Addington *et al*., 2004). Rubber tree exhibited a strong control of water losses through the relative stability of midday leaf water potential, in the dry season PLC was high. The hydraulic limitation hypothesis assumes that the plant maintains minimum leaf water potential above the critical value by closing the stomatal to prevent the embolism in the xylem (Cochard *et al*., 1996; Sperry *et al*., 2002). Sangsing *et al.* (2004) reported values of xylem pressure between -1.5 and -2.0 MPa was correlated to 50% of embolism in petioles in young rubber tree.

The principle of the xylem apparatus is used to measure the relative changing in xylem hydraulic conductance caused by the occurrence of air bubble in the xylem conduits (Sperry *et al*., 1998).

2.3.2.4 Leaf stomatal conductance (g_s)

Stomatal control of leaf transpiration and loss of hydraulic conductivity in twigs have been monitoring during the soil drought (Cruiziat *et al*., 2002). Stomata control the development of xylem embolism. Stomatal regulation is directly affected by plant water status and whole plant hydraulic structure (Frank, 2004). Stomatal closure occurred to maintain the minimum value of water potential above the cavitation threshold (Sperry and Tyree, 1988; Oren *et al*., 1999). Sangsing (2004) showed a strong relationship between stomatal conductance and leaf water potential in young rubber tree clone RRIM 600 and RRIT 251. The stomatal closure in the afternoon stimulated tissue rehydration which increased leaf water potential (Davies and Kozloski, 1997).

Stomata may respond to changes in plant hydraulic conductance. Previous studies assumed that stomata is sensitive to VPD (Fraqhuar, 1978). Addington *et al*. (2004) reported that reduction in stomatal conductance as hydraulic conductance decreased when VPD was high. The reduction in leaf water potential would cause cavitation of xylem that induced stomatal closure at high VPD (Sperry, 2000).

Measurement of stomatal conductance is difficult to measure under natural conditions because of the large size of the trees and variations of leaf age and position and boundary layer of the leaf (Ansley *et al*., 1992). Leaf-level stomatal conductance can be measured with an AP4 Porometer (Sangsing, 2004) and Li-Cor 6400 (Addington *et al*., 2004).

3. Plant water status and water stress

Under drought condition, predawn leaf water potential was closely related to soil moisture content and leaf stomatal conductance (Ansley *et al*., 1992). Kume *et al.* (2007) confirmed that the reduction in leaf water potential were caused by stomatal closure according to drought stress. Stomatal control is important in avoiding water stress under conditions of atmospheric and soil drought (Cunningham, 2004). Hence, closure of stomata is to maintain the water potential value above the critical threshold and to prevent the occurrence of embolism in the xylem under drought stress (Bond and Kavanagh, 1999; Poggi *et al*., 2007). In addition, predawn leaf water potential declined as maximum canopy conductance decreased in the water stress (O’Grady *et al*., 2008).

Variation in transpiration is sensitive to drought. Stand transpiration is strongly limited when soil water content declined below the threshold (Poyatos *et al*., 2005). Bond and Kavanagh (1999) found that transpiration of *Eucalyptus globules* trees were significantly reduced, and closely followed with canopy conductance when soil water deficit increased.

Under drought conditions, there is a relationship between stomatal function and plant hydraulic property (Cochard *et al*., 2002). Several reports showed that the plant in water stress increased the tension gradient of water flow along the shoot which induced embolism and loss of functional vessel. Therefore, shoot hydraulic conductivity decreased in response to water stress (Sperry and Tyree, 1990; Hargrave *et al*., 1994; Lovisolo and Schubert, 1998). The loss of hydraulic conductance induced stomatal closure that caused the cavitation in the xylem (Sperry, 2000).

Sangsing (2004) reported that young rubber trees provoked a strong stomatal closure and decreased in transpiration, xylem pressure and leaf water potential after the period of water stress. Several researchers have studied the influence of soil and atmosphere of drought on water relations of mature rubble trees (Chandrashekar *et al*., 1990; Gururaja Roa *et al*., 1990). Under drought conditions, minimum leaf water potential in both young and mature rubber reached -1.95 MPa. Transpiration and whole tree hydraulic conductance decreased during the period of leaf senescence and shedding in the dry season (Isarangkool Na Ayuthaya, 2010).

4. Tapping activity

Latex is the cytoplasm of specialized cells constituting the laticiferous tissue. This tissue can be found in every organ of the tree. Latex contains rubber particles, constituting 90% of the dry latex. Layer of laticiferous cell are regularly produced by the cambium, consist of phloem tissues (Webster and Baulkwill, 1989). Tapping activity is performed by cutting bark on one half of the trunk (the tapping panel) with a sharp knife, and severing 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). Rubber tree starts to tap when the average trunk girth attains 50 cm at 1.5 m height above the ground (Chandrashekar *et al*., 1998). The first cut is done 1.50 m from the ground. Trees are then tapped every 2 to 5 days, according to the tapping system. The regeneration of the bark occurs along with the cambium and can be tapped again (George and Jacob, 2000). After tapping, the cambial derivatives were produced in large numbers. The differentiation of these tissues was initiated after about one week. Newly different sieve tubes in the regeneration bark had a large diameter than those produced from the cambium in the uncut areas (Thomas *et al*., 1995).

MATERIALS AND METHODS

1. Plant materials

The rubber plantation (13.41 °N; 101.04 °E) is the part of Chachoengsao Rubber Research Center (CRRC), the Eastern region of Thailand, cover around 6.2 hectares plantation which consisted of 13-15 year-old rubber trees clone RRIM 600, the main clone in Thailand. The planting pattern was 7.5 m x 2.5 m and 9 m x 2.5 m. and the trees had been tapped for 6 years. The average girth of the trees at 1.80 m from the ground was 60-65 cm and the average height was about 21 m. Observation of 1-year-old slices of adult rubber trees from this plot showed that the cortex is approximately 7 mm-thick.

The climate is tropical and humid. Annual rainfall averaged 1,288 $mm.year^{-1}$. Rainfall usually starts in March. The peak appeared during the rainy season (September to October). The soil is clayey skeletal, kaolinitic, typic Paleustults (Kabin Buri soil series). Mean contents of sand, silt, clay, and organic matter is 49%, 16%, 35%, and 1.08%, respectively. It extended less than 1m deep before reaching a hard packed rocky underground consisting mainly of iron oxide.

The experiment was monitored for a long-term on rubber trees during 3 years starting from January 2007 to January 2010. The rubber plantation in CRRC have been tapped for 7 years. Annually, tapping activity generally starts in May and stops at the end of January, which allows 9 months of tapping and 3 months of resting period.

Figure 1 Rubber plantation at Chachoengsao Rubber Research Center (CRRC).

2. Methods

2.1 Climatic measurement

A weather station was located on a 25 m height tower inside the plot and recorded half hourly values of air temperature (T_a), relative humidity (RH), rainfall, net radiation (R_n), global radiation (R_g), photosynthetically active radiation (PAR) and wind speed (WS). The reference evapotranspiration (ETo, mm.day^{-1}) was calculated by Penman-Monteith equation and FAO recommended coefficients, under given conditions of ambient temperature, relative humidity, net radiation, wind speed and vapor pressure deficit.

ETo was used to represent the evaporative demand according to the FAO Penman-Monteith equation (Allen *et al*., 1998) was given by:

$$ET_o = \frac{0.408\Delta(R_n - G) + \gamma\frac{900}{T+273}u_2(e_s - e_a)}{\Delta + \gamma(1+0.34u_2)} \qquad (1)$$

where ETo = reference evapotranspiration (mm day^{-1}),
Rn = net radiation at the crop surface (MJ m^{-2}day^{-1}),
G = soil heat flux density (MJ m^{-2}day^{-1}),
T = air temperature (° C),
u_2 = wind speed (m s^{-1}) at 2m height,
e_s = saturation vapour pressure (kPa),
e_a = actual vapour pressure (kPa),
e_s- e_a = saturation vapour pressure deficit (kPa),
Δ = slope vapour pressure curve (kPa °C),
γ = psychrometric constant (kPa °C).

2.2 Soil water content

Soil water content was determined by gravimetric method. Soil samples were taken in a can at 20, 40, and 60 cm deep, in 3 locations in the plot. Sampling was done monthly from January 2007 to January 2010. Fresh samples were weighted, dried in an oven (24 hours at 105 °C), and the dry sample was weighted to find the mass of water removed.

2.3 Sap flow measurement

Sap flow was measured by heat dissipation method adapted from Granier (1985, 1987) using home-made 20 mm-long radial probes. The set consists of two sensor probes (needle) per set. One probe was continuously heated (0.2 W), and the other one was unheated and was used to measure the temperature of wood tissue and acts as reference probe (Figure 2). Campbell Scientific datalogger model 21X (Shepshed, UK) was used to collect temperature data. The initial calibration of our set of probes was done on a synthetic porous media (sawdust in PVC pipe) by Roupsard *et al*. (2006). Js was calculated as:

$$Js = \alpha K^{\beta} \qquad (2)$$

where Js is the sap flux density (Js, l $dm^{-2}h^{-1}$) and K is the sap flow index. Coefficients $\alpha = 312\times10^{-6}\ m^3m^{-2}s^{-1}$ and $\beta = 1.231$.

The sap flow index was calculated as:

$$K = \frac{\Delta T_o - \Delta T_i}{\Delta T_i} \qquad (3)$$

where ΔT_o is the daily maximum and ΔT_i is the current temperature difference between the two sensors of the probe.

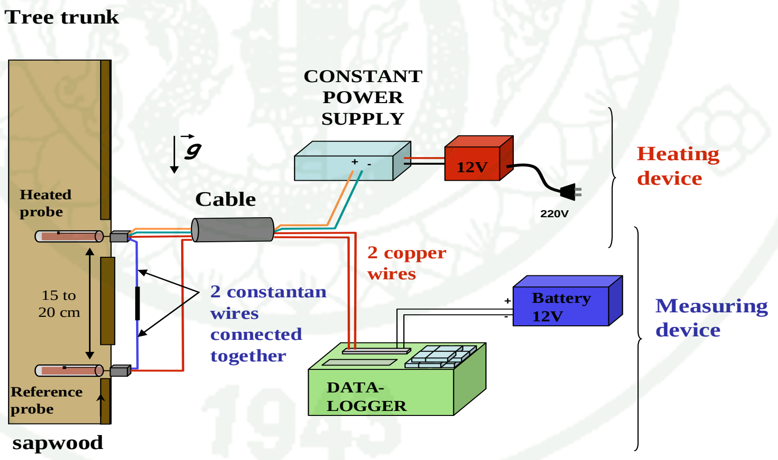

Figure 2 Granier system and installation of Granier sap flow probes on a rubber tree trunk.

2.3.1 Calibration of probes in the laboratory

The calibration of the home-made probes was done on four probes in the laboratory with reference to the gravimetric method, using high pressure flow meter (HPFM, Dynamax Co., Houston). Four probes were set on the four 5 cm diameter stems of 6 year-old rubber trees clone RRIM 600 to obtain five datasets: probe 1 stem 1 (P1S1), probe 1 stem 2 (P1S2), probe 2 stem 3(P2S3), probe 3 stem 4 (P3S4), and probe 4 stem 4 (P4S4). Sap flux density was calculated on total cross sectional sapwood area. Approximately 0.5 m long stem sections were cut in the field and the sections were soaked in distilled water for 12 hours overnight to avoid vessel blockage due to latex exudates. Both ends of each stem sections were re-cut off (about 2 cm) before connecting apical end to HPFM. After turning on the system pressure, water flowing out of the basal end was collected in a jar put on a 0.01 g accuracy balance (Adventurer, Ohaus, Pine Brook) and the sap flux densities obtained by weighting water on the balance were used as reference to calibrate the home-made probes. Water flow rate through stem sections was varied by step-wise increasing in pressure to obtain a range of flow densities from 0.5 to 5 l dm^{-2} h^{1}. Two probes per one home-made sensors were installed on each stem section. The distance between the sensor probes was 10 cm. The upper probe was continuously heated and the lower probe was unheated. Data were recorded by Campbell Scientific data logger model 21X (Shepshed, UK). The stem sections were left under zero flow conditions at night to determine ΔT_o. Sap flow index (K) was calculated according to equation 3 and parameters α and β in equation 1 were estimated from relationship between K and observed Js.

2.3.2 Spatial variations of sap flux density in stem

Four home-made probe sets were installed to two rubber trees under field conditions to study spatial variations of sap flux density in rubber stem. For each set of probe, two 4 cm^2 of bark were removed with a chisel, one above the another and each was separated about 10 cm. After the latex dried, holes were drilled about 2 cm into the exposed xylem and the aluminum tubes were inserted straight into the holes. The probes were then inserted into the aluminum tubes. Prior to insertion, probes were coated with silicone grease to ensure good thermal contact and easy removal of the probes and to protect the probes from rainfall.

This preliminary experiment aimed to establish the protocol for a long term monitoring program of the stand transpiration. We tested the influence of 4 sources of variations in stem flux density: (i) natural thermal gradients, (ii) azimuthal variability, (iii) axial variability, and (iv) radial variability.

(i) Natural thermal gradients were often shown to affect sap flux density considerably (Do and Rocheteau, 2002; Lundblad *et al*., 2001, Roupsard *et al*., 1999). Therefore, the daily variations of the natural vertical thermal gradient between the two probes were studied. Four probe sets were installed on four cardinal directions (north, south, east, west) of a tree stem at 1.80 m from the ground. The variations of dT between the two regions of the wood where two probes were installed were measured continuously for 6 days: the first 2 days with heating and the following 4 days without heating.

(ii) Azimuthal variability of sap flow was evaluated with probe sets located on each of the 4 cardinal directions (north, south, east, west) of the trunk, at 1.80 m from the ground. Sap flux density was measured for 6 days on 2 trees and the result were analyzed for correlations among different cardinal directions.

(iii) Axial variability of sap flux density was studied by measuring sap flux density for 3 days at different heights (130, 180, 230 cm) above ground on the stems of 2 trees, on north and south directions.

(iv) Radial variability of sap flux density was assessed using a set of 10 cm-long probes. The probe set was inserted at different depths (2, 4, 6, 8 or 10 cm) into the xylem to measure sap flux densities at different depths, This 10 cm-long probe set was first installed at 2 cm-depth and the sap flux density was measured for 3 days. It was then re-installed at 2 cm deeper into the xylem every 3 days until it reached the center of the stem. Sap flux density measured using another set of probes fixed at 2 cm depth on the opposite side of the same stem was used as a reference. The radial variability of sap flux density was studied on 2 trees of different girths (57.5 cm and 66.0 cm). Radial variability of sap flux density was modeled as functions of depth into the xylem. The model has two basic assumptions: (1) young xylem has maximum sap flux density and (2) sap flux density decreases linearly with depth into the xylem (and thus older xylem) towards the center of the stem. Relationship between sap flux density ($J_s/J_{s\text{-reference}}$) and depth into the xylem can be written as:

$$J_s/J_{s\text{-reference}} = J_{s\text{-young}}, \text{ if } J_{s\text{-old}} > 1 \text{ or } J_{s\text{-old}} = 1,$$
$$= J_{s\text{-old}}, \text{ if } J_{s\text{-old}} < 1 \qquad (4)$$

where $J_{s\text{-young}}$ and $J_{s\text{-old}}$ are sap flux densities of young xylem and old xylem, respectively, referenced to J_s measured at 2 cm depth intothe xylem. $J_{s\text{-young}}$ is given by:

$$J_{s\text{-young}} = 1 \qquad (5)$$

$J_{s\text{-old}}$ can be expressed as a linear function of depth into the xylem and is given by:

$$J_{s\text{-old}} = d_1 .D + d_2 \qquad (6)$$

where D is depth into the xylem, both d_1 and d_2 are empirical parameters; d_1 indicates the sensitivity of $J_{s\text{-old}}$ to D and $-d_2/d_1$ is the depth at which $J_{s\text{-old}}$ approaches zero.

The model was fitted to combined data set from 2 trees with d_1 = -0.1389 and d_2 = 1.568. The model explained more than 97% of variations of $J_s/J_{s\text{-reference}}$. Predicted vs. observed plot (not shown) exhibits satisfactory prediction of the model over a full range of depth into xylem studied.

2.3.3 Seasonal variation of stand transpiration

Seven trees were selected for long-term monitoring of sap flow and stand transpiration, from January to December 2007 and five trees were sampled for the experiment from January to March 2008. The trunk girth at 1.8 m above the ground averaged 62.5-65.5 cm and sapwood area averaged 250 cm^{-2}. Sap flux density (Js) was calculated as below.

$$Js = 312 \times 10^{-6} K^{1.231} \qquad (7)$$

where Js is the sap flux density (Js, $l\ dm^{-2}h^{-1}$) and K is the sap flow index. Sap flow index (K) was calculated according to equation 2. Tree transpiration was calculated as

$$T\ tree = Js \cdot A \qquad (8)$$

where T tree ($l\ h^{-1}$) is tree transpiration, Js ($l\ dm^{-2}\ h^{-1}$) is sap flux density and A is sapwood area (dm^2)

Assuming the trunk sap flow in a tree is equal to whole tree transpiration, then the stand transpiration was calculated as follow:

$$T = Js_{mean} \times A_{mean} \times N \qquad (9)$$

where T is stand transpiration of the rubber tree layer of the stand level ($mm\ h^{-1}$), Js_{mean} ($l\ dm^{-2}\ h^{-1}$) is mean sap flux density, A_{mean} is mean sapwood area, N is number of trees per hectare (1 ha = 10000 m^2)

2.4 Leaf water potential

Leaf water potential was measured from January 2009 to January 2010 with pressure chamber a Scholander-type pressure chamber (plant water status console, Soil Moisure Equipment Corporation, USA). Fully expanded mature leaves were sampled for leaf water potential measurements. Leaf water potential were performed rapidly after cutting, at predawn between 04:30 and 06:00 hours, and midday between 12:30 and 13:30 hours. Predawn leaf water potential measurement was related to soil water content.

2.5 LAI ratio

LAI ratio was estimated from the hemispherical photograph. The camera was set at height of 1 m above the ground at 20 positions along with the litter trap every week. The photos were taken by using digital cameras (COOLPIX995, 3.2 mega pixels, Nikon) with Fisheye converter (FC-E8, Nikon). Gap fraction from the images were calculated by Gap Light Analyzer (GLA) (Frazer *et al*., 1999).

$$\text{LAI Ratio} = \frac{\text{LAI}_i}{\text{LAI}_{\text{max}}} \qquad (10)$$

LAI_i : LAI fisheye every week

LAI_{max} : Maximum LAI fisheye of the year

2.6 Stomatal conductance

Stomatal conductance was measured by Li-Cor 6400 on intact mature leaves of rubber trees, in the study site. The hourly measurements of diurnal stomatal conductance were obtained between 08:00 and 17:00 hours. Stomatal conductance was measured on leaf exposed to sun on 6th April, 31st August, and 18th November 2007.

Stomatal conductance was measured with an AP4 Porometer (Delta-T Devices Ltd., Cambridge, England). The measurements were obtained on the leaflets randomly chosen on each tree between 1 tapped and 1 untapped tree near the tower as the same trees with sap flow and leaf water potential measurement between 11:30 and 13:00 hours. Stomatal conductance was measured on leaf exposed to sun at the middle of canopy from November to January 2010 during the dry season.

2.7 Percentage loss conductivity (PLC)

We measured PLC from 6 tapped trees and 6 untapped trees as the same tree with measurement of sap flux density, leaf water potential from March 2009 to January 2010. The percentage of loss of hydraulic conductivity (PLC) was measured on the petioles with the technique described by Sperry *et al*. (1988). The petioles were cut about 2-3 cm under the water to prevent air entry into the conduits and connected to the XYL'EM apparatus (Embolism Meter, INRA Licensed instrutec-France, Cochard *et al*., 2001). And then they were wrapped with teflon tape to prevent lateral leaks. The initial conductivity (Ki, mmol $ms^{-1}MPa^{-1}$) of each segment was measured with a hydrostatic pressure gradient of ca 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 air bubbles. After that the hydraulic conductivity (Km, mmol $ms^{-1}MPa^{-1}$) of the segments were determined again. PLC then was calculated from:

$$\mathrm{PLC} = \frac{100\,(\mathrm{Km} - \mathrm{Ki})}{\mathrm{Km}} \qquad (11)$$

2.8 Whole tree hydraulic conductance (gL)

Whole tree hydraulic conductance was calculated from concurring measurements of sap flow rate and leaf water potential following calculated ETo. The multi-points method plotted the diurnal changes of leaf water potential versus sap flux density, the slope of the assumed linear relationships representing the hydraulic resistance, the reverse of the hydraulic conductance. The single point method applied the simplified following formula (Cochard *et al*., 1996).

$$gL = \frac{J_s\,max}{(\psi_{predawn} - \psi_{midday})} \qquad (12)$$

where gL is Whole tree hydraulic conductance (l dm^{-2} $h^{-1}MPa^{-1}$), J_s max is the sap flux density (l dm^{-2} h^{-1}) between 11.00 to 13.00 hours, $\psi_{predawn}$, ψ_{midday} are predawn and midday leaf water potentials (MPa), respectively. $\psi_{predawn}$ is assumed close to soil water potential surrounding the roots. ψ_{midday} corresponds to the maximum of transpiration.

Experiment 1 Sap flow measurement of rubber (*Hevea brasilliensis* Muell Arg.) trees

The study was to check the calibration of the probes on the cut stems of rubber tree in the laboratory, to measure dynamics of sap flow rate of the rubber tree and to estimate stand transpiration of rubber plantation as related to environmental variables. The experiment was conducted in 13-15 year-old rubber (*Hevea brasilliensis* Muell. Arg.) trees, RRIM 600 clone under natural conditions at Chachoengsao Rubber Research Center (CRRC) from January 2007 to January 2010.

Firstly, the calibration of the home-made probes was done on four probes in the laboratory with reference to the gravimetric method, using high pressure flow meter (HPFM).

Secondary, sap flow probes were installed to rubber trees under field conditions to study spatial variations of sap flux density in rubber stem. We tested the influence of 4 sources of variations in stem flux density:

1. Natural thermal gradients, four probe sets were installed on four cardinal directions (north, south, east, west) of a tree stem at 1.80 m from the ground. The variations of dT between the two regions of the wood where two probes were installed were measured continuously for 6 days: the first 2 days with heating and the following 4 days without heating.

2. Azimuthal variability of sap flow was evaluated with probe sets located on each of the 4 cardinal directions (north, south, east, west) of the trunk, at 1.80 m from the ground.

3. Axial variability of sap flux density was studied by measuring sap flux density for 3 days at different heights (130, 180, 230 cm) above the ground on the stems of 2 trees, on north and south directions.

4. Radial variability of sap flux density was assessed using a set of 10 cm-long probes. The 10 cm-long probe set was inserted at different depths (2, 4, 6, 8 or 10 cm) into the xylem to measure sap flux density at different depths. Sap flux density measured using another set of probes fixed at 2 cm depth on the opposite side of the same stem was used as a reference. The model has two basic assumptions: (1) young xylem has maximum sap flux density and (2) sap flux density decreases linearly with depth into the xylem (and thus older xylem) towards the center of the stem.

Finally, seasonal variation of stand transpiration were estimated from sap flow measurement, average of 7 rubber trees (two probes per tree) in 2007, average of 5 individual rubber trees in 2008, and average of 4 individual rubber trees in 2009. Soil water content and climatic data were measured from January 2007 to January 2010. The soil moisture content was measured with gravimetric method at 20, 40 and 60 cm depth in rubber plantation. The climatic data was recorded with a weather station in half hourly interval. Data included air temperature (Ta) and relative humidity (RH), rainfall, net radiation (Rn), global radiation (Rg), and wind speed (WS). The reference evapotranspiration (ETo, mm h^{-1}) was calculated by Penman-Monteith equation and FAO recommended coefficients, under given conditions of ambient temperature, net radiation, wind speed and vapor pressure deficit.

Experiment 2 Transpiration and stomatal conductance of rubber trees in response to environmental variables

The study was to analyze the diurnal dynamics of stand transpiration and stomatal conductance. The experiment was conducted in 13 year-old rubber (*Hevea brasilliensis* Muell. Arg.**)** trees, RRIM 600 clone under natural conditions at CRRC

Seasonal variations of plant and soil water status and climatic datas were measured from January 2007 to December 2007. Plant water status was estimated with leaf water potential measurement by pressure chamber at different heights (12, 14, 16, 18, and 20 m from the ground). Soil water content was measured by Gravimetric method at 20, 40 and 60 cm depth, 3 locations in rubber plantation. The climatic data was recorded with a weather station in half hourly interval. Data included air temperature (Ta) and relative humidity (RH), rainfall, net radiation (Rn), global radiation (Rg), and wind speed (WS). The reference evapotranspiration (ETo, mm h^{-1}) was calculated from the meteorological data by Penman-Monteith equation and FAO recommended coefficients, under given conditions of ambient temperature, net radiation, wind speed and vapor pressure deficit.

For the large scale, we monitored stand transpiration (T) by measurement of trunk sap flow adapted from Granier (1985) method in seven untapped rubber trees. The reference evapotranspiration (ETo) was calculated from the meteorological data by Penman-Monteith equation and FAO recommended coefficients. On the tree scale, we measured stomatal conductance (g_s) by Li-Cor 6400 on the leaves exposed to the sun. We focused on difference three days along the year: (1) on 6th April, the new leaves occurred at the early of the rainy season, (2) on 31st August, the optimum soil water content was in the rainy season, and (3) on 18th November, it was the period of water stress. We want to analyze the diurnal dynamics of stand transpiration and stomatal conductance.

Experiment 3 The effect of tapping activity on water relation in rubber trees

The study was to estimate the effect of tapping on plant water relations in rubber trees (January 2009 to January 2010). Sap flow measurement, leaf water potential, whole tree hydraulic conductance (gL), and the percent loss of conductivity (PLC) were used as indices of water relation in this study. The sap flow measurement was measured in 2 tapped trees and 2 untapped trees. Two fully expanded leaves from 6 tapped trees and 6 untapped trees were selected for leaf water potential measurement. gL was calculated from concurring measurements of sap flux density and water potential between plant and soil. PLC was measured by XY'LEM apparatus in the same trees. The soil moisture content was measured with gravimetric method at 20, 40, and 60 cm depth between tapped and untapped trees in rubber plantation. The tapping activity was started in May after rainfall event and stopped in February. The climatic data was recorded with a weather station in half hourly (January 2009 to January 2010), values collected included air temperature (Ta) and relative humidity (RH) rainfall, net radiation (Rn), global radiation (Rg), and wind speed (WS). The reference evapotranspiration (ETo, mm h^{-1}) was calculated from the meteorological data by Penman-Monteith equation and FAO recommended coefficients, under given conditions of ambient temperature, net radiation, wind speed and vapor pressure deficit. We focused on the effect of tapping activity on plant water relations of rubber trees.

Place and Duration

The research was conducted in laboratory at Khon Kaen University located in Khon Kaen Province and rubber plantation located in Chachoengsoa Rubber Research Center (CRRC), Sanamchaikhet District, Chachoengsao Province, Thailand. The research was investigated from January 2007 to January 2010.

RESULTS

Experiment 1 Sap flow measurement of rubber (*Hevea brasilliensis* Muell. Arg.) trees

1. Laboratory calibration of probes

The results showed a non-linear relation between K and sap flux density from gravimetric method (Figure 3a; R^2=0.90).

The whole data set was fitted to a power function passing through 0 (Figure 3a):

$Js = \alpha K^{\beta}$

where $\alpha = 11.24$ l dm^{-2} h^{-1} (or 312 x 10^{-6} m^3 m^{-2} s^{-1}) and $\beta = 1.235$

The results showed that the data obtained from different probes on the same cut stem or from one single probe on different cut stems can be fitted by the same function. There was a strong linear relationship between calibrated sap flux density and gravimetric sap flux density (Figure 3b; R^2= 0.90).

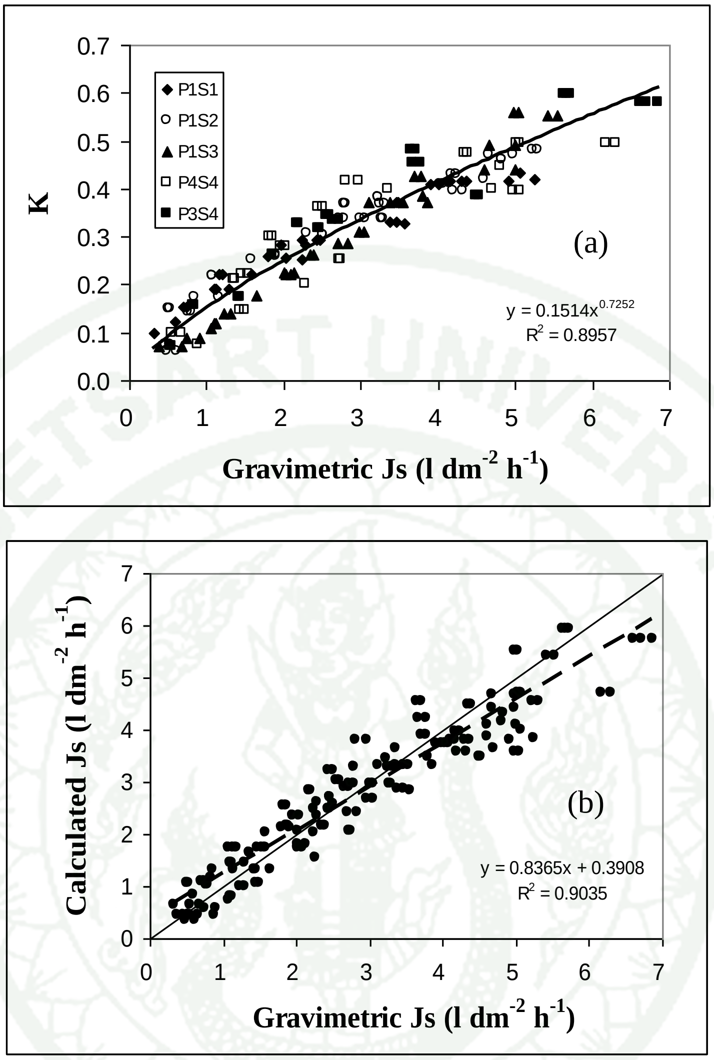

Figure 3 Calibration of home-made sap flow probes using CTD method with the gravimetric method in laboratory: (a) values of sap flow index (K) versus sap flux density (Js) from gravimetric method. Squares show results from the same probe with 2 different stem sections (empty square: probe 1 stem 1, and closed square: probe 1 stem 2), (closed triangle: probe 2 stem 3), other symbols show different probes in the same stem section (cross: probe 3 stem 4 and closed rhomb: probe 4 stem 4), and (b) Relationship between calculated sap flux density (Calculated Js) using a power function with newly estimated coefficients and gravimetric sap flux density (Gravimetric Js). The solid line is the 1:1 line and the broken line was the linear trend line fitted to the whole data set.

2. Field setup of the probe

No significant natural vertical gradient was observed between the two probes in all 4 sets installed at four cardinal directions of rubber stems as the signal averaged only 0.0032 mV (Figure 4). The heating of the upper probes significantly increased the variations of temperature between the two regions of the wood where the two probes were installed and thus the signal varied with an averaged span of 0.20 mV.

Circumferential variations were observed on two trees, with flows being sometimes close to 2-fold higher on one side of the trunk than the other sides. This indicated that it is necessary to take this variability into account when calculating the total sap flow of a given tree. For each tree, good correlation were found between flows measured on different azimuths (Table 1), Significant circumferential differences in flow were showed in Table 2.

There was a little difference in flux density measured at different heights on the trunk of a rubber tree (Table 2). Sap flux density is highest at 180 cm height on the trunk.

Two different radial profiles were obtained, first tree (n°1, girth of 66.0 cm), a larger girth, and the second tree (n°2, girth of 57.5 cm), of thinner trunk (Figure 5). The model for the radial distribution was capable to predict the sap flux density of rubber tree. Sap flux density at 0-4 cm depth below trunk surface was high and stable. Then sap flux density started to decrease after 4 cm depth into the xylem toward the center of the stem. However, the model underestimated for higher assimilation rate (Figure 6)

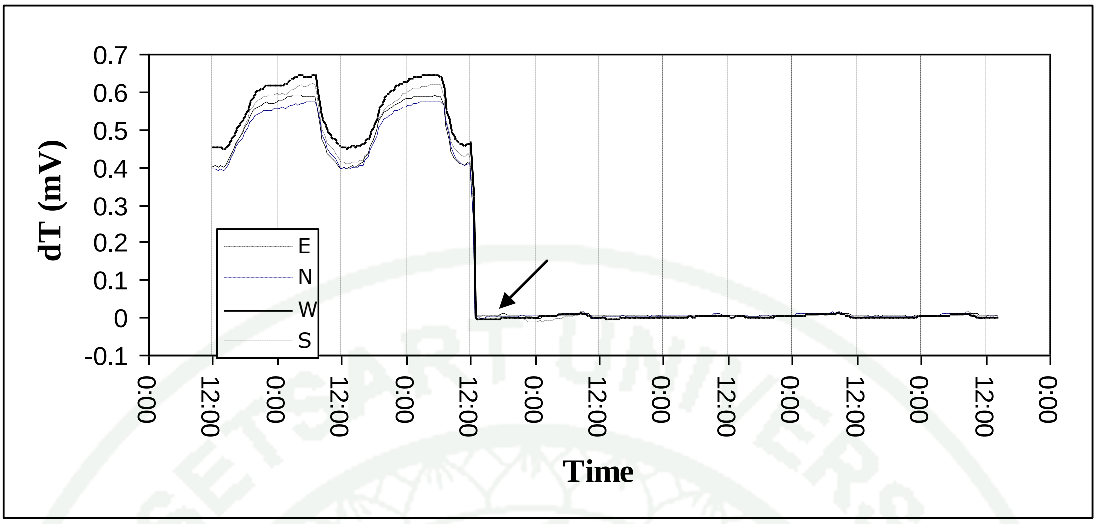

Figure 4 Temperature difference between the two needles of sap flow probes with (before arrow) and without (after arrow) heating. Data without heating give an estimation of the natural gradient of temperature in the sapwood. dT is different temperature of the sapwood.

Table 1 Coefficient of correlation between time series of sap flux density measured by 4 probes install at 4 azimuths.

	Azimuth	East	North	South	West
Tree 1	East	1	0.94	0.95	0.96
	North		1	0.99	0.98
	South			1	0.98
	West				1
Tree 2	East	1	0.99	0.99	0.96
	North		1	0.99	0.98
	South			1	0.97
	West				1

Table 2 Sap flux density (Js) measured by 4 probes install at 4 azimuths in 2 trees and 3 different heights.

Treatment	Tree1		Tree2		Tree3
	Daily Js (l/dm^2/day)	Max Js (l/dm^2/h)	Daily Js (l/dm^2/day)	Max Js (l/dm^2/h)	Max Js (l/dm^2/h)
Azimuth					-
North	62.56 b	4.10 b	69.27 b	4.80 b	-
East	93.12 a	7.38 a	49.49 c	3.52 c	-
South	60.99 b	4.62 b	103.09 a	7.31 a	-
West	106.28 a	6.68 a	54.54 bc	4.48 b	
Height					
130cm	-	-	-	-	4.3 a
180cm	-	-	-	-	5.6 a
230cm	-	-	-	-	4.9 a

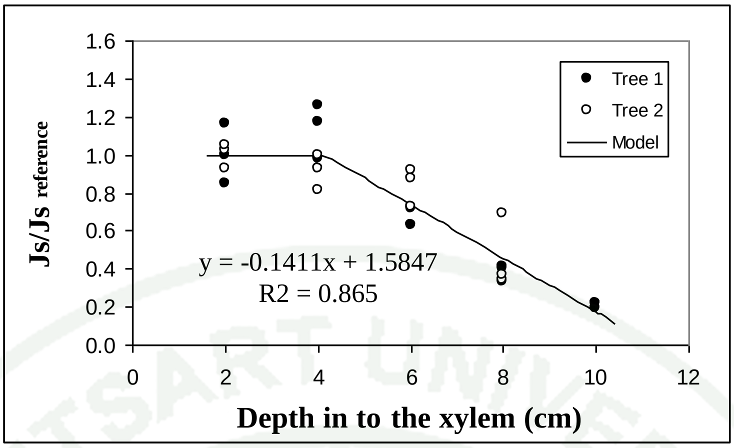

Figure 5 Radial sap flux density of two rubber trees. Tree 1 is a large tree, girth of 66.0 cm while tree 2 is a smaller tree, girth of 57.5 cm. Js was averaged over at least 3 days for each depth. The model was fitted as a function of relative depth into the xylem (R^2 = 0.865). The sap flux density at 2 cm is considered as a reference.

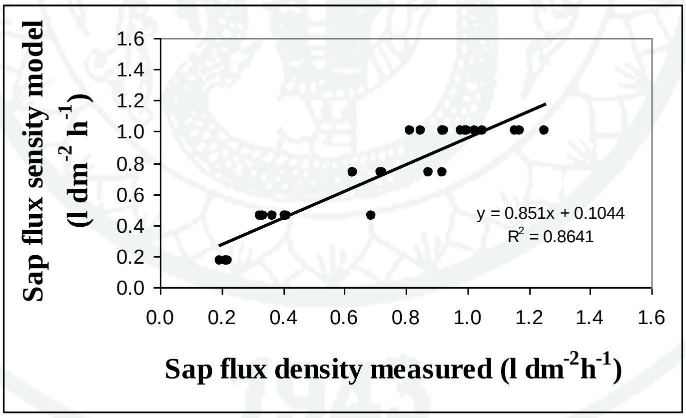

Figure 6 Relationship between sap flux density measured and stimulated by the model for 3 days. The line indicates the regression between sap flux density measured and stimulated by the model for 3 days.

3. Seasonal variation of stand transpiration and ETo

3.1 Dynamics of stand transpiration and ETo

Figure 7 shows the diurnal dynamics patterns of ETo and stand transpiration (T) for 3 periods: (i) refoliation period during the dry season (February 2007, Figure 7a), (ii) beginning of the rainy season with fully expanded leaves (May 2007, Figure 7b) and (iii) beginning of the dry season including the leaf-shedding period (December 2007, Figure 7c). ETo and T showed similar diurnal dynamics, increasing from zero in the morning and peaking in early afternoon. However, there was often a time lag between evaporative demand (showed by ETo) and stand transpiration, particularly during leaf shedding/refoliation periods. During refoliation period (early February), which occurred just after defoliation completed, daily stand transpiration increased rapidly, although this was still the dry season. In this time, the new leaves fully expanded within 2-3 weeks (Figure 7a). Thereafter, stand transpiration was generally high and showed rather constant diurnal patterns throughout vegetative growth period, extending to the rainy season. However, stand transpiration was limited during high rainfall events (Figure 7b, 13-15 May). Stand transpiration slightly decreased before defoliation period, and became very low, during leaf shedding, although it never stopped, as few leaves always remained (Figure 7c).

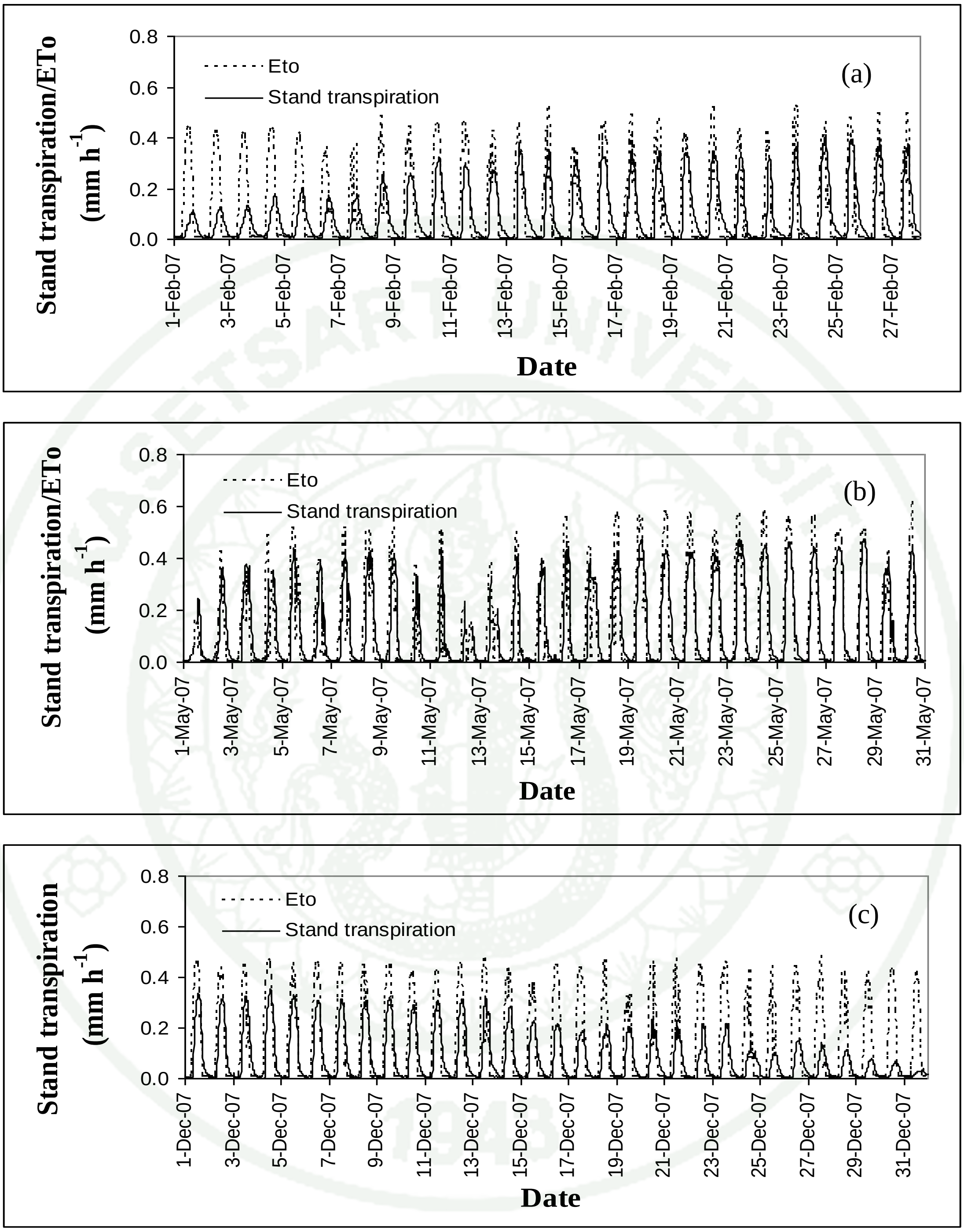

Figure 7 Diurnal dynamics of stand transpiration estimated from sap flow measurements (solid line) and potential evapotranspiration (dotted line): (a) during the refoliation period (February), (b) during the vegetative growth perio (May), and (c) during the defoliation period (December). We measured only on untapped trees.

3.2 Seasonal variations of stand transpiration, ETo and environmental conditions

Figure 8a showed rainfall started in March. The rainfall was high and varied in the rainy season. The rainy season started from March to October. After that it decreased at the early of the dry season. There was no rain in the dry season. The dry season started from November to February. Total rainfall in 2008 was higher than those in 2007 and 2009 (Table 3). In 2007, it had less rainfall during the rainy season about 2 weeks in June and August. However, in 2009, there was the period of without rain in the rainy season.

Vapor pressure deficit (VPD) was high in the dry season. After that it decreased and was rather constant in the rainy season. However, in 2009 the value of VPD was high in the rainy season as the rain dropped in August.

Soil water content was remarkable changes along the year for 3 yeas. Soil water content was low in the dry season and increased slightly in March after rainfall started. Soil water contents of both top and bottom soil layers were high in the rainy season (Figure 8b). The maximum value of soil water content appeared in July and September in 2007 and 2008 whereas the maximum value of soil water content in 2009 occurred in April after the rainfall started. However, in 2009 soil water content dramatically decreased during the rainy season (June, July and August) and increased again when the rainfall occurred in September. Therefore, there was the soil drought during the rainy season. Later on, soil water content decreased slightly at the onset of the dry season (November to February).

ETo was low in the dry season and increased following the rainfall event (Figure 7a). The values of ETo were high and varied in the rainy season. ETo decreased in the onset of the dry season. ETo was not different between 3 years (Table 3).

Seasonal variations in stand transpiration showed the same pattern with LAI ratio (Figure 9a). Stand transpiration increased rapidly after the new leaves occurred in January and February according to the flushing of new leaves. The peak of stand transpiration occurred in the rainy season. During full canopy, stand transpiration fluctuated around 3.0-4.0 mm day^{-1}, very close to ETo value for all three years. ETo decreased in the dry season with increasing soil water deficit and high VPD. The minimum stand transpiration reached 0.5 mm day^{-1} during defoliation period (end of December) when there was few leaves. However, in 2009 stand transpiration dramatically decreased down to 1.5 mm day^{-1} during the rainy season in June, where the stand transpiration did not follow the ETo and declined again in August when the rainfall stopped, after that it increased again when rainfall occurred in September. The peak of stand transpiration could be corresponded to high ETo and rain occurrence in the dry season. Stand transpiration declined slightly whereas ETo also declined as minimum stand transpiration during defoliation period.

LAI ratio was correlated with rainfall and soil water content at 20 cm depth in the soil. Despite some variability between trees in the leaf shedding/refoliation periods were showed in Figure 9b. The peak of LAI ratio was highest in 2008, immediate in 2007, and lowest in 2009. Seasonal changes in stand transpiration on a stand scale showed the same pattern with LAI ratio. The maximum LAI ratio was lowest in 2009.

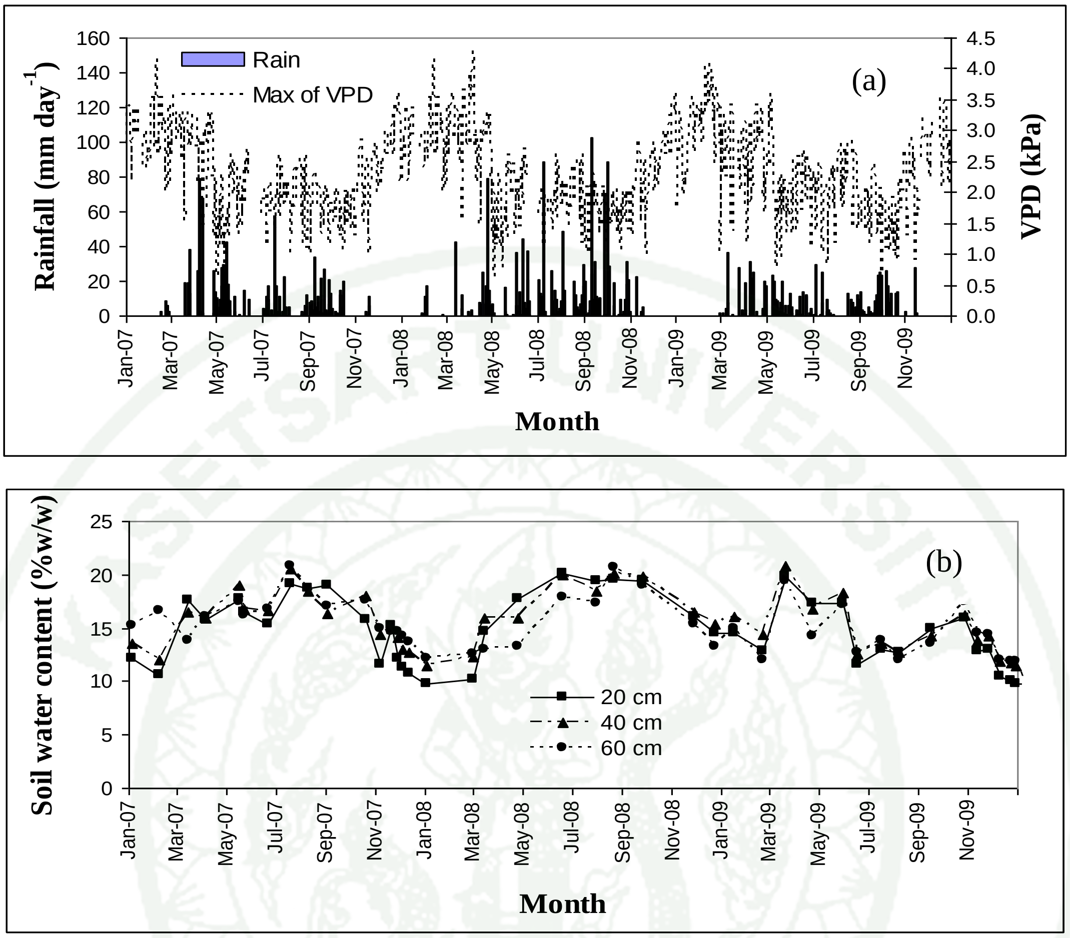

Figure 8 Seasonal variations of climate and soil water content from January 2007 to January 2010: (a) rainfall (columns), maximum of vapor pressure deficit (VPD; dotted line), (b) soil water contents at 20 cm (closed square with black line), 40 cm (closed triangle with dotted line), and 60 cm depths (closed circle with dotted line).

Table 3 Annual rainfall and evapotranspiration (ETo) in 3 consequent years of this experiment

year	Total rainfall (mm/year)	Total ETo (mm/year)
2007	1,361.8	1,877.3
2008	1,886.4	1,809.5
2009	1,177.5	1,835.3

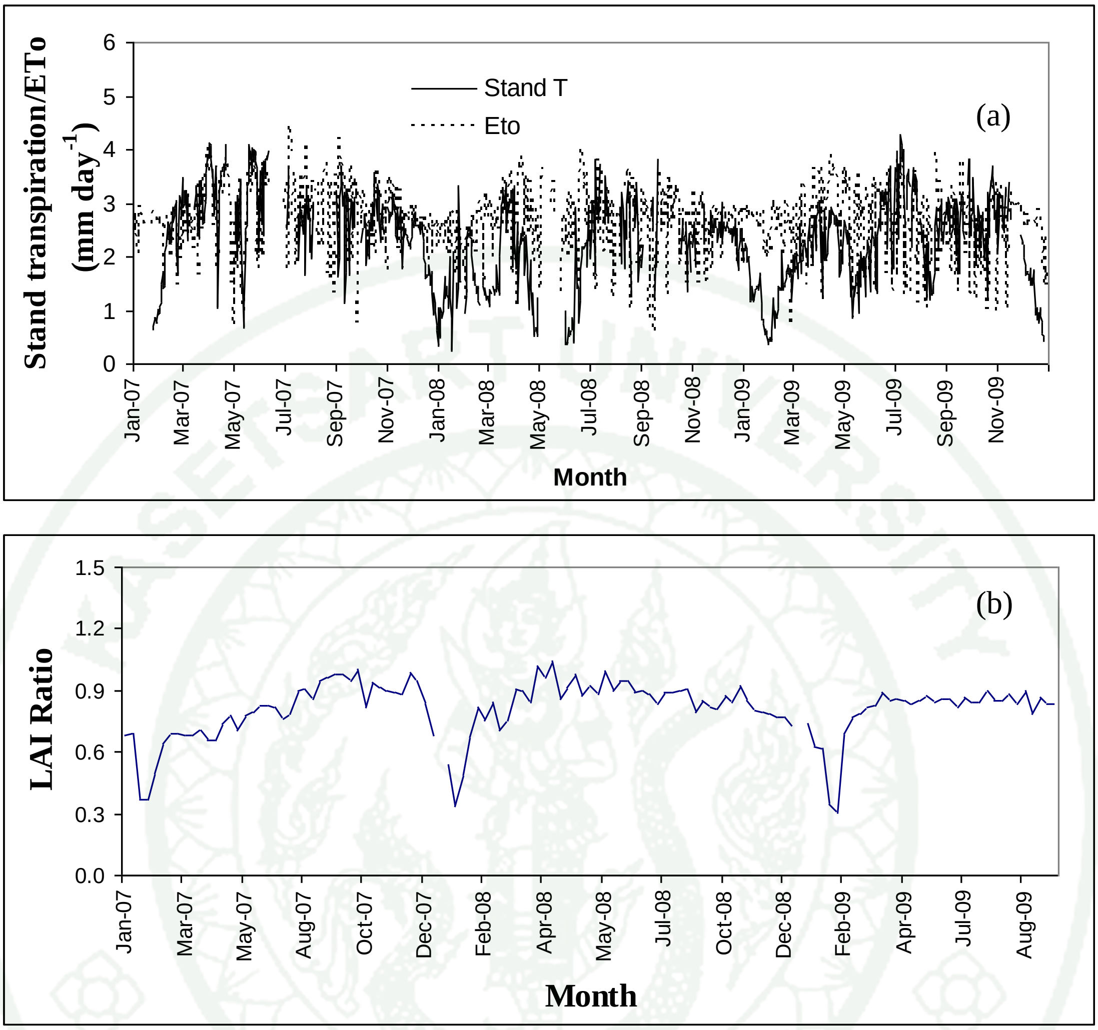

Figure 9 Seasonal variations of stand transpiration, evapotranspiration (ETo), and LAI ratio from January 2007 to January 2010: (a) daily stand transpiration (black line) and evapotranspiration (ETo, dotted line), and (b) LAI Ratio estimated from hemispherical photographs, 20 positions in the rubber plantation.

3.3 Relationship between stand transpiration and ETo, VPD and soil water content

Figure 10 showed that there was a relationship between daily stand transpiration and daily ETo. In well-watered condition during the rainy season, stand transpiration followed ETo. Conversely, stand transpiration was no related to ETo in the dry period in both the early and the end of the year when the leaves shedding occurred and returned flushing.

Figure 11 showed that stand transpiration was less related to maximum of VPD. Firstly, stand transpiration was high and varied with increasing VPD in the rainy season. Secondly, it was reduced as high VPD in the dry season for 3 years.

Figure 12 showed that the relationship between stand transpiration and soil water content. When soil water content was less than 15%, stand transpiration decreased rapidly in the dry season. There was no different in three years.

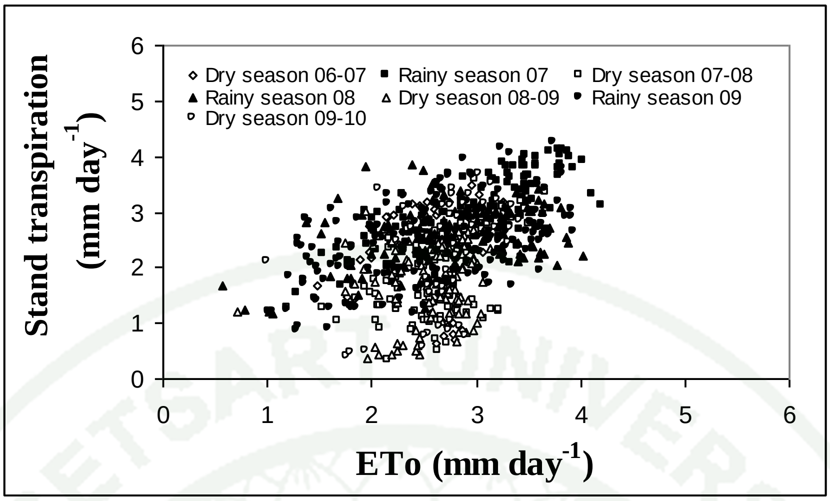

Figure 10 Plots of stand transpiration versus evapotranspiration (ETo). 3 years data from January 2007 to January 2010. Stand transpiration was calculated from sap flow measurement. ETo was calculated by Penman-Monteith equation and FAO recommended coefficients.

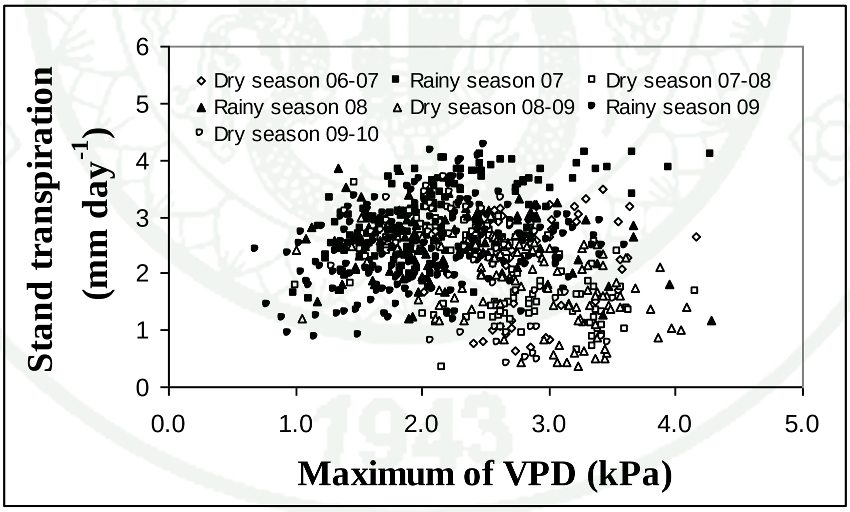

Figure 11 Plots of stand transpiration versus maximum of VPD. 3 years data from January 2007 to January 2010. Stand transpiration was calculated from sap flow measurement.

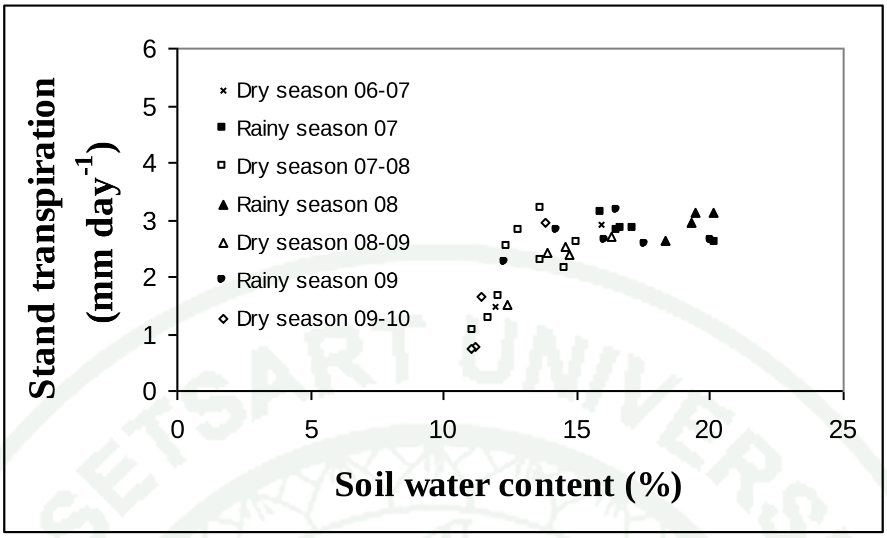

Figure 12 Plots of stand transpiration versus average of soil water content in different depths. 3 years data from January 2007 to January 2010.

Experiment 2 Transpiration and stomatal conductance of rubber trees in response to environmental variables

1. Environmental conditions and seasonal changes

The seasonal variations of environmental conditions during the experimental period were shown in Figure 13. The highly seasonal of water status in soil, plant and air were affected by rainfall event. The rainfall started in May. After that it varied throughout the rainy season. The rainfall declined at the end of the rainy season and stopped in the dry season (December). The cumulated amount of 1,085 mm was 15.76% below the long-term average of 10 years in this area (Figure 13a). Vapor pressure deficit (VPD) was high in the dry season (January and December), the maximum values was 1.8 kPa, but it was low in the rainy season (average 1.2 kPa) (Figure 11a). Soil water content was low in the dry season (10-12 %). When the rainfall events occurred in March, soil water content increased slightly first in the upper part of the soil. Later on, it remained high throughout the rainy season (16-20%) and declined at the end of the year during the dry season (Figure 13b).

2. Seasonal changes in plant water status

Leaf water potential expresses in plant water status. The seasonal variations of predawn leaf water potential (ψ_{predawn}) at 12, 14, 16, 18, and 20 m height, respectively was shown in Figure 13c. The values of predawn leaf water potential was high (-0.20 to -0.45 MPa) in the the rainy season when the rainfall events started and soil water content increased slightly. It was a little declined and was rather constant throughout the rainy season following the optimum soil water content (June to October). Then, it decreased slightly at the end of the year during the soil dried (the values reached -0.72 MPa).

3. Diurnal variation of environmental conditions, stand transpiration and stomatal conductance

Figure 14 showed the diurnal variation of net radiation (Rn) and VPD. Rn increased rapidly around 10 am in the morning. Maximum value of Rn appeared before midday. It decreased sharply in the afternoon. There were no difference of maximum Rn between April and August (680-700 Wm^{-2}), but higher than November (420 Wm^{-2}). Vapor pressure deficit (VPD) increased in the morning. Maximum value of VPD appears around noon. Then it decreased at the late afternoon. The maximum VPD was highest in April (2.8 kPa), and lower in August (1.8 kPa) and November (2.2 kPa). Time lags between VPD and Rn were about 5 hours in April, 2 hours in August and November.

Figure 15 showed the diurnal pattern of evapotranspiration (ETo), stand transpiration, and stomatal conductance for three days of intensive measurements on 6 April 2007, 31 August 2007, and 18 November 2007. ETo increased rapidly around noon whereas the peak of VPD appeared. It decreased in the afternoon. The maximum of ETo was higher in April and August (0.62 mm h^{-1}) than those in November (0.43 mm h^{-1}). Stand transpiration (T) increased in the morning as radiation and VPD increased. T generally reached maximum around midday and then it declined in the afternoon as low light level and high VPD. Stand transpiration was highest in April (0.45 mm h^{-1}), intermediate in August (0.4 mm h^{-1}), and lowest in November (0.3 mm h^{-1}). Similarly, stomatal conductance increased rapidly in the morning result from stomatal opening under condition of high radiation and high air temperature and low VPD (Figure 15b). Maximum g_s occurred around 10 a.m. before the occurrence peak of T. Ater that it declined more steeply after stand transpiration continued to increase until midday. Then stomatal conductance was more sensitive to climatic changes than stand transpiration. The maximum of g_s in August (461 $mmolm^{-2}s^{-1}$) was higher than in April (274 $mmolm^{-2}s^{-1}$) but was lowest in November (216 $mmolm^{-2}s^{-1}$). There were time lags between stomatal conductance and stand transpiration throughout the year.

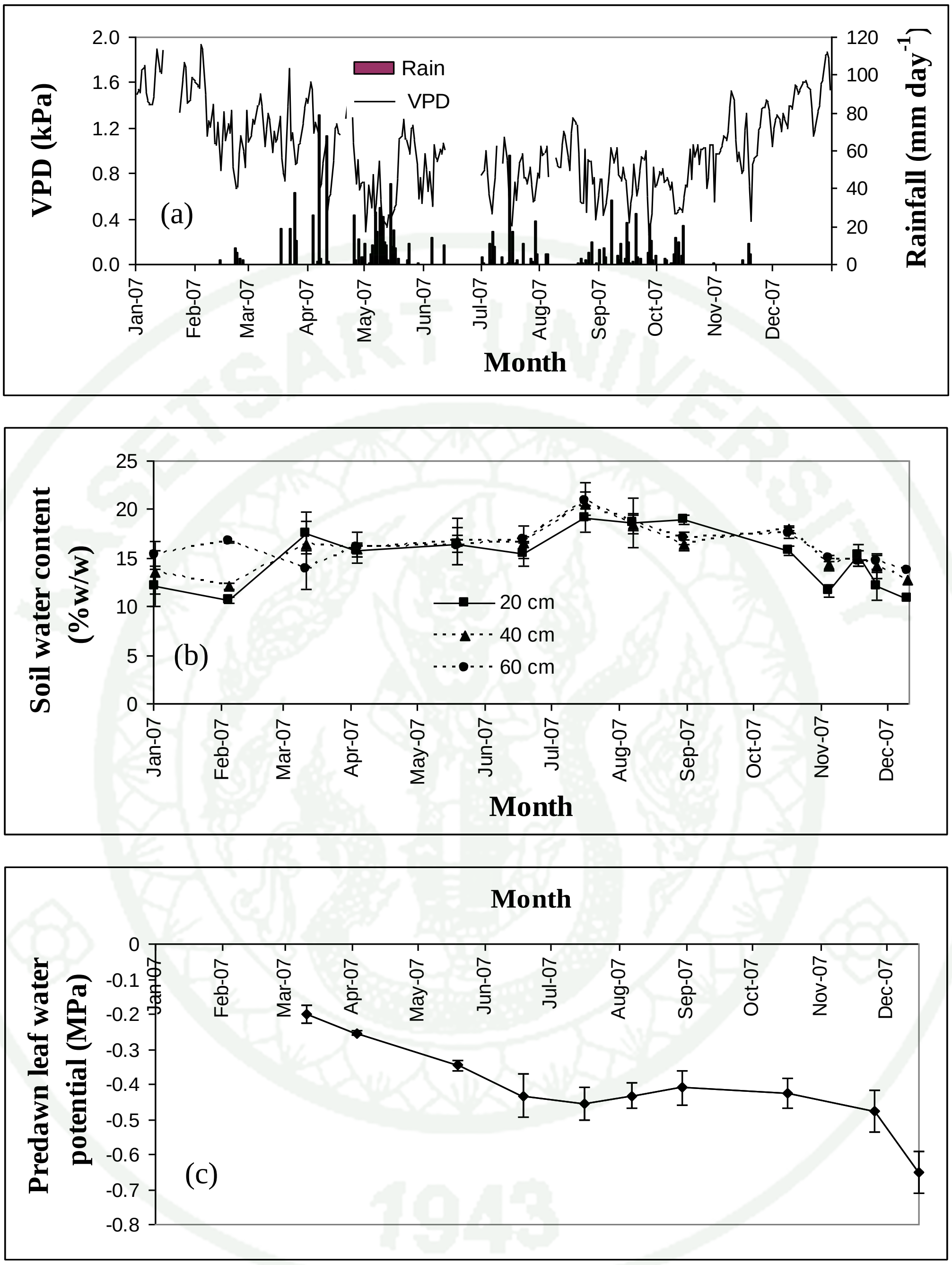

Figure 13 The environmental conditions and leaf water potential during January to December 2007: (a) rainfall (columns), vapor pressure deficit (VPD; blacked line), (b) soil water contents at 20 cm (closed square with black line), 40 cm (closed triangle with dotted line) and 60 cm depths (closed circle with dotted line), and (c) average of 2 individual rubber trees in leaf water potential at 12, 14,16,18, and 20 m height.

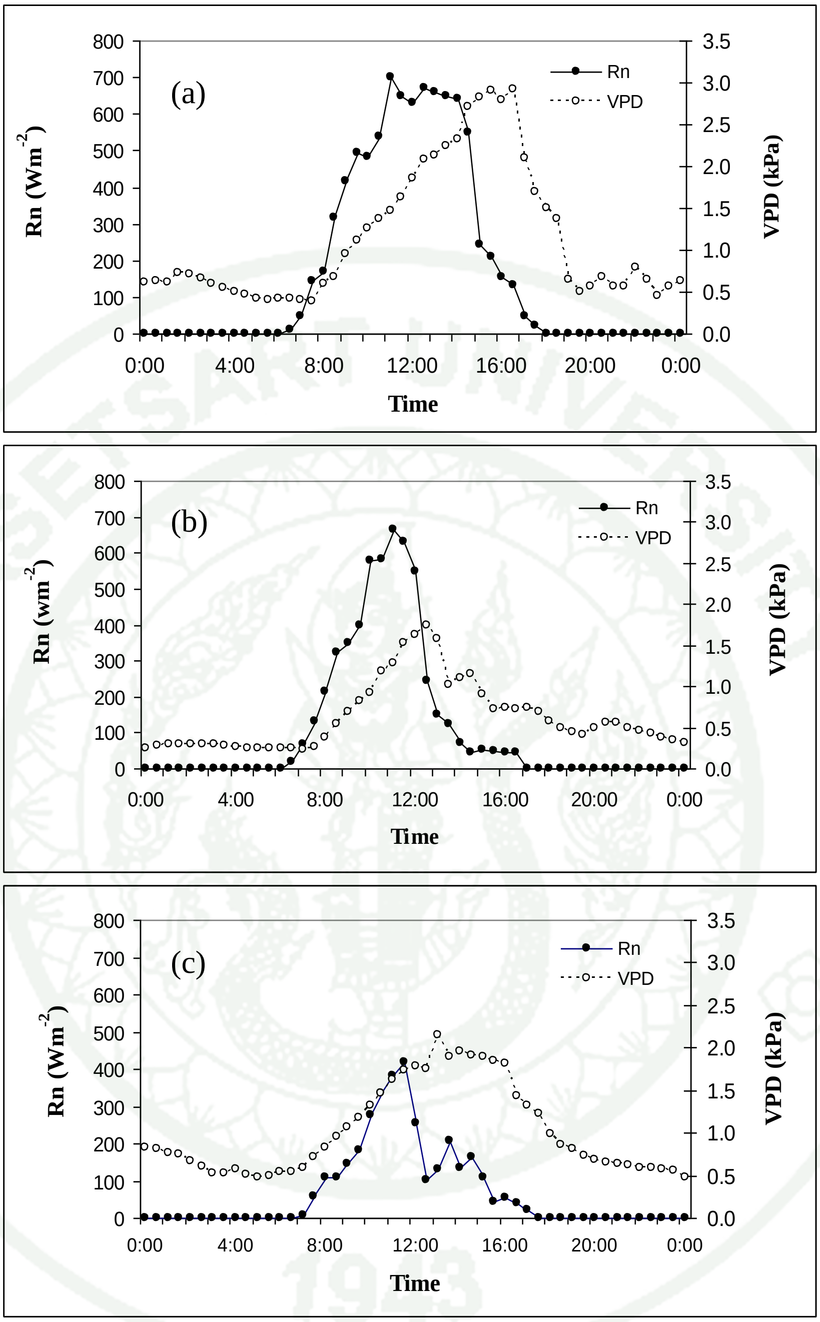

Figure 14 Diurnal variations of net radiation (Rn), and VPD during on (a) 6th April: the end of dry season, (b) 31st August: the rainy season, and (c) 18th November: the early of dry season.

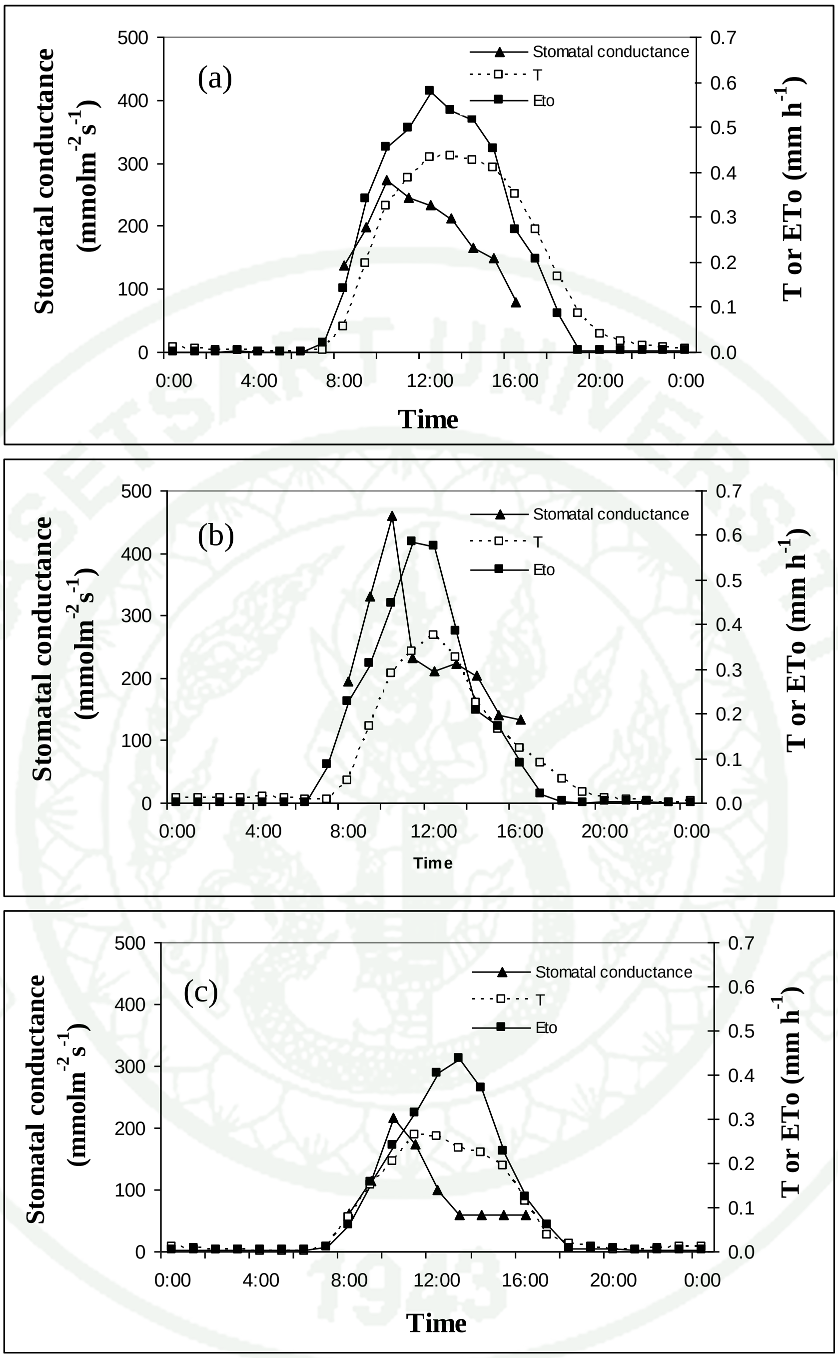

Figure 15 Diurnal variations of evapotranspiration (ETo, blacked line and closed square), stand transpiration (T, dotted line and empty square) and stomatal conductance ($g_{s,}$ blacked line and closed triangle) during on (a) 6th April: the end of dry season, (b) 31st August: the rainy season, and (c) 18th November: the early of dry season

4. Relationship between stand transpiration, stomatal conductance, evapotranspiration (ETo), radiation and VPD

The relationship between stand transpiration and evapotranspiration (ETo), Rn and VPD were hysteresis pattern. Diurnal stand transpiration (T) was a positively correlated with diurnal evapotranspiration (ETo) (Figure 14). A strong relationship between stand transpiration (T) and net radiation (Rn) was demonstrated in rubber trees (Figure 17). In addition, the results showed the relationship between T and VPD for the three measurement days (Figure 18). The degree of linear significant correlation between T and VPD (R^2 = 0.64-0.96) was generally higher than T and Rn (R^2 = 0.62-0.93). The relationship between T, ETo, radiation and VPD in the morning were greater than in the afternoon. Moreover, The relationship between T, ETo, radiation and VPD were low in the dry season.

Stomatal conductance (g_s) was strongly related to net radiation for three days, on 6th April 2007 (R^2 = 0.53), 31st August 2007 (R^2 = 0.90), and 18th November 2007 (R^2 = 0.70) (Figure 19). Stomatal conductance increased as radiation increased in the morning. Moreover, stomatal conductance was related to VPD on 6th April (R^2 = 0.59), 31st August (R^2 = 0.65) and 18th November (R^2 = 0.44) (Figure 20). The degree of diurnal correlation between g_s and Rn was greater than for VPD, indicating that diurnal g_s was more dependent on Rn. However, stomatal conductance declined in response to increasing VPD in the afternoon. The slope of the relationship between g_s and VPD reflected the sensitivity of stomatal to VPD. Then the higher stomatal sensitivity to VPD occurred in the rainy season and lower stomatal sensitivity appeared in the dry season. The stomatal closure occurred when VPD reached 2.2 kPa in the rainy season whereas stomata closed when VPD was more than 2.5 kPa in the dry season.

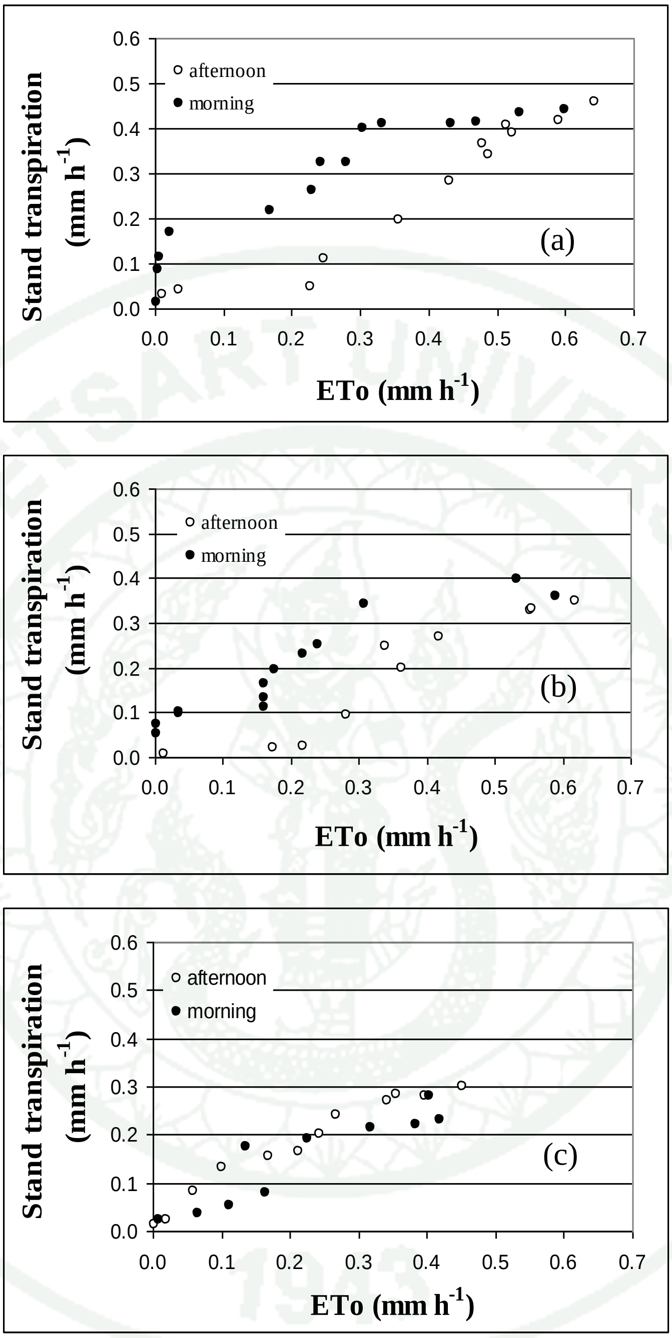

Figure 16 Relationship between diurnal stand transpiration estimated from sap flow measurements and diurnal evapotranspiration (ETo) on (a) 6th April 2007 (in the morning, R^2 = 0.94; in the afternoon, R^2 = 0.79), (b) 31st August 2007 (in the morning, R^2 = 0.96; in the afternoon, R^2 = 0.79), and (c) 18th November 2007 (in the morning, R^2 = 0.96; in the afternoon, R^2 = 0.80).

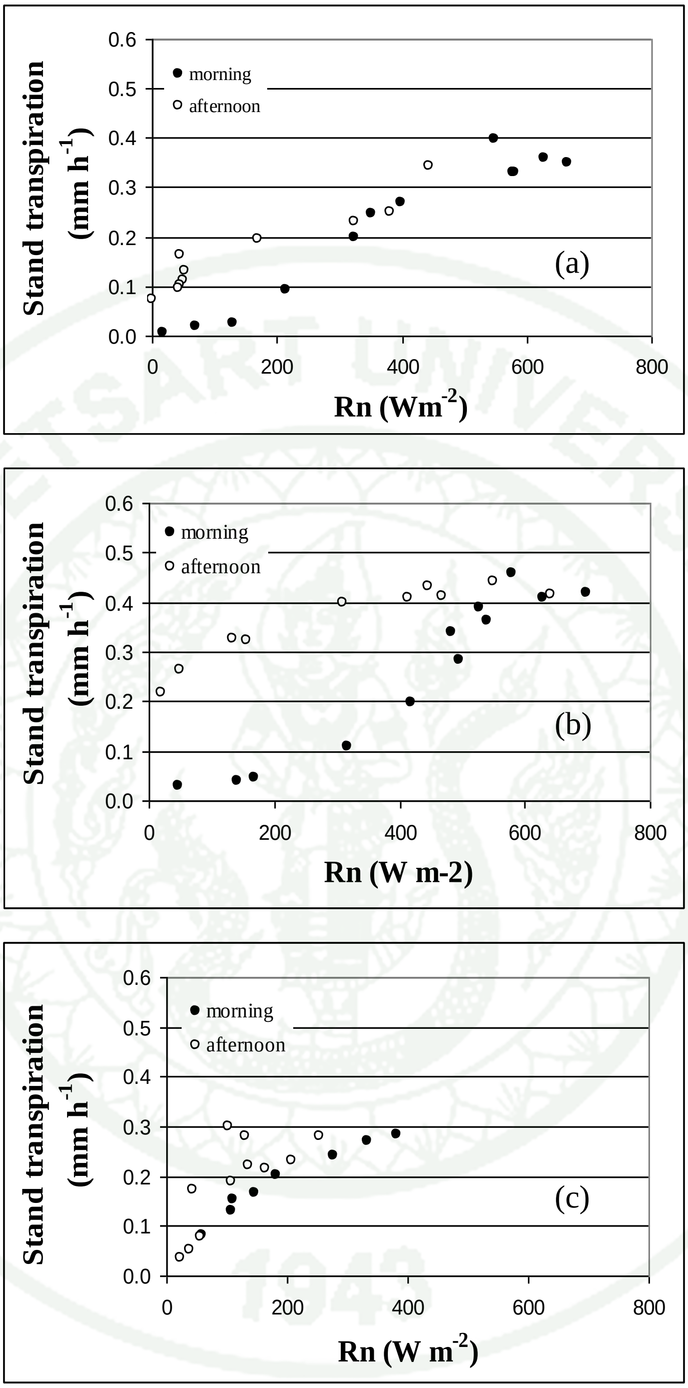

Figure 17 Diurnal relationship between stand transpiration and net radiation (Rn) on (a) 6th April 2007 (in the morning, $R^2 = 0.93$; in the afternoon, $R^2 = 0.62$), (b) 31st August 2007 (in the morning, $R^2 = 0.91$; in the afternoon, $R^2 = 0.88$), and (c) 18th November 2007 (in the morning, $R^2 = 0.87$; in the afternoon, $R^2 = 0.65$).

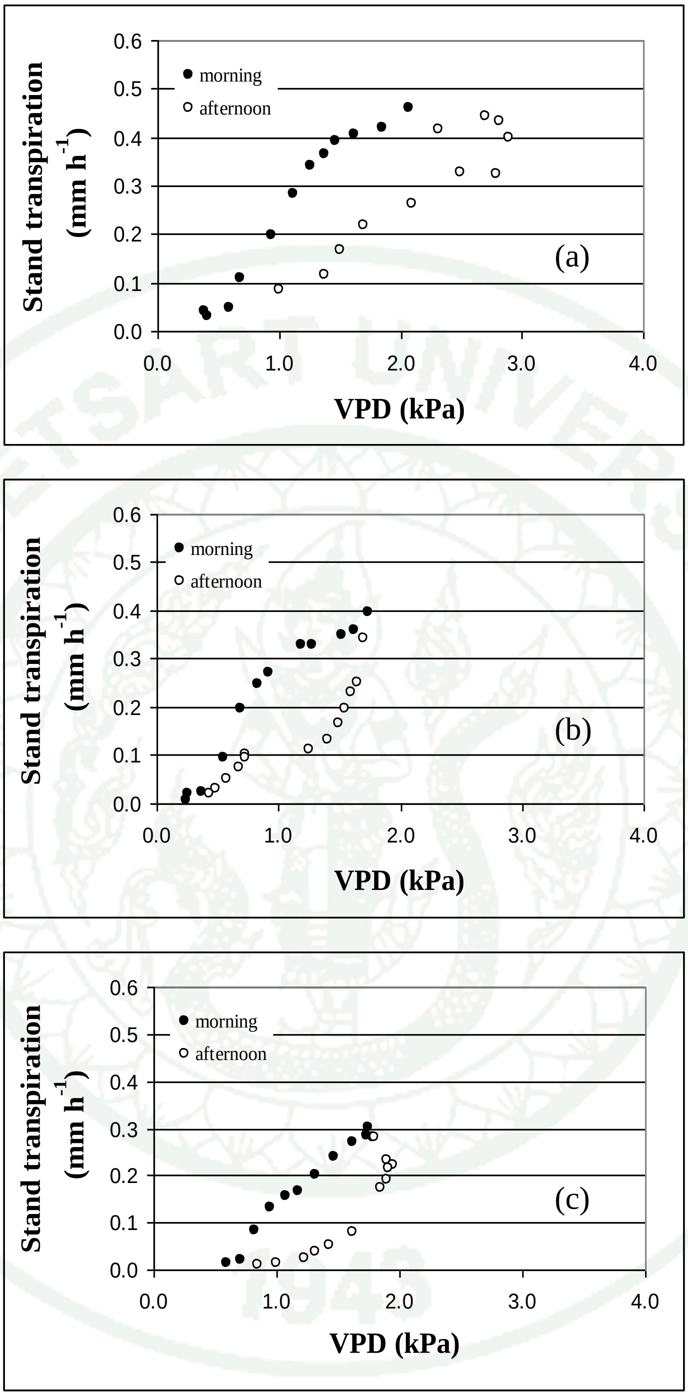

Figure 18 Diurnal stand transpiration and vapor pressure deficit (VPD) on (a) 6th April 2007 (in the morning, R^2 = 0.96; in the afternoon, R^2 = 0.79), (b) 31st August 2007 (in the morning, R^2 = 0.94; in the afternoon, R^2 = 0.92), and (c) 18th November 2007 (in the morning, R^2 = 0.97; in the afternoon, R^2 = 0.64).

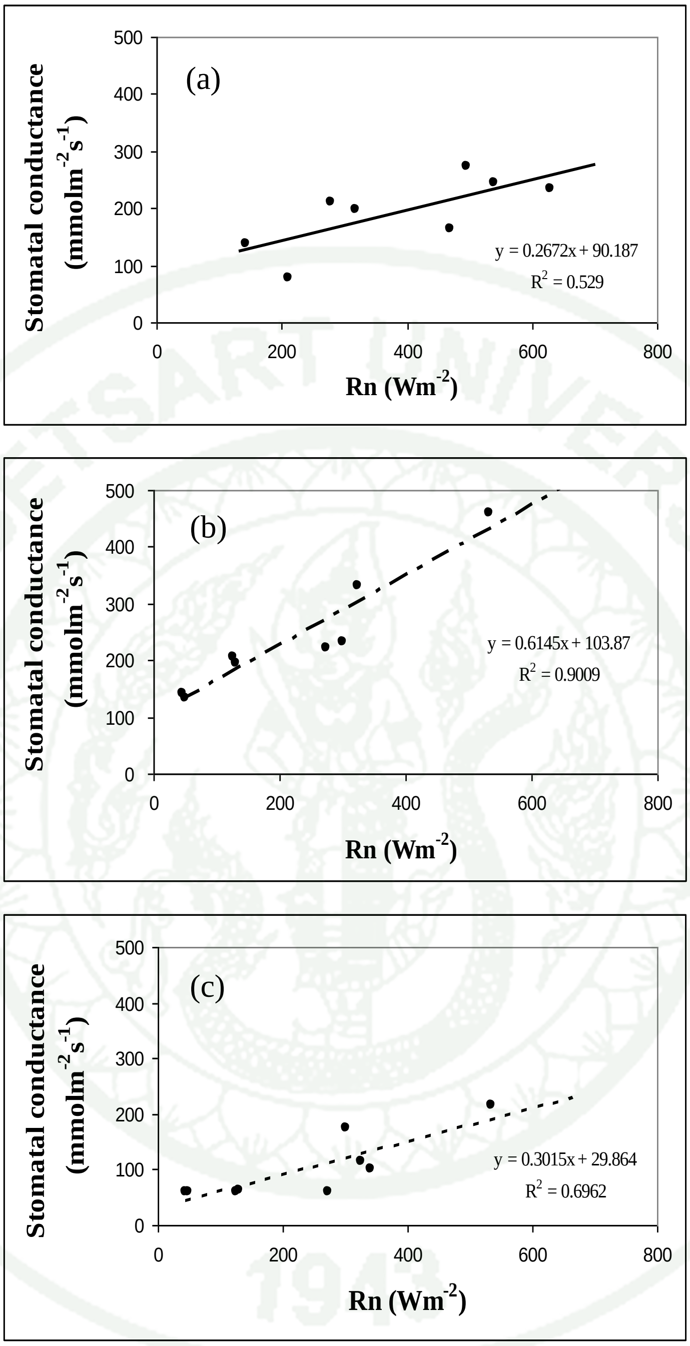

Figure 19 Diurnal relationship between diurnal stomal conductance (g_s) and net radiation (Rn). Stomatal conductance was measured using Li-Cor 6400 on individual leaves of four rubber trees in each day on (a) 6th April 2007 (R^2 = 0.53), (b) 31st August 2007 (R^2 = 0.90), and (c) 18th November 2007 (R^2 = 0.70). The line indicates the respective curve regression between g_s and Rn of three days.

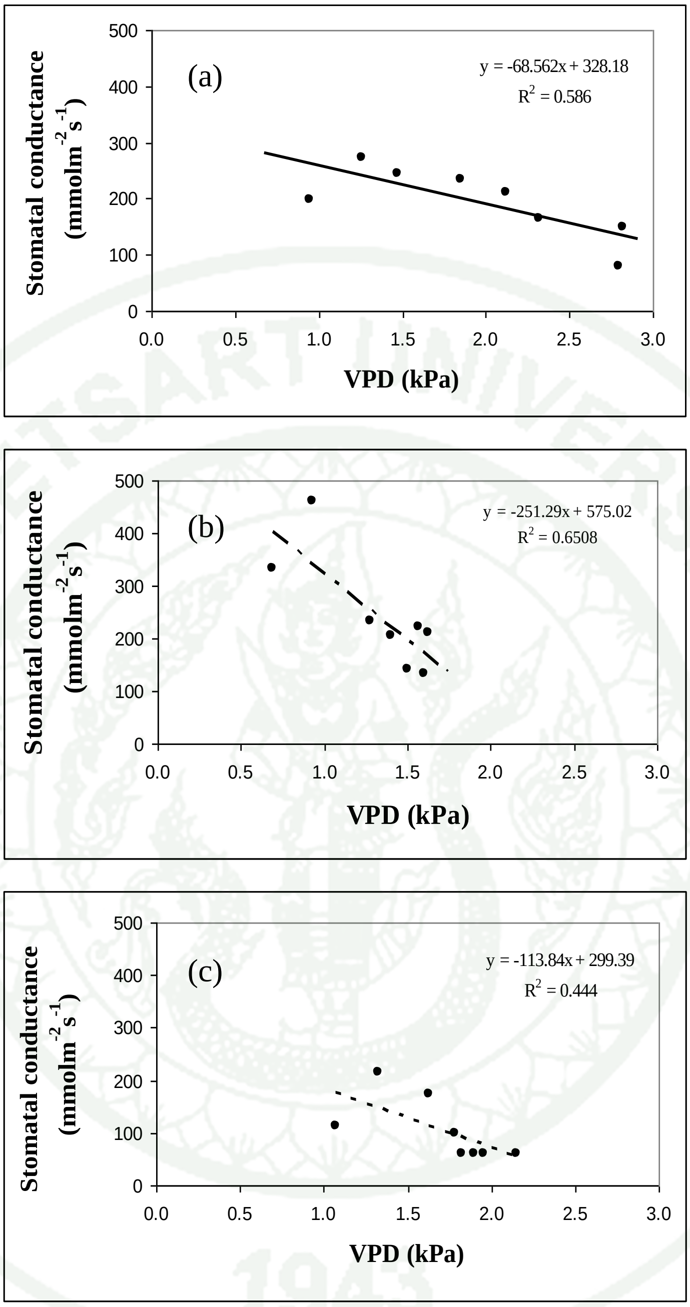

Figure 20 Diurnal relationship between stomal conductance (g_s) and vapor pressure deficit (VPD). VPD was calculated from air temperature and relative humidity. Stomatal conductance was measured using Li-Cor 6400 on individual leaves of four rubber trees in each day on (a) 6th April 2007 (R^2 = 0.59), (b) 31st August 2007 (R^2 = 0), and (c) 18th November 2007 (R^2 = 0.29). The line indicates the respective curve regression between g_s and VPD of three days.

Experiment 3 The effect of tapping activity on plant water relation in rubber trees

1. Seasonal variation of environmetal conditions and plant water status

Figure 21 showed that there was no rain from November to February. Rainfall started in May and varied from 2 to 36 mm day^{-1} during the rainy season. The rain dropped in August. Evapotranspiration (ETo) was varied largely from 1.05 to 4.10 mm day^{-1}. ETo decreased after the onset of the rainy season when rainfall dropped in August. Despite full canopy, stand transpiration showed similarly pattern to ETo. Stand transpiration was generally high at the onset of rainy season (3.5 – 4.0 mm day^{-1}). However, stand transpiration dramatically decreased to 1.2 mm day^{-1} during the rainy season in August when the rain stopped. In the dry season, stand transpiration declined slightly whereas ETo also declined strongly as minimum stand transpiration during defoliation period.

Soil water content changed along the year. Soil water content increased in March after rainfall occurred and it was high at the early of the rainy season. After that it dramatically decreased from 23 % to 13 % in June, July and August. Soil water content declined slightly from 15% to 10% at the onset of the dry season. Soil water content in 40 cm was highest values in the dry season. There was no difference in soil water content among any depths of soil.

Figure 22 showed that predawn leaf water potential ($\psi_{predawn}$) was high and stable in the rainy season, values ranging between -0.35 and -0.30 MPa. However, the value of predawn leaf water potential dropped in August (-0.42 MPa) following the soil water stress and then it increased at the end of the rainy season. Predawn leaf water potential decreased strongly in the dry season. It ranged from -0.72 to -0.35 MPa. Midday leaf water potential (ψ_{midday}) was high and rather constant in the rainy season (between-1.1 and -1.2 MPa). In contrast, Midday leaf water potential was unaffected by change in soil water content in the rainy season after that it decreased slightly from -1.55 to -1.2 MPa in the dry season. There was no difference in predawn leaf water potential ($\psi_{predawn}$) and Midday leaf water potential (ψ_{midday}) between tapped tree and untapped tree.

Seasonal variation of percent loss of hydraulic conductance (PLC) was shown in figure 23. PLC increased continuously from 26.5 to 45% at the early of the rainy season and was rather constant between 45.6 and 47.5% in the rainy season, after that it increased slightly from 47.5 to 55.5% in the early of the dry season. There was no difference in PLC between tapped tree and untapped tree (p-value = 0.56).

Seasonal variation of whole tree hydraulic conductance was shown in figure 24. Whole tree hydraulic conductance (gL) was high and varied between 5 and 6 l $dm^{-2}h^{-1}$ MPa^{-1} throughout the rainy season and then it decreased strongly from 5 to 0.3 l $dm^{-2}h^{-1}$ MPa^{-1} in the dry season. There was no difference in whole tree hydraulic conductance (gL) between tapped tree and untapped tree (p-value = 0.85).

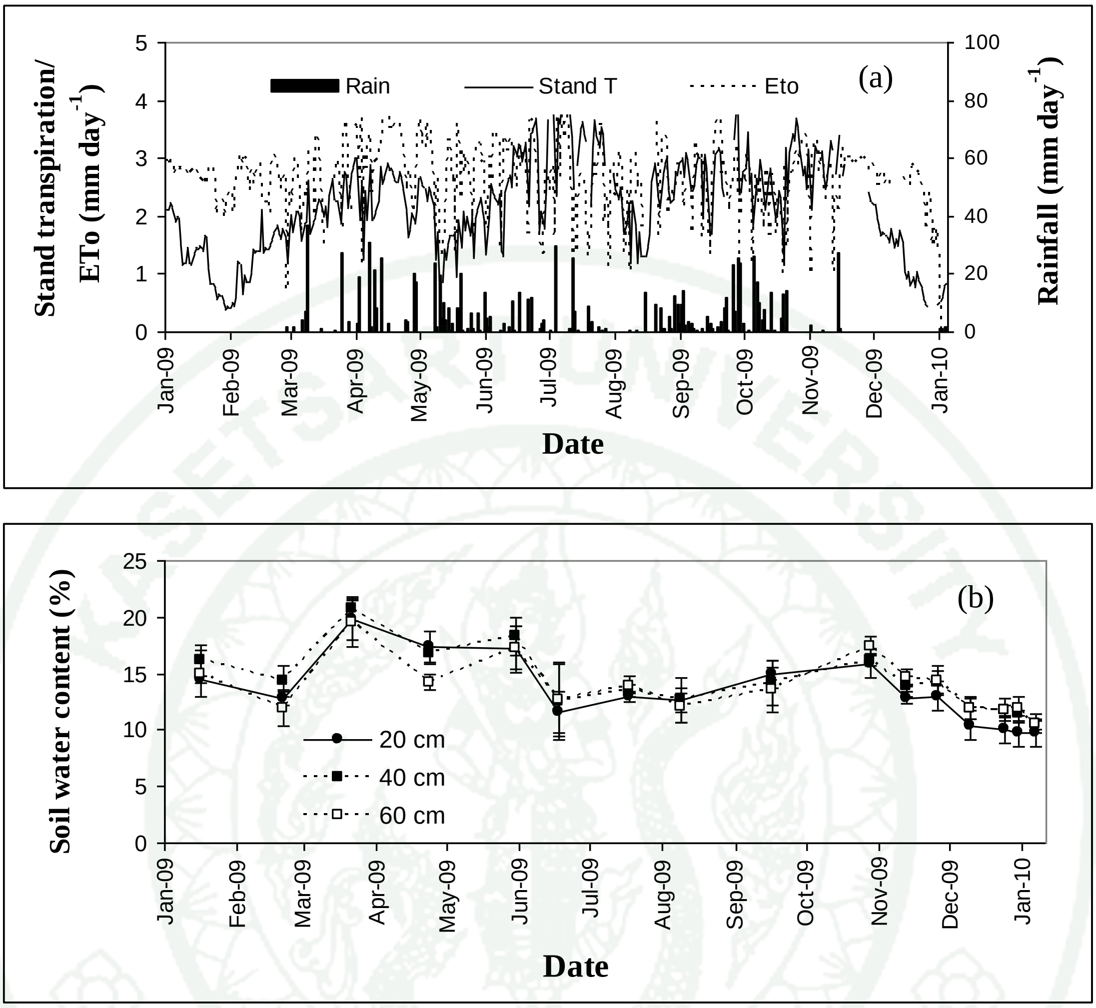

Figure 21 Daily variations of stand transpiration and evapotrnaspiration (ETo) from January 2009 to January 2010. (a) Rainfall (columns), evapotranspiration (ETo; dotted line) and stand transpiration (black line), and (b) Soil water content at 20 cm (closed circle with black line), 40 cm (closed square with dotted line) and 60 cm (opened square with dotted line).

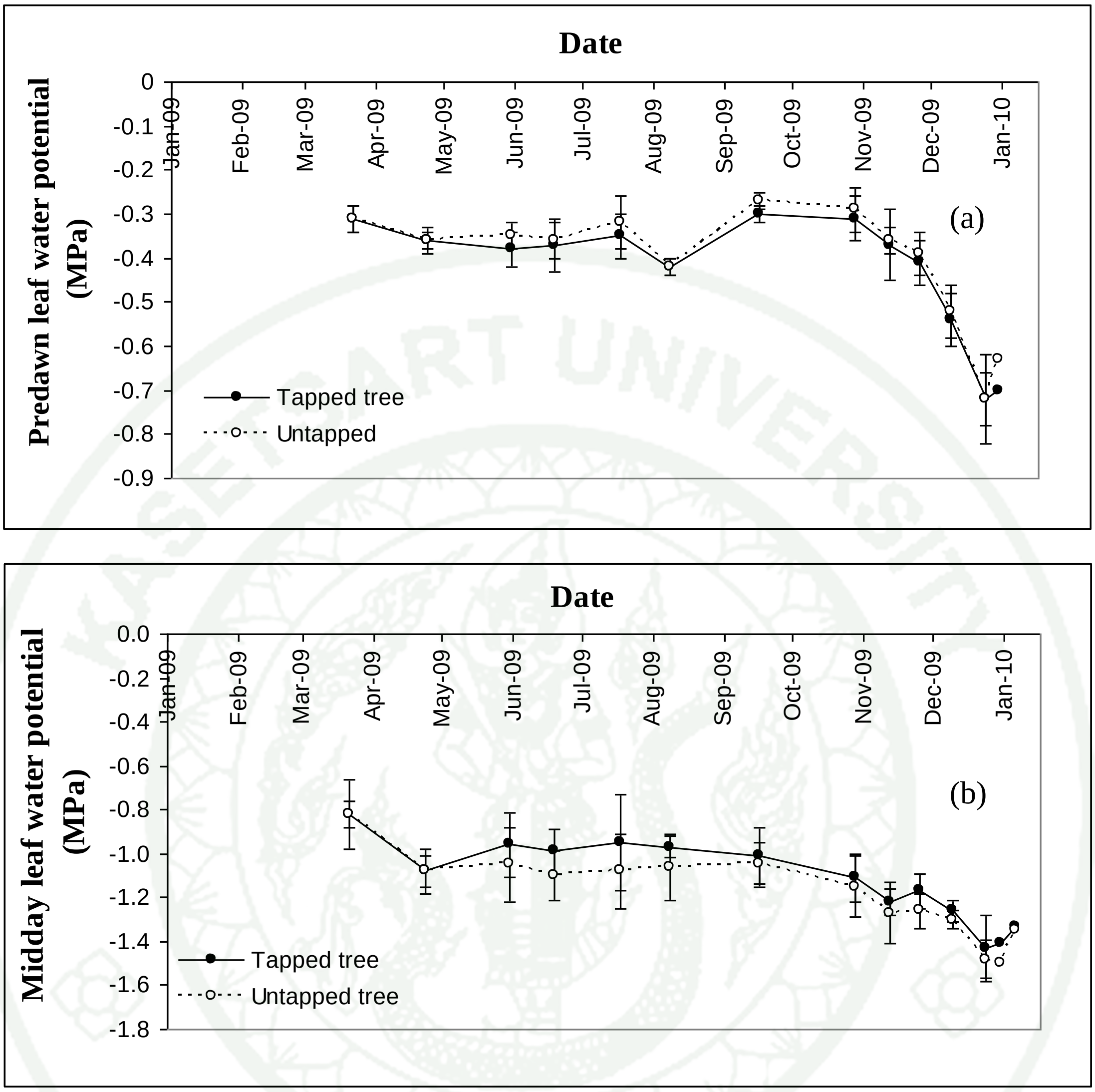

Figure 22 Seasonal variations of predawn and midday leaf water potentials of both tapped and untapped trees from March 2009 to January 2010: (a) predawn leaf water potential, and (b) midday leaf water potential. We measured from 6 tapped trees and 6 untapped trees. There was no significant between tapped and untapped trees. Black vertical bars represent the standard error, N = 12 (N is the leaf samples of each treatment).

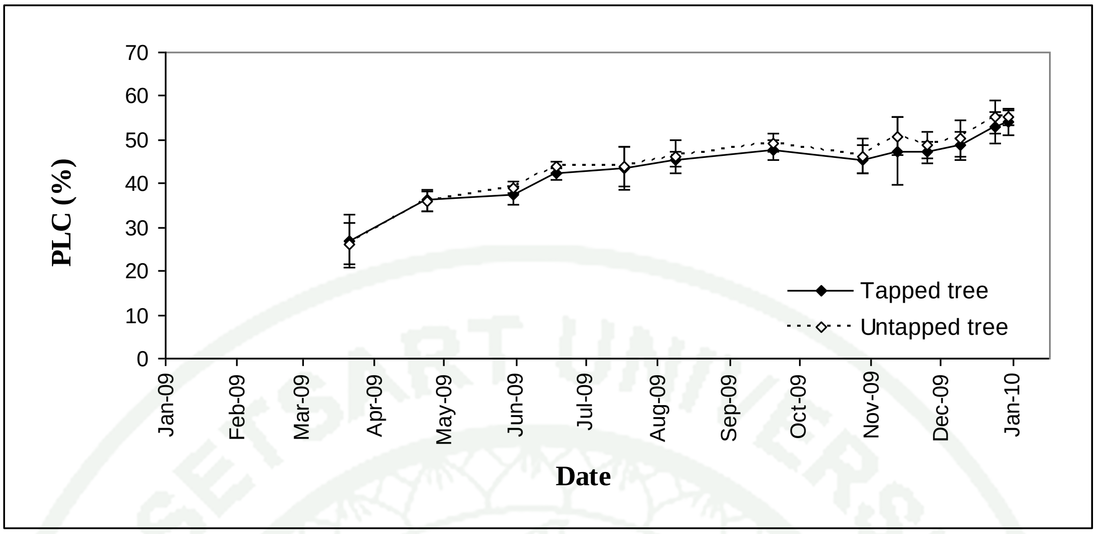

Figure 23 Seasonal variation of percent loss of hydraulic conductance (PLC) of rubber trees from March 2009 to January 2010. We measured from 6 tapped trees and 6 untapped trees. There was no significant between tapped and untapped trees. Black vertical bars represent the standard error, N = 12.

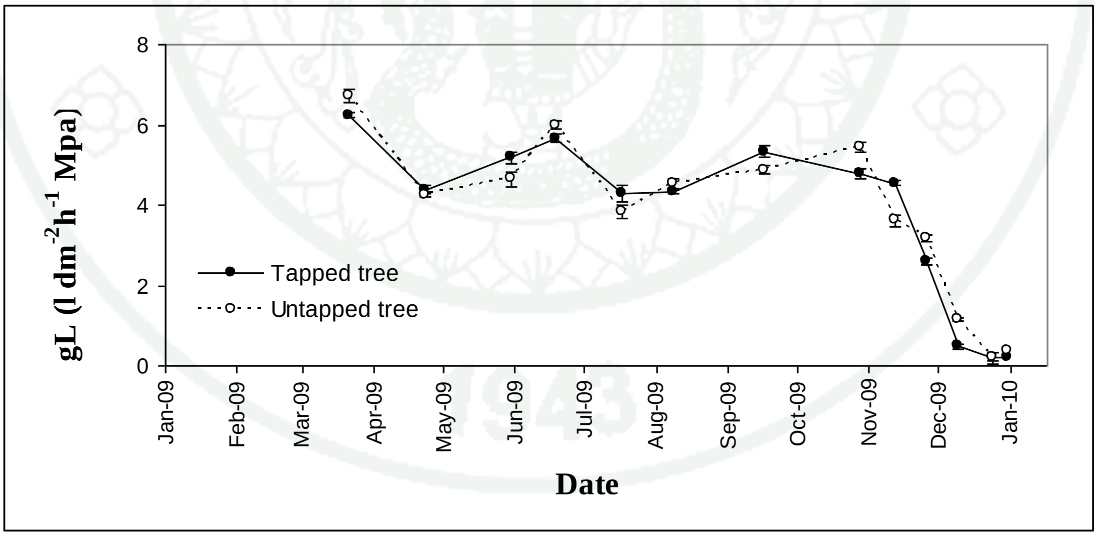

Figure 24 Seasonal variations of the whole tree hydraulic conductance (gL) of rubber trees from March 2009 to January 2010. gL was calculated from concurring measurements of sap flow rate and leaf water potential in the same time.

2. Relationship between stand transpiration, leaf water potential, PLC and soil water content

Predawn leaf water potential ($\psi_{predawn}$) was strongly related to soil water content in both tapped and untapped trees (Figure 25). Predawn leaf water potential ($\psi_{predawn}$) remained stable in the rainy season whereas it decreased in the dry season.

Percent loss of hydraulic conductance (PLC) was related to midday leaf water potential (Figure 26). Fifty percentage of embolism was obtained in the petioles for leaf water potential between -1.55 and -1.30 MPa in the dry season.

Stand transpiration was strongly linear related to predawn leaf water potential ($\psi_{predawn}$) in both tapped and untapped trees (Figure 27). Stand transpiration increased whereas predawn leaf water potential ($\psi_{predawn}$) also increased.

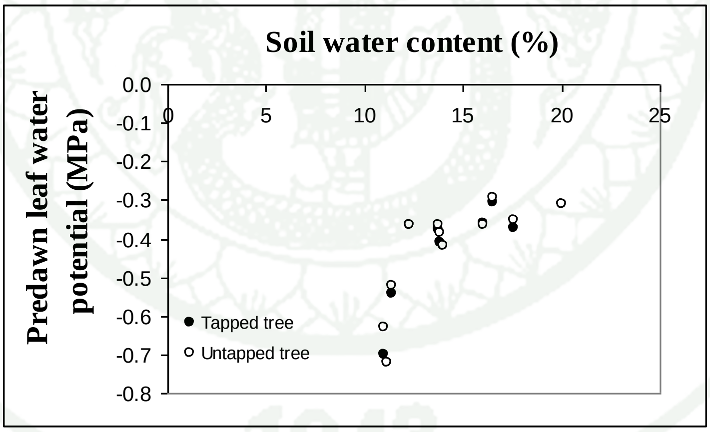

Figure 25 The relationship between predawn leaf water potential ($\psi_{predawn}$) and soil water content along the year.

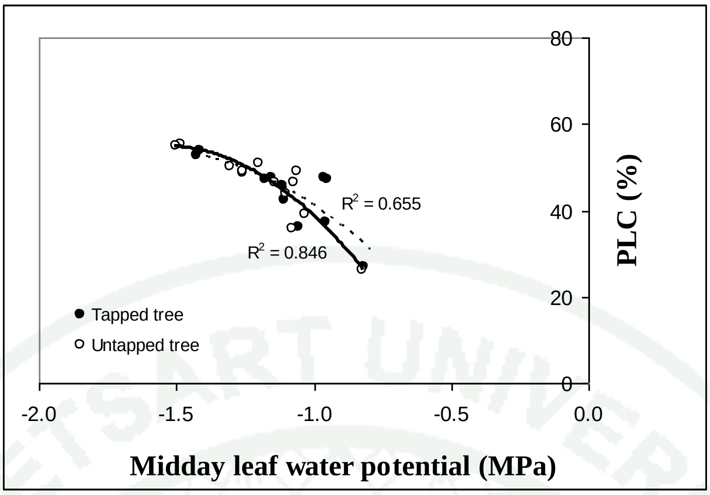

Figure 26 The relationship between midday leaf water potential (ψ_{midday}) and percent loss of hydraulic conductance (PLC). The line indicates the regression of tapped trees (R^2 = 0.846) and the dotted line indicates the regression of untapped tree (R^2 = 0.655).

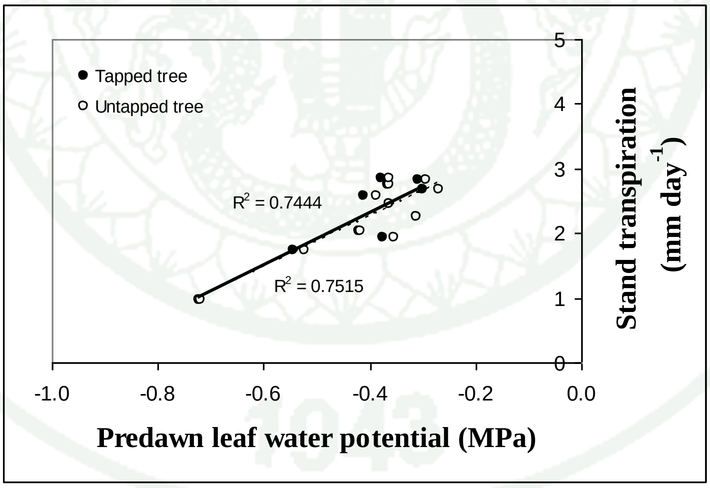

Figure 27 The relationship between stand transpiration and predawn leaf water potential (ψ_{predawn}) along the year. The solid line indicates the regression of tapped trees (R^2 = 0.744) and the dotted line indicates the regression of untapped tree (R^2 = 0.752).

3. Relationship between whole tree hydraulic conductance and PLC, stomatal conductance, and predawn leaf water potential

Figure 28 showed that whole tree hydraulic conductance (gL) was correlated with percent loss of hydraulic conductance (PLC), stomatal conductance (g_s) and predawn leaf water potential ($\psi_{predawn}$) in both tapped and untapped trees. The values of PLC decreased while gL increased. Whole tree hydraulic conductance started to decrease after PLC reached 50%. The values of hydraulic conductance (gL) increased while stomatal conductance (g_s) also increased. Stand transpiration increased whereas $\psi_{predawn}$ also increased.

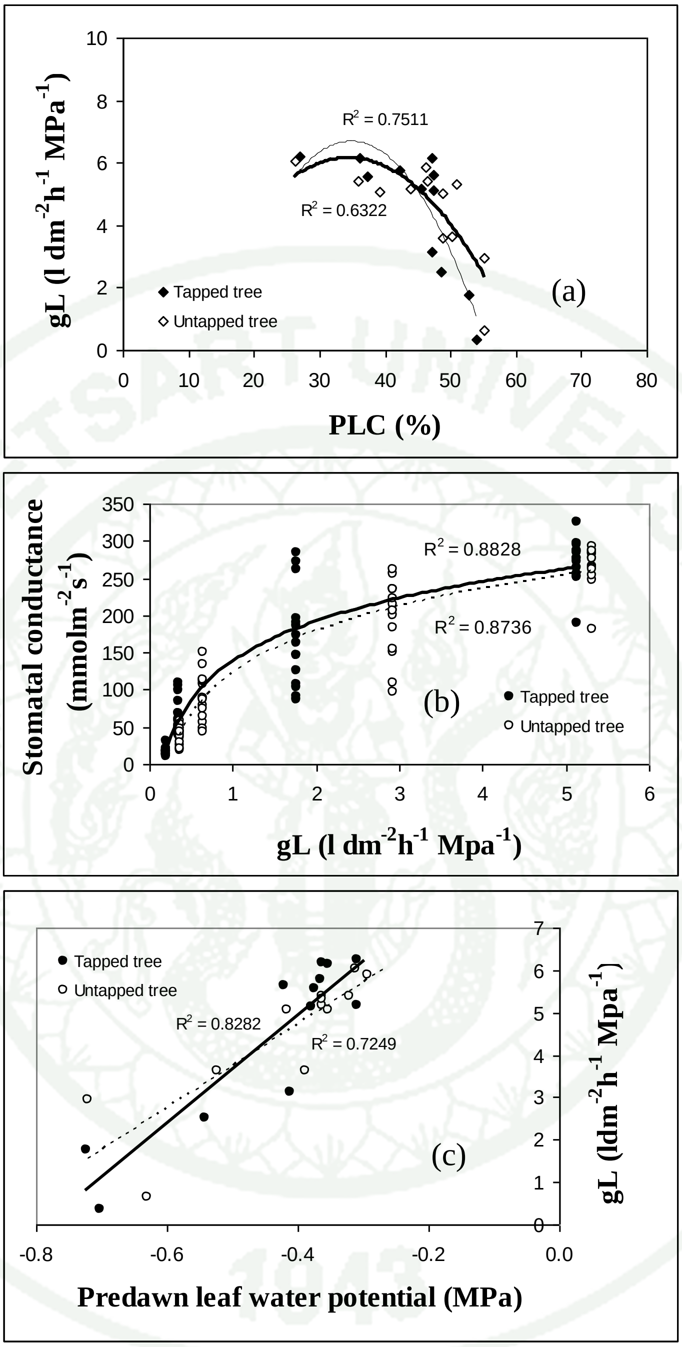

Figure 28 The relationship between whole tree hydraulic conductance (gL) and percent loss of hydraulic conductance (PLC, a), stomatal conductance (g_s, b) and predawn leaf water potential ($\psi_{predawn}$, c) in both tapped tree and untapped trees. The solid line indicates the regression of tapped trees and the dotted line indicates the regression of untapped tree.

4. Effect of tapping activity on plant water status and yield

Figure 29 showed the dynamics of sap flux density (Js) of both tapped and untapped tree in rubber tree. Before tapped activity started, sap flux density of both tapped and untapped tree were no different. During well-watered conditions, sap flux density of both tapped and untapped tree were also no different. However, sap flux density of tapped tree was lower than untapped tree during the dry season.

Figure 30 showed that stomatal conductance (g_s) rapidly reduced in the dry season. The value of g_s decreased strongly from 276 to 16.5 mmol $m^{-2}s^{-1}$. The variation of stomatal conductance was similar to whole-tree hydraulic conductance in the dry sesson. There was no difference in g_s between tapped and untapped trees at the early of the dry season, but g_s of tapped tree was significant lower than untapped tree during defoliation period in the dry season.

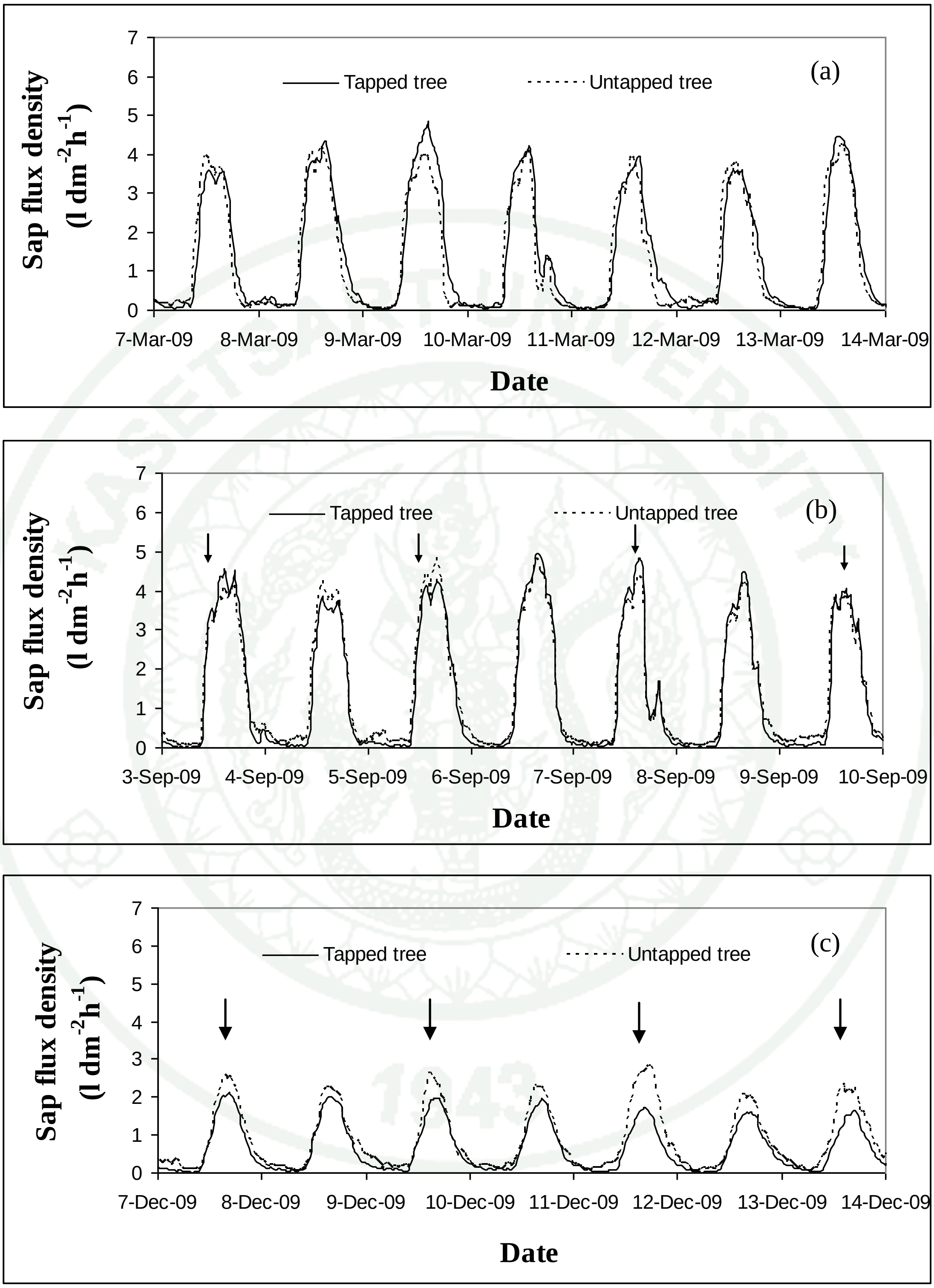

Figure 29 Diurnal courses of sap flux density (Js) for tapped and untapped rubber trees. (a) before tapping activity**,** (b) during well-watered conditions, and (c) during the dry season. The arrows express the tapping days.

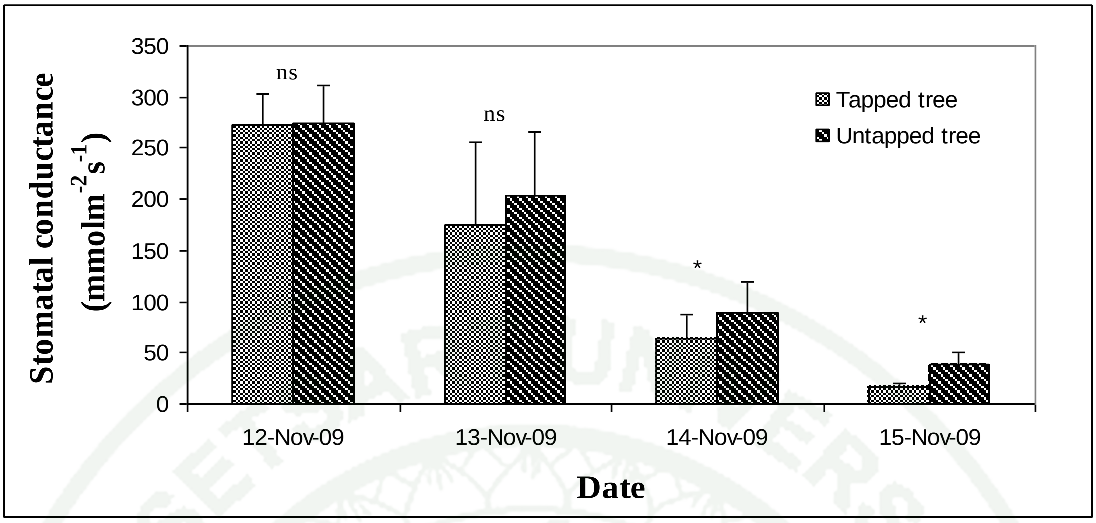

Figure 30 The values of leaf stomatal conductance (g_s) started after the rainfall stopped at the early of the dry season. Values are mean ±SE (n=10) an asterisk (*) indicates a significant difference at $P<0.05$ between tapped and untapped trees. Abbreviations: ns = no significant.

DISCUSSION

Experiment 1 Sap flow measurement of rubber (*Hevea brasilliensis* Muell. Arg.) trees

1. Sap flow measurement and estimates stand transpiration

1.1 Calibration the probes in the laboratory

The calibration of home-made probes were carried on the cut stem of rubber tree with CTD method by Granier (1985). The shape of the curve was similar to that reported by Roupsard *et al*. (2006) and the coefficients (α, β) were very close to the calibration obtained with sawdust when expressed in m^3 m^{-2} s^{-1} (Figure 3). These results showed that calibration is independent of woody species. We assumed that the calibration coefficients of sap flow probe are similar in many type of trees but also artificial medias (Lu *et al*., 2004). Conversely, the calibration curve of these probes was different from the calibration curve obtained in the same species by Isarangkool Na Ayutthaya *et al*. (2010) who showed a strong linear relationship between K and sap flux density. The calibration by Isarangkool Na Ayutthaya *et al*. (2010) used the Transient Thermal Dissipation method by Do and Rocheteau (2002). In the transient conditions, the temperature signal became time-related. It was the difference between the temperature reached at the end of the heating period and the temperature reached after the cooling period. For the CTD method, the flow index was considered as the ratio of signal at zero flow to the signal at measured flow. However, the results showed that the variability between the different cut stems and between the different probes was in the same range, similarly to the results with TTD method (Isarangkool Na Ayutthaya *et al*., 2010). The variability between cut stem samples tested with the same probe may have different causes. Firstly, the probes may be inserted partly in non-conductive sapwood. The error may occur when small stem or branches of fast-growing species are incorrectly assumed to be comprised entirely of sapwood. The risk is lower in *Hevea* than in ring-porous species where sapwood layer can be less than 20 mm in depth (Swanson, 1994; Phillips, 1996). Clearwater *et al*. (1999) suggested that the best approach for heat dissipation methods may be use relatively short probes and to avoid contact with inactive xylem. Secondly, the variability may result from a more or less tight contact between the probe and the sapwood. ΔT is a good indicator of such contact. The variations of ΔT within the same cut stem reflected mainly the variations of heat dissipation by conduction according to the quality of contact between probe and sapwood (Isarangkool Na Ayutthaya *et al*., 2010). Thirdly, variability can result from variable water flow around the circumference of individual cut stem. Lu (1997) described a method to reduce this error: two sets of heat dissipation probes were inserted in the same cut stem, in parallel to provide mean ΔT. Fourthly, gradients in sap flow may occur along the length of the heated probe and that may lead to underestimation of sap flow. The error can be minimized by using shorter probes. (Clearwater *et al*., 1999). Finally, McCulloh *et al*. (2007) demonstrated that a rather large inter tree variability can occur when the responses of CTD method is compared with gravimetric measurement. Then, a large number of samples is necessary to better calibrate CTD probes with cut stem experiments. As the species or artificial medium used for calibration seem to have little effect, the best way to calibrate a given type of CTD probes could be to combine new sets of data with previously published data obtained with the same kind of probes.

1.2 Spatial variation in sap flux density in stem

Preliminary experiment was set to adjust the heat dissipation method to rubber tree. The results showed that no significant natural vertical gradient was observed between the needles of a given probes. However, these small natural thermal variations occur everyday around dawn, which seems to indicate that they are artifacts from ambient thermal gradients which were directly exposed to sunlight on the trunk, it is possible related to the “morning peak” reported by Lu *et al*. (2004). This verification is critical because in case of important natural variation between two needles, the estimated sap flux density would have been much more complex. It would be required a parallel monitoring of the natural thermal gradient on each tree (adding another probes with no heating) (Verdier, unpublished data). Therefore, the constant power supply to the heating element is required. It is also desirable that heating system is based on constant current voltage to avoid the effect of the variation in natural vertical gradient (Lu *et al*., 2004).

We found that the significant azimuthal variations were obtained on around all trees. It was similar to the reported by Lu *et al*. (2000) in mango trees. azimuthal variations often depends on the canopy or branches exposed sunlight in the forest stand (Granier, 1987). Peak of sap flux density appeared around noon of different branches. In addition, the sap flow rate in the main stem will be a composite of all branches. Moreover, the relative position between the heated needles and large branch (or scar of a removed branch) seemed to exert the most influence on circumferential variation in sap flow in the trunk (Lu *et al*., 2000). Sap flow in large branch was higher than small branch. Then, sap flow of the trunk, a position close to the large branch was higher than the other sides. In addition, Sap flow in the trunk, a position close to girdling branch decreased while sap flow at the trunk on the opposite side of the girdling branch increased slightly (Lu *et al*., 1998). The xylem system in one branch could be connected more effectively to a specific zone of xylem tissue in the trunk (Lu *et al*., 1998). As a result, whole tree sap flow may be integrated in the trunk following branch manipulation. azimuthal variation in sap flux density was closely correlated with soil water content and root system (Lu *et al*., 2004). In the rainy season, sap flux density is highest in the shallow roots and in the outer stem xylem on the trunk. In contrast, when the soil was dry, the deep root and the inner stem xylem was highest flow rate. For the radial profile around the trees is highly asymmetric radial pattern because the differences in conducting activity of sapwood layer (Nadzhdina *et al*., 2002). Therefore, it is necessary to use more than one probe on each tree during the long-term monitoring. However, the relationship between two probes on the both North and South side of same tree were more than the other sides. Then the results suggested we should install the two probes on the North and South.

Although differences were not significant, the daily sap flux density was slightly higher at 1.80 m than at other heights. Because sap flux density below 1.80 m was closely related to the tapping panel. Then the sap flux density was lower than at the higher level. Rubber tree trunks are straight and short main trunk with low axial variations of the trunk's radius, it is reasonable no difference in sap flux density. In this case, it close to the first branches (around 3 m height), or close to the ground because root or branches would probably be deviated the xylem vessel (Verdier unpublished data). It may also be equilibrium between branch and trunk water conductive system (Lu *et al*., 2000).

Changes in sap flux density were closely correlation with different depth into the xylem of the stem. Values of sap flux density was high at 2-4 cm and decreased toward the center of the stem. Possibly, the outer xylem is very active for sap flow whereas the conductive xylem at the center of the sapwood is less active. Nevertheless, the conductive functions of the active sapwood differed within the tree (Nadezhdina *et al*., 2002). Isarangkool Na Ayutthaya *et al*. (2010) showed the xylem area in rubber tree was schematically divided into four rings: the outer ring comprised between 100% and 60% of xylem radius, the intermediate ring between 60% and 30%, the inner low-conducting ring between 30% and 5% and non conductive pith. Therefore, The results were assumed that the differences in sap flux density occurred in the radial variations within the stem that sap flux density is usually high, close to the cambium and declines in the old sapwood (Swanson, 1994). The patterns of radial variation in sap flux density along the sapwood were observed in many tree species (Hotton *et al*., 1995; Phillips *et al*., 1996; Lu, 1997; Lu *et al*., 2000; Ford *et al*., 2004). The radial profiles can be grouped into two types. The first showed a peak in sap flux density about 0-4 cm beneath the cambium. The second showed a more even profile, beyond 6 cm below the sapwood, both groups of profiles were similar (Lu *et al*., 2000). The maximum sap flux density appeared in the outer sapwood because the outer xylem often connects the leaves exposed to sun whereas low sap flux density in deep layer of sapwood may reflect an undeveloped conducting system at the center of the stem (Nadezhdina *et al*., 2002). This research improved the model of sap flux density. The model showed that sap flux density of young xylem (outer xylem) was high and stable whereas the sap flux density of old xylem (inner xylem) decreased linearly toward the center of the stem.

1.3 Seasonal variation of stand transpiration and ETo

ETo is driven by the meteorological conditions (Pereiera *et al*., 2006). In addition, ETo is always directly related to soil moisture content and LAI (Guardiola-Claramonte, 2010). ETo inducing saturating transpiration appeared in the rainy season, during well-watered soil condition. However, some peaks of transpiration saturated above the value of ETo at low ETo as the same reported by Isarangkool Na Ayutthaya (2010). The results found that some peaks of transpiration reduced on rainy days because transpiration stopped when the foliage was wet according to low ETo and rain occurrence (Granier, 1987). Conversely, ETo was high whereas transpiration decrease slightly in the dry season. During the dry season water consumption is mostly governed by environmental variables that directly affect rubber phenology, vapor pressure deficit, temperature and radiation (Guardiola-Claramonte, 2010).

During the year, seasonal change in stand transpiration reflected both leaf phenology and climatic conditions. The leaf flushing occurred in February that followed by increasing transpiration during the dry season. After return pre-flushing, root growth appeared in the deep soil. In addition, water can remove from deep to shallow roots at night when soil surface is dry (Caldwell *et al*., 1998). It is an important strategy for tree survival in the dry conditions. When the rainfall occurred in March, the fine root density was obtained in the top soil layer (Gonkhamdee *et al*., 2009). They could increase soil to root conductance. After leaf flushing, rubber trees increased the hydraulic conductance of leaves due to the development of the new xylem conduits for the new leaves (Isarangkool Na Ayutthaya, 2010).

Furthermore, stand transpiration was generally high and rather constant in the stable full canopy (maximum LAI) that obtained in the rainy season. In at time, LAI is maximum and constant leaf area index and close to optimum soil water availability. Leaf area is a key factor of whole-tree transpiration when the soil water is non-limiting factor. During vegetation completely shades the ground, it can be assumed that the transpiring surface is equivalent to the ground area (Pereira *et al*. 2006). Similarly, in oil palm, Dufrene *et al.* (1992) found transpiration response to large LAI when the soil water level was close to field capacity. Despite well-water soil conditions, transpiration did not follow evaporative demand and saturated above a critical value of ETo. The results found that some peaks of transpiration reduced on rainy days because transpiration was limited when the foliage was wet according to low ETo and radiation, and rain occurrence (Granier, 1987).

Stand transpiration was slightly decreased during defoliation period (December). It is possible that conductance is limited. During drought period, soil water content decreased. The decreasing of the soil water movement to root and declining contact between soil and roots might be the cause of this event (Isarangkool Na Ayutthaya, 2010). The period of leaf senescence and shedding change in hydraulic conductance of whole trees. Because the stage of leaf senescence preceding leaf shedding, the trees can form the abscission zone in the petiole (Taiz and Zeiger, 2006). This abscission zone can induce to decrease the hydraulic conductance between of twigs and leaves. Leaf yellowing and shedding should reduce the total hydraulic conductance (Isarangkool Na Ayutthaya, 2010). Hydraulic system in rubber tree is high vulnerability to cavitation (Sangsing *et al*., 2004). The results suggested that stomatal control of transpiration has been monitored during the drought (Cruiziat *et al*., 2002). Stomatal closure occurs during the period of soil drought to prevent water potential falling to dangerous level and risking serious xylem dysfunction (Frank *et al*., 2007). Transpiration rate decreased with increasing soil water deficit (Roupsard *et al*., 2006).

1.4 Relationship between stand transpiration and ETo, VPD and soil water content

ETo can be used to predict transpiration of the trees. ETo is driven by the meteorological conditions and it depends on plant and soil water status (Pereiera *et al*., 2006). Stand transpiration was high and very close to ETo value around 3 mm day^{-1} at the end of the rainy season according to the low VPD and high radiation. Transpiration of a forest stand depends on interactions between environmental variables and stomatal behavior of the plants (Meinzer *et al*., 1997). Therefore, increasing the radiation loaded on the leaf was due to an increase in stomatal conductance (Pieruschka *et al.*, 2010). Gururaja Roa *et al*. (1990) showed that the mature rubber trees did not saturating transpiration under high evaporative demand. They found high transpirations in the dry season. However, stand transpiration steadily declined during the dry season when the soil water content was less than 15%. The minimum of stand transpiration reached 0.5 mm day^{-1} at the end of December. The transpiration decreased during the dry season due to high VPD and soil water deficit (Wullschleger *et al.*, 2001). Stomatal closure corresponded to high VPD that occurred to prevent minimum leaf water potential above a critical value (Cochard *et al.*, 1996; Sperry *et al.*, 2002). Transpiration rate decreased with increasing soil water deficit (Roupsard *et al.*, 2006). Stand transpiration was high and stable when the soil water content was more than 15%. This might be caused by the stomatal aperture occurred following low VPD and high soil moisture during the rainy season.

Experiment 2 Transpiration and stomatal conductance of rubber trees in response to environmental variables

2. Responses of plant water status to environmental variables

2.1 Seasonal changes of plant water status

Plant water status is the dynamic property and would be changed following water availability in soil and atmosphere. Leaf water potential is the thermodynamic expression, which is a reliable indicator of plant water status (Kramer and Kozlowski 1979; Larcher, 2001). Predawn leaf water potential was high and remained constant in the rainy season and after that it decreased slightly in the dry season in response to increasing soil water deficit. This pattern was similar to the report in mature rubber trees by Isarangkool Na Ayutthaya (2010) found that predawn leaf water potential ranged between -0.44 and -032 MPa in the well-water period. It slightly decreased -0.47 to -0.54 MPa in the mid drought period and reached -0.72 to -0.83 MPa at the peak of drought. O' Grady *et al*. (2008) found that the decline in predawn leaf water potential in several species correlated with increasing VPD and decreasing soil water availability in the dry season. It provides a strong evidence of the existence of a critical minimum leaf water potential as soil water stress and is consistent with isohydric regulation of plant water status (West *et al*., 2007). As predawn leaf water potential declined, maximum stomatal conductance also declined in the dry season (Figure 1c and 3b). Leaf water potential is regulated by stomatal conductance that observed in many species (Myers *et al*., 1997). Sangsing (2004) shown a strong relationship between stomatal conductance and leaf water potential in young rubber tree clone RRIM 600 and RRIT 251. Tree regulates stomatal apertures to avoid excessive loss of water and maintain leaf water potential above a critical threshold, protecting the xylem cavitation (Tyree and Sperry, 1989; Sperry, 2000; Cochard *et al*., 2002; David *et al*., 2004).

2.2 Diurnal variation of climatic conditions, stand transpiration and stomatal conductance

Diurnal stand transpiration (T) and leaf stomatal conductance (g_s) were similar pattern (Figure 15). The variations in stand transpiration and stomatal conductance occurred throughout the day and. The results were obtained that the maximum g_s occurred around 10 a.m. following high radiation and low VPD in the morning. The maximum T appeared around midday whereas g_s continued to decrease with increasing VPD. Thus stomatal conductance was more sensitive to climatic variations than stand transpiration. The results implied that T and g_s decreased in the afternoon and the dry season. Stomatal closure occurred to limit transpiration despite high VPD and low soil water content (Meinzer, 1993; Franks, 2004). Thereby, water loss through transpiration was regulated by stomatal and driven by atmospheric demand (Jackson *et al*., 2000). We monitored actual transpiration from leaves representative outside the canopy, exposed to the sun by stomatal conductance, while the stand transpiration was estimated from sap flow measurement at the stem and integrated with foliage throughout the canopy. There were time lags between stomatal conductance and stand transpiration. Stand transpiration in April was higher than those in August and November according to high VPD and radiation. Stand transpiration and stomatal conductance were lowest in November at the early of the dry season. The results may be caused by xylem cavitation that reduces the xylem hydraulic conductivity and impairs the water transport to the leaves. Moreover, there was a strong limitation of transpiration with increasing VPD resulted from progressive stomatal closure as high VPD and soil water deficit (Bovard *et al*., 2005).

We found a strong linear relationship between stand transpiration and reference evapotranspiration (ETo) (Figure 16). Poyatos *et al*. (2005) found that daily stand transpiration was a strong linear relation to ETo in a partial only.

2.3 Relationship between stand transpiration, stomatal conductance, ETo, radiation and VPD

Transpiration was mainly regulated by radiation and VPD. There was a strong relationship between stand transpiration and net radiation (Figure 17). If Rn is low, transpiration may decrease despite high VPD (Meinzer *et al.*, 1997). Stand transpiration exhibited in relation to VPD (Figure 18). The peak of stand transpiration was correlated with VPD. This result may suggest the time lags of T response to VPD. The gradient of water vapor between inside the stomata and ambient air drives transpiration. This may suggest that VPD controls the magnitude of daily water uptake. It was found that stand transpiration increased with increasing VPD (O’ Grady *et al.*, 1999; Motzer *et al.*, 2005; Granier *et al.*, 1996; Wullschleger *et al.*, 2000). And it decreased at high VPD (Cunningham, 2004). The relationship between stand transpiration, ETo, radiation and VPD in the morning were greater than in the afternoon. Increasing radiation leads to increase in transpiration. Therefore, stand transpiration and ETo increased rapidly in the morning with increasing Rn and VPD. However, transpiration generally declined despite high VPD in the afternoon.

Stomatal conductance was regulated by radiation and VPD. Stomatal conductance was related to radiation (Figure 19). This result showed stomatal sensitive to radiation. The maximum stomatal conductance affected radiation-induced stomatal opening shortly after sunrise when radiation increased and VPD was low (Will and Teskey, 1999). Therefore, increasing the radiation loaded on the leaf increased stomatal conductance (Pieruschka *et al.*, 2010). However, there was a relationship between stomatal conductance and VPD (Figure 20). Stomatal conductance decreased strongly in the afternoon with diminishing sunlight and high VPD that induced stomatal closure. (Motzer *et al.*, 2005). The curves of relationship between stomatal conductance and VPD may be revealed as the result of a stomatal closure response to increasing VPD, supporting a mechanism to maintain tree transpiration (Montieth, 1995; David *et al.*, 2004). It is commonly observed that greater sensitivity is associated with higher maximum g_s at low VPD and well-watered conditions. Conversely, it appears that lower stomatal sensitivity to VPD is correlated with low rainfall and high VPD (Oren *et al.*, 1999; Cunningham, 2004). Rubber trees showed high stomatal sensitivity to VPD in the rainy season and low stomatal sensitivity to VPD in the dry season.

Experiment 3 The effect of tapping activity on plant water relations in rubber trees

3. Plant water status in responses to environmental conditions and tapping activity

This results might be suggested the regulation of plant water status following the variation of soil water content and environmental conditions. Moreover, tapping activity may affect water relation in rubber trees.

3.1 Responses of transpiration to environmental conditions

Evapotranspiration (ETo) and stand transpiration increased at the end of the dry season when leaves were mature, with high stomatal conductance, some rains, and high soil water content. ETo inducing saturating transpiration appeared during well-watered conditions. However, stand transpiration did not follow to ETo as the same results reported by (Isarangkool Na Ayutthaya, 2010) and other species (David *et al*., 2004). Our results showed that ETo and stand transpiration decreased in August, due to soil water stress during the rainy season. Because the plant are necessary to limit the loss of water from plant tissue by closing their stomata as soil water limitation (Jackson *et al*., 2000). This suggests that soil water stress in the rainy season and the onset of the dry season induced decreasing of stand transpiration in rubber trees. However, ETo was high and constant whereas transpiration decrease slightly during the dry season.

3.2 Responses of leaf water potential to environmental conditions

Predawn leaf water potential ($\psi_{predawn}$) is often used as indicator of soil water potential or soil water availability in the root zone (Frank, 2007). For instance, Ansley *et al*. (1992) found the relationship between predawn and soil water content. $\psi_{predawn}$ increased at the end of the dry season after rainfall started, while soil water content increased. Then $\psi_{predawn}$ decreased in August following the soil water stress. Midday leaf water potential (ψ_{midday}) remained rather constant throughout the rainy season. This pattern expressed an isohydric behavior which maintains leaf water potential above a critical value (West *et al*., 2007). The value of ψ_{predawn} and ψ_{midday} under soil water stress (November and December) were closely to soil water content in the dry season. The reduction in leaf water potential would cause cavitation in the xylem during the dry season (Sperry, 2000). In addition, leaf water potential is regulated by stomatal conductance. Then stomatal closure appear to maintain leaf water potential above the critical threshold (Oren *et al*., 1999). Moreover, reduction of transpiration through stomatal regulation could decrease leaf water potential.

3.3 Responses of whole tree hydraulic conductance and PLC to environmental conditions

The rubber tree started to have embolism in the xylem at the beginning of leaves after the leaves return to mature. The rubber tree was high vulnerable to embolism (Sangsing *et al*., 2004). PLC remained rather constant in the rainy season, according to high soil water content and increasing the whole tree hydraulic conductance. However, PLC tended to increase at the end of the rainy season. When the soil water content dropped in August that induced embolism occurrence in the xylem although rainfall occurred in September. 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 values, following soil water stress (Sperry and Tyree, 1988; Cochard *et al.* 1996). The results from the relationship between PLC and ψ_{midday} suggest that rubber trees are likely to induce embolism in the xylem vessel as minimum leaf water potential below a critical threshold. Sangsing *et al*. (2004) found the values of 50% of embolism in the petioles when midday leaf water potentials were between -1.5 and -2.0 MPa. Under drought conditions, there is a relationship between stomatal function and plant hydraulic (Sperry *et al*., 2002; Cochard *et al*., 2002). The loss of hydraulic conductance induced stomatal closure that caused the cavitation in the xylem (Sperry, 2000). Stomatal closed during the period of soil drought as it prevents water potential falling to dangerous level and risking serious xylem dysfunction (Frank *et al*., 2007).

Whole tree hydraulic conductance (gL) was high after the new flushing leaves returned to mature leaves in rubber trees. In this time, the root growth obtained in the subsoil (Gonkhamdee *et al*., 2010). The process of leaf and root developing can increase the relative contribution of hydraulic conductance of the soil to root and root to canopy. However, gL decreased during the rainy season, due to soil drought in August. The decline of gL decreased the soil to root conductance and decreased contact between soil and roots (Isarangkool Na Ayutthaya, 2010). gL started to decrease after PLC reached 50%. The xylem embolism developed in the petioles and reduced the xylem hydraulic conductance (Tyree and Sperry, 1988). Moreover, drought-induced changes in hydraulic conductance. Hydraulic conductance was related to soil water deficit. In this case, The declined of hydraulic conductance from the soil to root surface might be explained (Cruiziat *et al*., 2002). These studies have suggested that the reduction in gL may be revealed as the result of stomatal closure that caused the cavitation in the xylem. Then gL was controlled by stomatal behavior. Moreover, g_s is tightly regulated to maintain minimum leaf water potential above the critical threshold (Tyree and Sperry, 1988; Cochard *et al*., 1996). We showed that a declined in gL with decreasing $\psi_{predawn}$. When leaf water potential decreases, water transport of the xylem and tension developed in the water column may be limited by xylem cavitation (Cochard *et al*., 1996).

3.4 Effect of tapping activity on water status and yield

The results of diurnal courses of sap flux density were high and a relatively low difference between tapped and untapped trees in the rainy season. The maximum sap flux density decreased during the dry season. It was found that sap flow of several tree species decreased under conditions of high VPD and soil water stress during the dry season (Granier *et al*., 1992). The maximum sap flux density in tapped trees was lower than untapped trees, especially in the tapping day. Sap flow is expected to be fully compensated by uptake of water by root and water use by transpiration (Pataki *et al.*, 1998). The flow of water through the trunk of tapped trees was lower than untapped trees, due to water loss with latex flow after tapping.

Stomatal conductance was substantially more reduced in the dry season. The results suggest that the reduction in plant water status induced stomatal closure at high VPD and soil water deficit to maintain the minimum leaf water potential above the cavitation threshold (Sperry and Tyree, 1988). There was no difference in g_s between tapped and untapped trees at the early of the dry season but g_s of tapped tree was significant lower than untapped tree during defoliation period in the dry season. Because the tapped tree losses water through latex production. Therefore, rubber tree exhibited a strong control of water losses by closing the stomatal to prevent the embolism in the xylem during the dry season (Cochard *et al*., 1996).

CONCLUSION

1. We confirmed that the Granier method can be used in research on sap flux density and to estimate stand transpiration of rubber trees. This results showed that the calibration curve was similar to the calibration made by Roupsard et al. (2006) and Isarangkool Na Ayutthaya et al. (2010). The calibration of sap flow probes were independent of woody species and madias. Variations of sap flux density in the rubber stem were significant in azimuthal and radial variability. There was a little difference in axial valiability. The seasonal variation of stand transpiration was very clearly related to LAI, ETo, and soil water content. In addition, stand transpiration was closely related to evapotranspiration (ETo), VPD, and soil water content.

2. We found that environmental conditions are important interacting controls plant water status in rubber trees. Plant water status was correlated with VPD and soil water content. Stand transpiration (T) and stomatal conductance (g_s) were mainly controlled by radiation and VPD. Both T and g_s increased with increasing radiation in the morning. Maximum g_s occurred earlier than T peak occurrence. T and g_s decreased in the afternoon. There were time lags between T and g_s throughout the year. Stomatal conductance was more sensitive to climatic changes. The relationship between climatic factors and transpiration varied along the year.

3. The result suggested that the changes of plant water relations was related to climatic conditions and soil water content. Under soil water stress during the rainy season, the decrease of stand transpiration was mainly corresponded to a decrease of whole tree hydraulic conductance (gL) and predawn leaf water potential ($\psi_{predawn}$). Conversely, PLC and midday leaf water potential (ψ_{midday}) were stable and did not decrease according to soil water stress. During the dry season, the results showed that stand transpiration, stomatal conductance, predawn and midday leaf water potential, PLC and gL were related to climatic variables and soil water stress. Leaf water potential ($\psi_{predawn}$, ψ_{midday}) and PLC were not affected by tapping. Tapping activity would not change much water balance of rubber trees. However, tapping activity reduced sap flux density and stomatal conductance in the dry season, particularly in the tapping day.

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