

Water Balance Modeling of Rubber Tree (*Hevea brasiliensis*) Plantation under Tropical Conditions

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A Thesis Submitted in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy in Plant Science

Prince of Songkla University

2015

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	Plantation under Tropical Conditions
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Major Program	Plant Science
Academic Year	2014

ABSTRACT

The rubber plantations have largely expanded into climatically sub-optimal areas in the north and northeast of Thailand. The dynamic of land use is similar to that in other rubber producing countries, with expansions also recorded in northeast India, the highlands and coastal areas of Vietnam, Southern China and the Southern plateau of Brazil. In such areas, rubber tree can be constrained by drought, low temperature and high altitude or conversely by periodic heavy rainfall.

The thesis presented here investigated the effect of climatic gradients consequently to soil and atmospheric drought on water relations of rubber plantations. It is to understand the effect of drought on the performance of rubber tree. The bucket water balance model; BILJOU99 to analyze constraints on tree transpiration and the consequences on soil water balance, growth and production in areas of limited data with daily scale has been developed. The three representative mature stands of rubber: RRIM 600 where trees faced full ranges of soil water over the complete phenological cycle and along the gradient line of climatic regimes were selected in this study.

The simple framework based on reduction factors of potential transpiration was tested to evaluate the water constraints on seasonal transpiration in tropical sub-humid climates. The implementation of a regulation of transpiration at high evaporative demand whatever soil water availability was necessary to avoid large overestimates of transpiration. The details of regulation were confirmed by the analysis of canopy conductance response to vapour pressure deficit. In the tested environmental conditions, the impact of atmospheric drought appeared larger importance than soil drought contrary to expectations. The evolution of modeling was applied to evaluate transpiration of three representative mature stands in drought-prone and traditional areas. The classical concept of regulation by climate, leaf area index and soil moisture was approved globally. But the saturation of transpiration by high evaporative demand showed the regional differences. The implementation of modeling, including threshold of high evaporative demand is required locally in sub-tropical climate and drought prone area. However, such framework induces underestimation in mildly drought prone and optimal area.

In addition the results from BILJOU and relationship between leaf area index (*LAI*) and latex yield showed that *LAI* pattern was the prior factor influence to the latex yield production. The variations of latex yield lagged behind *LAI* pattern and related a little with water use and transpiration. However, there was poor correlation between latex yield and climatic factors in this study. These evidences support the hypothesis that the majority of latex yield initiated from the carbohydrate reserve. It is suggested that around three months after photosynthesis; the carbon assimilation at canopy is spent to metabolize latex. Those support the ability of agro-climatic on transpiration and soil moisture estimation, consequently to latex production.

ชื่อวิทยานิพนธ์	แบบจำลองสมคุลของน้ำในแปลงยางพาราภายใต้สภาพภูมิอากาศแบบเขตร้อน
ผู้เขียน	นายเจษฎา โสภารัตน์
สาขาวิชา	พืชศาสตร์
ปีการศึกษา	2557

บทคัดย่อ

ปัจจุบันการปลูกขางพาราได้มีการขยายพื้นที่ปลูกไปยังพื้นที่ต่างๆ ทั่วโลก เช่น ภาคเหนือ และภาคตะวันออกเฉียงของประเทศไทย พื้นที่ด้านตะวันออกเฉียงเหนือของประเทศ อินเดีย พื้นที่ราบสูงและแนวชายฝั่งของประเทศเวียดนาม ตอนใต้ของประเทศจีน และพื้นที่ราบสูง ทางใต้ของประเทศบราซิล ซึ่งพื้นที่ส่วนใหญ่มีความจำกัดด้านสภาพภูมิอากาศ โดยเฉพาะอย่างยิ่ง สภาพภูมิอากาศที่มีความแห้งแล้งในภาคตะวันออกเฉียงของประเทศไทย การปลูกยางพาราในพื้นที่ ดังกล่าวจึงอาจได้รับผลกระทบ จากสภาพภูมิอากาศที่ไม่เหมาะสม

วิทยานิพนธ์นี้จึงศึกษาอิทธิพลของสภาพภูมิอากาศ ต่อสภาพความความชื้นในดิน และความแห้งแล้ง ที่มีผลกระทบต่อยางพารา เพื่อทำความเข้าอิทธิพลของสภาพภูมิอากาศ และ ความแห้งแล้งต่อการใช้น้ำและการคายน้ำของยางพารา การศึกษาเป็นการประยุกต์ใช้แบบจำลอง สมดุลของน้ำที่มีชื่อว่า BILJOU99 วิเคราะห์ปัจจัยที่ควบคุมการคายน้ำของยางพารา และจำลอง สมดุลของปริมาณน้ำในดิน ภายใต้สภาพภูมิอากาศที่แตกต่างกันของแต่ละภูมิภาคในประเทศไทย โดยทำการทดลองในแปลงยางพาราพันธุ์ RRIM 600 ที่เปิดกรีดแล้ว จำนวนสามแปลง ซึ่งตั้งอยู่ใน พื้นที่ที่มีการกระจายของปริมาณฝนแตกต่างกัน

การคำนวณการคายน้ำในแบบจำลองใช้หลักการอย่างง่าย ด้วยการคำนวณการคาย น้ำสูงสุดที่เป็นไปได้ และหารูปแบบความสัมพันธ์กับปัจจัยที่จำกัดการคายน้ำ ได้แก่ ความชื้นดิน สภาพอากาศ และดัชนีทรงพุ่ม แบบจำลองถูกพัฒนาขึ้นเพื่อจำแนกระดับอิทธิพลของปัจจัยแต่ละ อย่าง ที่มีผลต่อการคายน้ำของยางพารา จากการศึกษา พบว่า ค่าความแห้งของบรรยากาศ เป็นปัจจัย สำคัญอันดับต้นที่มีอิทธิพลต่อควบคุมการคายน้ำของยางพารา ในสภาพพื้นที่ที่ก่อนข้างแห้งแล้ง ของภาคตะวันออกเฉียงเหนือ เนื่องจากหากสภาพอากาศมีก่าความแห้งของบรรยากาศสูง จะชักนำ ให้ยางพาราปิดปากใบ และมีการคายน้ำที่คงที่ การคำนวณการคายน้ำที่ไม่พิจารณาปัจจัยของค่า ความแห้งของบรรยากาศ โดยพิจารณาเฉพาะความชื้นในดินเป็นหลัก จึงทำให้ก่าการประมาณการ กายน้ำที่กำนวณได้มีก่าสูงกว่าก่าจริง การพัฒนาแบบจำลอง BILJOU99 วิเคราะห์การคายน้ำของยางพาราในพื้นที่ที่มี การกระจายของฝนแตกต่างกันสามพื้นที่ พบว่า การคำนวณที่พิจารณาเฉพาะปัจจัยสภาพอากาศ ดัชนีพื้นที่ใบ และความชื้นในดิน ซึ่งเป็นแนวทางหลักในการคำนวณการคายน้ำของพืชโดยทั่วไป โดยไม่พิจารณาอิทธิพลของค่าความแห้งของบรรยากาศ ให้ค่าการคายน้ำของยางพาราในระดับที่ ยอมรับได้ อย่างไรก็ตามการตอบสนองของยางพาราต่อค่าความแห้งของบรรยากาศที่มีผลต่อการ กายน้ำมีรูปแบบความสัมพันธ์ที่คล้ายคลึงกัน แต่มีระดับการตอบสนองที่แตกต่างกันในแต่ละพื้นที่

การคำนวณการคายน้ำของยางพาราโดยการใส่อิทธิพลของค่าความแห้งของบรรยากาศในสมการ จะชักนำให้ค่าที่คำนวณได้ต่ำกว่าค่าจริง โดยเฉพาะในพื้นที่ที่มีปริมาณฝนเพียงพอ และปานกลาง สำหรับยางพารา ดังนั้นปัจจัยหลักที่อิทธิพลต่อการคายน้ำของยางพารา ในพื้นที่ที่มีปริมาณฝน เพียงพอ จนถึงปานกลาง จึงมีเฉพาะปริมาณความชิ้นดิน สภาพอากาศ และดัชนีพื้นที่ใบ หรือ คุณสมบัติของทรงพุ่ม ขณะที่พื้นที่ที่มีปริมาณฝนจำกัดในภาคตะวันออกเฉียงเหนือ ค่าความแห้ง ของบรรยากาศจะมีอิทธิพลสูงที่สุด

การศึกษาเพิ่มเติม โดยใช้ผลการคำนวณปริมาณความชื้นดิน ด้วยแบบจำลอง BILJOU99 และการวิเคราะห์ความสัมพันธ์ของผลผลิตและปัจจัยต่างๆ พบว่า ดัชนีพื้นที่ใบเป็น ปัจจัยหลักที่ควบคุมปริมาณผลผลิตของยางพารา ผลผลิตแปรผันตามการเปลี่ยนแปลงของดัชนี พื้นที่ใบ และมีระยะเวลาห่างกันประมาณ 80 วัน หลังการเปลี่ยนแปลงของดัชนีพื้นที่ใบ ทั้งนี้ไม่พบ ความสัมพันธ์ที่ชัดเจนระหว่าง การคายน้ำ ปริมาณความชื้นดิน สภาพอากาศ ที่มีต่อผลผลิต อย่างไร ก็ตามผลการศึกษา ช่วยยืนยันแนวคิดที่ว่า ยางพารามีการสะสมการ์ โบไฮเดรตในลำต้น และผลผลิต ในรูปของน้ำยาง มาจากการ์ โบไฮเดรตสะสม มากกว่าจะเป็นการสังเคราะห์โดยตรงจากกระบวน การสังเกราะห์แสง และการศึกษานี้ช่วยยืนยันว่า แบบจำลองเพื่อคำนวณการคายน้ำ และปริมาณ ความชื้นดิน สามารถประยุกต์ใช้เพื่อการประเมินการตอบสนองของยางพาราต่อปัจจัยสิ่งแวคล้อม และอาจดัดแปลงเพื่อการศึกษาผลผลิตได้

ACKNOWLEDGEMENTS

Remind to the people who are honorable and involving in my thesis, I would like to give my sincere gratitude to my thesis advisors, Assoc. Prof. Dr. Sayan Sdoodee, Assoc. Prof. Dr. Charlchai Tanavud and my thesis supervisors, Dr. Philippe Thaler, Dr. Frederic C Do and Dr. Frederic Gay. I do appreciate their valuable supervision, suggestions, criticism, support, guidance and encouragement throughout the period of my study. I would like give a special thanks to Dr. Frederic C Do for his taking care my first paper and good academic practice in analyzing data and writing paper to up level in publication. And I do appreciate Dr. Frederic Gay, for his helps and suggestions in anything when I was doing field works. I would like to express my sincere gratitude to the chairperson of thesis examination, Prof. Dr. Sompong Te-chato and the examination referee, Dr. Jessada Phattaralerphong for their helpful suggestions. And it is indispensable to express my sincere appreciation to the plantation owner at Songkhla province, Mrs. Tanom Tammashotang who welcomed me kindly in her rubber plantation. I would like to express my sincere gratitude to Dr. Supat Isarangkool Na Ayutthaya and Dr. Sumit Kunjet who was in charge the field works at Buri Ram and Chachoengsao province, respectively. This work inside a PhD study was supported by the Higher Education Research Promotion and National Research University Project of Thailand (NRU) and the Graduate School, Prince of Songkla University. The field experiments at Buri Ram province were particularly supported by the funding of the French Institute for Rubber (IFC) and associate companies (Michelin, Socfinco, SIPH). The field experiments at Chachoengsao and Songkhla province were supported by Centre de Coopération Internationale en Recherche (CIRAD). Moreover, I would like to thank to UMR Eco&Sols, INRA, Montpellier for a nice place for training, thesis writing and some supporting.

Finally, I would like to express my sincere gratitude and appreciation to my parents and my family for giving me encouragement. Particularly, above all I would like to give all appreciations to my father (Mr. Jin Sopharat) who strongly supported me encouragements, helping in field works and pushing me to achievement.

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LIST OF ABBREVIATIONS AND SYMBOLS

BILJOU	BILan hydrique JOUrnalier; the daily water balance model
ETo	reference evapotranspiration (mm d ⁻¹)
ET0 _{max}	maximum reference evapotranspiration (mm d ⁻¹)
R_n	net radiation (MJ $m^{-2} d^{-1}$)
G	soil heat flux density (MJ $m^{-2} d^{-1}$)
Tem	air temperature (°C)
<i>u</i> ₂	wind speed at 2 m height (m s^{-1})
e_s	saturation vapour pressure (kPa)
e_a	actual vapour pressure (kPa)
e_s	saturation vapour pressure deficit (kPa)
Δ	slope vapour pressure curve (kPa °C ⁻¹)
γ	psychrometer constant (Pa K ⁻¹)
Т	transpiration (mm d^{-1})
$T_{ m mea}$	measured transpiration (mm d^{-1})
$T_{\rm max}$	maximum transpiration (mm d^{-1})
$T_{ m mod}$	estimated transpiration (mm d^{-1})
$T_{\rm mod_ET0c}$	estimated transpiration including with
	threshold of evaporative demand (mm d^{-1})
$T_{\rm mod_REWc1.0}$	estimated transpiration including with
	threshold of evaporative demand and $REW_{c} = 1.0$
ET_{\max}	maximum evapotranspiration (mm d^{-1})
$K_{ m phen}$	reduction coefficient by phenology
Tem _{min}	minimum temperature (°C)
VPD	vapor pressure deficit (kPa)
VPD _{max}	maximum vapor pressure deficit (kPa)
DL	photoperiod or day length
f(Tem _{min})	reduction function by minimum temperature
f(VPD)	reduction function by vapor pressure deficit

f(DL)	reduction function by photoperiod or day length content
	between two successive
ΔW	change of the soil water stock
Р	precipitation (mm d ⁻¹)
Ir	irrigation
Cr	capillary rises
ΔSF	difference between entering and outgoing lateral subsurface
	flow
In	rainfall interception (mm d ⁻¹)
R_o	surface run-off
$E_{\rm S}$	soil evaporation (mm d^{-1})
D	drainage or deep percolation (mm d^{-1})
Th	through fall (mm d^{-1})
E_{u}	evaporation from understorey plus soil (mm d ⁻¹)
$T_{\rm clim}$	transpiration limited by climatic demand (mm d^{-1})
Ψ_{leaves}	leaf water potential (MPa)
Ψ_{crit}	critical leaf water potential or minimum leaf water potential
	(MPa)
${arphi}_{ heta}$	soil matric potential (MPa)
$T_{ m crit}$	critical transpiration resulted by ψ_{crit}
${arphi}_{mid}$	midday leaf water potential (MPa)
F_{soil}	reduction coefficient by soil moisture
heta	volumetric water content in the soil
$ heta_{ ext{max}}$	maximum soil water content or soil water
	at field capacity
$ heta_{ m wilt}$	minimum soil water content or soil water
	at wilting point
$F_{c \text{lim}}$	reduction coefficient by climatic variables

PET	potential evapotranspiration (mm d ⁻¹)
F_{phen}	reduction coefficient by phenological factor
LAI	leaf area index
LAI _{max}	maximum leaf area index
LAI _{mea}	measured leaf area index
$LAI_{\rm mod}$	estimated leaf area index
PAI	plant area index
REW	relative extractable soil water
<i>REW</i> _c	threshold of relative extractable soil water (0.4)
REW_i	relative extractable water in each soil layer <i>i</i>
REW_{mod}	relative extractable soil water by estimation
EW	extractable water
W	available soil water
EW_m	maximum extractable water
W_{f}	soil water content at field capacity
W_m	minimum soil water or soil water at wilting point
SWD	soil water deficit (mm)
I_s	water stress index
$J_{_S}$	sap flux density $(L.dm^{-2}.h^{-1})$
$J_{ m out_day}$	sap flow density measured in the outermost
	ring of the sapwood
K_{f}	flow index (dimensionless)
K_{a}	thermal index of the transient thermal dissipation method
$\Delta T_{\rm max}$	maximum temperature difference between the heated and
	non-heated probe measured at zero flux (°C),
ΔT	measured temperature different between the heated and
	non-heated probe (°C)

$\Delta T_{\rm on}$	temperature difference reached at the end of the 10-min
	heating period
$\Delta T_{\rm off}$	temperature difference before heating
α	coefficients depending on the quantity of heat applied
	$(\alpha = 315 \times 10^{-6} \mathrm{m}^{-2}.\mathrm{s}^{-2})$
β	coefficients depending on the quantity of heat applied
	(β=1231)
A_s	sapwood area
<i>8</i> _c	canopy conductance (mm s ⁻¹)
$g_{c_{\mathrm{md}}}$	midday canopy conductance (mm s ⁻¹)
λ	latent heat of water vaporization (J kg ⁻¹)
C_p	specific heat of dry air at constant pressure $(J kg^{-1} K^{-1})$
ρ	atmospheric density (kg m ⁻³)
g _a	aerodynamic conductance (m s ⁻¹)
<i>z</i> ₀	surface roughness
h	mean tree height
d	zero plane displacement
k	von Kármán constant
u	wind speed at measurement point (z)
Ω	decoupling coefficient
ε	change of latent heat relative to the change in sensible heat
	of saturated air
rm	maximal transpiration versus
	reference evapotranspiration
rLAI	reduction coefficient by leaf area index
rREWc	reduction coefficient by relative extractable soil
rEToc	reduction coefficient by evaporative demand water content
%DRC	percent of dry rubber content

mm s^{-1}	millimeter per second
$mm d^{-1}$	millimeter per day
BRR	Buri Ram province, Thailand
CCS	Chachoengsao province, Thailand
SKL	Songkhla province, Thailand

Chapter 1

Introduction

1. Background and Rational

Climate change poses the significant uncertainties and risks to the environment and development in many countries. Thailand and Indonesia respectively the top producer and the biggest plantation area of rubber are prone to the effects of climate changes; the impact of higher temperatures, changes in rainfall patterns, rising of sea level, shift of seasons and increasing a number of extreme climate events. The primary economic sector, particularly agriculture and cropping are in risks (Thomas, 2008; Ketsomboon and von der Dellen, 2013). Some of these events are occurring in some areas, while in other areas no changes are currently evident. Hence the appropriate strategies and adaptations to promote the sustainability for agriculture have been required (Salinger *et al.*, 2000). The main question of interest here is the following: how important will climate change with increase of CO_2 be in shaping crop yields for future. This question helps to set the challenge of adaptations in context (Lobell and Gourdji, 2012).

Rubber tree (*Hevea brasiliensis*) is an important crop for natural rubber production. At present more than 9.82 million hectares (UNCTAD, 2013) in about 40 countries are devoted to rubber tree cultivation with a production about 6.5 million tons of dry rubber each year. The world supply of natural rubber is barely keeping up with a global demand for 12 million tons of natural rubber in 2020 (Venkatachalam *et al.*, 2006). *Hevea* is native from rain forests of the equatorial region in the Amazon basin (Priyadarshan *et al.*, 2005). The equatorial belt and humid zones of tropical and monsoonal climate are traditional plantation areas (Raj *et al.*, 2005). The increase in world rubber consumption and pleasing prices has been the driving force behind the current boom in rubber markets in New Asia, (China, India and the ASEAN countries). It has resulted in the rapid expansion of plantation areas (Nhoybouakong *et al.*, 2009). The plantations have been expanded in the new and non-traditional areas where rubber can be constrained by drought, low temperature, high altitude or conversely by periodic heavy rainfall (Priyadarshan *et al.*, 2005).

However, a greater frequency of extreme events (flooding, drought) in rainy season and increase of temperature and evaporative demand in dry season are serious problems in traditional and new plantation areas (Ketsomboon and von der Dellen, 2013). Consequently plants have to cope with variations and unpredictable levels of constraints. The increase of plantation areas in suboptimal areas (Isarangkool Na Ayutthaya *et al.*, 2011) is hence questioned to the sustainability of rubber cultivation and the degradation of environments. The expansion of rubber in new plantation areas is required to answer whether to contribute carbon sequestration, increase accumulation of soil organic matter, impact on soil fertility and water balance (Chantuma *et al.*, 2012; Fox *et al.*, 2014; Guardiola-Claramonte *et al.*, 2010; Yang *et al.*, 2004).

To prevent excessive drought and xylem cavitation by maintain minimum leaf water potential posted the rubber (clone RRIM 600) as an isohydric species (Sangsing *et al.*, 2004a; Cochard *et al.*, 1996; Isarangkool Na Ayutthaya *et al.*, 2011). The response of stomatal controls has been approved (Kobayashi *et al.*, 2014). With this basis, whole tree hydraulic property and atmospheric drought has been applied to predict transpiration of rubber trees (Isarangkool Na Ayutthaya *et al.*, 2011).

However, the effect of tropical climate under different regimes consequently to soil and atmospheric drought on water relations of rubber plantations has been yet practically studied. It is therefore necessary to understand the effect of drought on the performance of rubber tree. The ability of a water balance model to analyze constraints on tree transpiration, soil water balance and latex production on the long term and in areas of limited data is a key issue (Boithias *et al.*, 2012; Carr, 2012). The daily scale models are required in this case basis (Hoogenboom, 2000).

The general objectives were to develop the daily agro-climatic and water balance model (BILJOU99; Granier *et al.*, 1999) to evaluate the annual basis of environmental constraints on tree transpiration of rubber and be able to use for the long term estimation of transpiration and up scaling for several areas. We selected three representative mature stands where trees faced full ranges of soil water over the complete phenological cycle and along the gradient line of climatic regimes. It was to evaluate comparatively the annual variation of transpiration and soil moisture between traditional and new plantation areas, to evaluate the constraint variables on transpiration between traditional and new plantation areas. It was hypothesized that the totally annual soil water along the gradient of climate zones which resulted from the different rainfall distributions was the prior factor of constraint compare to other constraints. And it was to test if the evaporative demand corresponded with soil moisture hold response to isohydric behavior of rubber. It was also hypothesized that the degree of isohydric regulation could be held similarly under the gradient of climatic regimes.

2. The objectives

1. To evaluate the generic controls of transpiration implemented with simple agro-climatic model (BILJOU framework): through evaporative demand, leaf area index and relative extractable water and propose an evolution of model to predict annual transpiration of rubber.

2. To evaluate transpiration and water balance of rubber plantations under different rainfall regimes with the simplified water balance model.

3. To evaluate the ability of simple soil water balance model on tree transpiration and the consequences on soil water balance and latex production.

3. The scope of the research

This study has focused on the estimation of transpiration by sap flow measurement. The simple model has developed to estimate transpiration and water balance of rubber tree plantations with the contribution of climate and annual phenology. Consequently, it related to the development of understanding on soil water balance and latex production which globally related with plant phenology and environmental variables.

Chapter 2

Review of Literature

1. Botany, plantations, tree characteristics and yield of rubber tree

1.1 Botany

The rubber tree originates from the Amazon forest. The genus *Hevea*, of the family Euphorbiaceae, includes ten species that would seem to have differentiated as the forest evolved in the last hundred thousand years. *Hevea brasiliensis*, which is a tall tree that can reach heights of 20-35 m in forests, with a trunk circumference of 1-2 m, has the particularity of producing a latex rich in natural rubber particles. This species, *Hevea brasiliensis*, which is virtually the only source of natural rubber, is the only one commercially planted and usually grown in clone form (Cilas *et al.*, 2004).

1.2 Plantations

The rubber tree is the major source of natural rubber. The economic life-span is around 30-35 years (Rao *et al.*, 1998). The biggest commercial plantations are based in South-Aast Asia and displayed over several continents of the world: Asia, Africa and South-America (Priyadarshan *et al.*, 2005). *Hevea* is a brevi-deciduous tree (1-2 weeks), native from the tropical rainforest in the Amazon Basin. Its habitat is characterized by small variations in air temperature 24-28 °C, precipitation, 1500-2000 mm and rainy days 100-150 days throughout the year. Rubber's natural habitat extends between 10 ° north and south of the equator and to at most 600 m above mean sea level. Thailand is the first producer and exporter natural rubber. Rubber plantation in Thailand covered 2.7 million hectares (or 16.89 million rais), produced 3.16 million tons in 2009. The traditional area of plantation is the southern part of the country (RRIT, 2010). However, due to the demand increasing and pleasing price, rubber has been cultivated at the new areas include the Central Highlands of Vietnam (12 °N), north-central Vietnam, northern India (29 °N), south-west China (22 °N), the southern plateau of Brazil (23 °S) and north-eastern Thailand (19 °N), where rubber can be constrained by drought, low temperature, high altitude or conversely by periodic heavy rainfall (Priyadarshan *et al.*, 2005; Guardiola-Claramonte *et al.*, 2010; Carr, 2012). Traditionally, it has been cultivated in the equatorial belt and more humid zones of tropical and monsoonal climates. Areas of higher production are characterized by adequate rainfall distribution and less fluctuations in temperature and humidity conditions (Rao *et al.*, 1990, 1998). The RRIM 600 has been a universally accepted clone with its wider adaptability growing in sub-optimal conditions over several countries (Priyadarshan *et al.*, 2005). The optimum plant density for rubber is in the range 500-700 trees per hectare, based on comparisons mainly done under wet conditions (Rodrigo, 2001).

1.3 Tree characteristics, leaf phenology, growth and yield

The rubber tree is a quick-growing, erect tree with a straight trunk and a bark which is usually grey and fairly smooth. In the natural wild, it may grow up to over 40 m and live for over 100 years, but in plantations they rarely exceed 25 m height, and they are replanted after 25-35 years when latex yields become uneconomic (Webster and Paardekooper, 1989). The leaves are trifoliate, and the laminae hang downwards with a bronze color when emerge. The leaf expansion follows a sigmoid curve. During the first 5 days after leaf unfolding, the expansion increases slowly and then rapidly from 5-12 days; the leaf becomes fully expanded thirteen days after unfolding (Sangsing et al., 2004a) (Figure 1). The mature laminae are shiny dark green on their upper surface and light green below. From emerged to mature of leaves takes approximately 35 days. The leaves exhibit a full rate of photosynthesis 50 to 60 days after emergence (Samsuddin and Impens, 1979). Rubber trees older than 3 or 4 years are subject to 'wintering', which is the term used to describe the annual shedding of senescent leaves. The leaf shedding is partial or complete for a short period of few weeks (Webster and Paardekooper, 1989). Latex yields usually decreased slightly at the onset of leaf fall, and are more markedly reduced during re-foliation. Leaf fall is normally followed within 2 weeks by the terminal bud bursting and by the expansion of new leaves within further weeks (Rao et al., 1998). In the south part of northeastern of Thailand, leaf yellowing usually starts at the end of December. Massive leaf shedding occurs

between the end of January and the onset of February; starting of dry season, and bud emergence is noticed at the end of February. The phenological stage of fully mature leaves eventually last from May to November. However, it is late around one and half month in Southern Thailand.

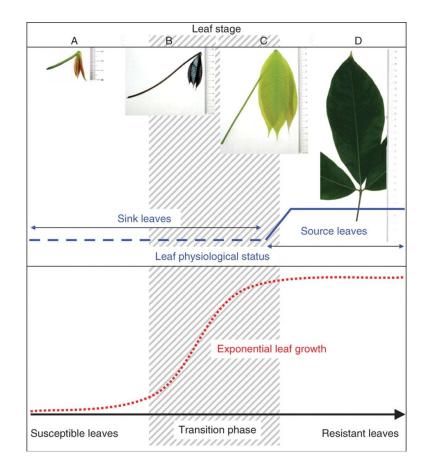


Figure 1 The development stage of rubber leaf Source: Lieberei (2007)

In Thailand, the tree is considered mature when the girth attains 50 cm at 150 cm height above ground, ready for tapping. This maturity is usually achieved around 5-6 years after planting in traditional conditions and around 8-10 years in sub-optimal conditions. More generally, growth of rubber tree varies from clone to clone (Sangsing *et al.*, 2004b), planting density, climatic season, air temperature, drought occurrence, irrigation, tapping systems and others. Typical radial growth pattern in water-limited areas of Thailand, starts at the onset of rainy season and lasts until the onset of dry season, girth growth completely ceases in the driest period (Isarangkool Na Ayutthaya, 2010).

Latex is issued from a secondary metabolic pathway and exuded from the trunk after a deep tapping of the bark. The latex contains on average 60 to 70% of water, so the tree water status and the availability of water in the soil are important limiting factors of rubber production (Pakianathan *et al.*, 1989 cited by Isarangkool Na Ayutthaya, 2010). Latex yield related with meteorological parameters, particularly maximum temperature. Vapor pressure deficit has the negative correlation, whereas only rainfall is positively correlated with latex yield (Rao *et al.*, 1990, 1998). And the yield decreases in the dry season. The highest flow rates of latex generally occur during wet months when growth rate are maximal (Pakianathan *et al.*, 1989 cited by Isarangkool Na Ayutthaya, 2010).

1.4 Responses to water and environmental factors

Leaf flushing during the dry season implies that the rubber tree must have sufficient reserves of water and carbohydrate for the following expansion of new leaves. Significantly, deep root water uptake takes place during leave flushing. While shedding reduces transpiration, simultaneous root water uptake increases stem water potential which required for subsequent leaf flushing. Importantly, the water is extracted from the soil column (i.e. basin storage), but is not released to the atmosphere until new foliage is grown. It is believed that trees will show different phenological stage depending on the local water balance during the dry season, with the degree of deciduousness increasing with rising water stress. Shedding and flushing shows strong synchronicity, with important root water uptake associated with these two processes. (Guardiola-Claramonte *et al.*, 2010). It is suggested that phenology of rubber tree has been influenced by soil water status and deep root water uptake.

The models based on climatic or/and hydraulic variables have been developed to estimate canopy conductance and evapotranspiration of rubber plantation (Guardiola-Claramonte *et al.*, 2008; Guardiola-Claramonte *et al.*, 2010; Isarangkool Na Ayutthaya, 2010; Isarangkool Na Ayutthaya *et al.*, 2011). It was stated that the model would perform better if phenological information would be included (Rodrigo *et al.*, 2001). A recent study by Guardiola-Claramonte *et al.* (2010) proposed a generalized, bioclimatic index that depends on minimum temperature (Tem_{min}), vapor pressure deficit (VPD) and photoperiod (DL) to predict foliar phenology. Herein,

they proposed the phenological coefficient that depends on phenology (K_{phen}) to estimate transpiration (T) as following:

$$T = ET_{\max} K_{phen}$$
[1]

$$K_{phen} = f(Tem_{\min})f(VPD)f(DL)$$
[2]

where ET_{max} is maximum evapotranspiration, $f(T_{min})$, f(VPD) and f(DL) are the reduction functions associated with the three environmental variables; minimum temperature, vapor pressure deficit and photoperiod, respectively (f = 1 when the vegetation is fully active and f = 0 when inactive).

Soil moisture deficit could retard latex flow and thereby reduce yield of rubber (Samarappuli *et al.*, 2000). It is therefore necessary to understand the effect of soil water stress on the performance of rubber tree and to provide appropriate agricultural practices such as ground cover management, fertilizer program, clone selection and field establishment practices to overcome the adverse effects of soil water stress (Samarappuli *et al.*, 2000). Therefore, the water balance model is the promising tool to deal with these phenomena.

2. Water balance modeling

The balance equation is an account of flows and changes in inventory of mass or energy for a system (Scott, 2000). The general soil water balance equation is hence including a total of these parameters (Saint-André et al., 2007):

$$\Delta W = P + Ir + Cr + \Delta SF - In - R_o - T - E_s - D$$
[3]

where (all expressed in mm); ΔW = variation of the soil water stock; P = precipitation; Ir = irrigation; Cr = capillary rises; ΔSF : difference between entering and outgoing lateral subsurface flow; In = interception; R_o = surface run-off; T = transpiration; E_s = soil evaporation; D = drainage or deep percolation.

Based on soil water content, the simple water balance model can indicate as the equation [4] and [5]. The balance of input-output of water is the conceptual idea of water balance modeling. The main purposes of a water balance model are to predict temporal variations in soil water content and to assess the water stress conditions actually experienced by a crop or a forest stand (Granier *et al.*, 1999).

$$\Delta W = P - In - T - E_{\mu} - D$$
^[4]

$$\Delta W = Th - T - E_u - D$$

$$\Delta W = Th - T - E_u - D$$
[5]

where ΔW is the change of soil water content between two successive days, *P* is rainfall, *In* is rainfall interception, *Th* is throughfall; the difference between total rainfall (*P*) and rainfall interception (*In*), *T* is tree transpiration, E_u is evaporation from understorey plus soil and *D* is drainage at the bottom of soil layers.

The major part is a combination of evapotranspiration modeling. It is a relationship between transpiration by tree, evaporation by soil and additional transpiration by understorey (Lundblad and Lindroth, 2002). These combinations are mainly influenced by evaporative demands linked to the climatic variables and hydraulic gradients through the flux pathway (Jarvis, 1976; Javis and McNaughton, 1986; Cochard *et al.*, 1996; Whitley *et al.*, 2008, 2009; Isarangkool Na Ayutthaya *et al.*, 2011). Because the transpiration is the majority related with tree, therefore the transpiration was focused in this study. The combination of climatic and physiological variables of plant was then the main items.

3. Transpiration and water flow

3.1 Isohydric and anisohydric behavior

The cohesion-tension theory of sap ascent for vascular, homeohydric plants states that: (i) evaporation of water from leaf tissues makes the microfibril cellulose matrix of cell walls develop capillary tensions (negative hydrostatic pressures) and (ii) thanks to the cohesion of water molecules, such tensions are transmitted downwards, all the way to root hairs, through continuous xylem tissue, literally pulling water upwards. The continuity of water columns from soil pores throughout the plant to leaf cells, linked to evaporative flux, is known as the soil-plantatmosphere continuum. The association between water transport capacity and carbon gain is unrelated to the role of the water molecule as a substrate in photosynthesis (involving only about a molecule of water per molecule of carbon), or to water storage in newly formed tissues (about 10 times larger but still small). There is a much larger requirement for water because of the need to display a large surface of fully hydrated cells to obtain carbon dioxide, which happens to be in desiccating air; that is why higher plants transpire between 100 and 1000 water molecules per molecule of assimilated carbon. As this need cannot be met by water stored in the plant, it has to come from an external reservoir - the soil, causing a huge mass flow, with nearly all the water that enters the roots being lost by leaf transpiration a few hours or days later. Any shortage in water supply in relation to the requirements of leaves results in water deficit and plant stress; thus there is a strong selection for preventing such deficits without missing opportunities to acquire carbon for growth (Maseda and Fernández, 2006).

As a physical process, T is determined by the evaporation of water molecules in the substomatal cavity of leaves. Hence, T is first determined by evaporative demand, which can be defined by climatic variables; solar radiation and *VPD*. Climatic demand combined with stand evaporative characteristics sets an upper physical limit (T_{clim}) to T. T may equal T_{clim} when T_{clim} is relatively low, for instance on cloudy rainy days. But there are a number of situations in which T_{clim} largely overestimates T. Hence, several authors have reported that even under well-watered soil conditions plants exhibit tight stomatal regulation of T under high climatic demand. And the decline in transpiration under low soil water availability is a more well-known process.

Through stomatal closure regulation, plants can be typically divided into high and low sensitive response, i.e., isohydric and anisohydric species, respectively. Plants with isohydric tendency exert tight stomatal control of transpiration. They operate over a short range of leaf water potential (ψ_{leaves}) and maintaining above critical of ψ_{leaves} (ψ_{crit}) independently of soil water and atmospheric constraints. It is prevention transpiration from exceeding critical rates (T_{crit}), results in xylem water potentials associated with hydraulic and symplastic failure (ψ_{crit}). Conversely, plants with anisohydric tendency exert less strict stomatal control. They operate over a larger range of leaf water potential when midday leaf water potential (ψ_{mid}) significantly decreases as a function of increasing soil drought (Fernández *et al.*, 2009; Fisher *et al.*, 2006; Franks *et al.*, 2007; Isarangkool Na Ayutthaya *et al.*, 2011; McDowell *et al.*, 2008).

3.2 Reference evapotranspiration (ETo)

The reference evapotranspiration (*ETo*) is used to represent the evaporative demand according to the details given by Allen *et al.* (1998):

$$ET_0 = \frac{0.408\Delta(R_n - G) + \gamma \frac{900}{Tem + 273}u_2(e_s - e_a)}{\Delta + \gamma(1 + 0.34u_2)}$$
[6]

where ET_0 is reference evapotranspiration (mm d⁻¹), R_n is net radiation (MJ m⁻² d⁻¹), G is soil heat flux density (MJ m⁻² d⁻¹), *Tem* is air temperature at 2 m height (°C), u_2 is wind speed at 2 m height (m s⁻¹), e_s is saturation vapour pressure (kPa), e_a is actual vapour pressure (kPa), e_s is saturation vapour pressure deficit (kPa), Δ is slope vapour pressure curve (kPa °C⁻¹) and γ is the psychrometer constant.

3.3 The contribution of climatic and soil water

In the simple concept of modeling, the transpiration varies between zero and maximum (T_{max}) , according to soil moisture in root zone as the following equation (described by Small and McConnell, 2008);

$$T = F_{soil}T_{\max}$$
^[7]

where the reduction coefficient is due to soil moisture (F_{soil}) as following;

$$\begin{aligned} F_{soil} &= 0 \text{ for } \theta < \theta_{wilt} \\ F_{soil} &= \left(\frac{\theta - \theta_{wilt}}{\theta_{\max} - \theta_{wilt}} \right), \text{ for } \theta_{wilt} < \theta < \theta_{\max} \end{aligned}$$

$$F_{soil} = 1.0$$
, for $\theta \ge \theta_{max}$

where θ is volumetric water content in the soil, θ_{wilt} is the minimum soil water content or the water content at which transpiration cease and θ_{max} is the maximum soil water content or soil water at field capacity.

The next level of modeling is to include the dependence of transpiration on climatic variables. This concept allows the seasonal changes in transpiration (Small and McConnell, 2008).

$$T = F_{soil} \cdot F_{c\,\lim} \cdot T_{\max} \tag{8}$$

where $F_{c \text{lim}}$ is the reduction coefficient by climatic variables.

The common method to represent the maximum transpiration is to use the potential evapotranspiration (*PET*) as following;

$$T = F_{soil} \cdot F_{c\,\text{lim}} \cdot PET \tag{9}$$

Under non limiting soil moisture the transpiration is dependent on evaporative demand. However, the above mentions accounted only the effects of climatic variables and soil moisture, it has yet considered the effect of variations of leaf area index or phenology (Granier and Bréda, 1996).

3.4 The contribution of phenology and environment

The whole tree hydraulic conductance model has been concluded that it is sufficient to describe water use regulation of the mature rubber tree stand (Isarangkool Na Ayutthaya *et al.*, 2011). This approach has been proved in several species; *Betula occidentalis* (Saliendra *et al.*, 1995), *Pinus taeda* (Ewers *et al.*, 2000), *Eucalyptus gomphocephala* (Franks *et al.*, 2000),

al., 2007). However, such approach requires the hydraulic function and importantly to calibrate with leaf water potential and hydraulic conductivity data set. Another way to estimate transpiration is combination between environmental limitation and phenological models.

To simplify and address the dependence of transpiration on phenology, the transpiration model including the parts of soil water, climatic and phenological factor can be showed as following;

$$T = F_{soil} \cdot F_{c\,\text{lim}} \cdot F_{phen} \cdot PET$$
[10]

where F_{phen} is reduction coefficient by phenological factor. The annual variations of *LAI* were used to represent as the phenological factor in this study.

4. Influence of leaf phenology on drought response

4.1 General features

To prevent excessive dehydration plants can express short term reversible responses by stomatal closure. This effect can induce also the long term responses; reduce transpiring leaf area as deciduous behavior, increase root development in wetter soil layers and decrease active sapwood area. Reducing leaf area is a major adaptation of deciduous trees to seasonal drought in the dry tropics. The different stages of leaf phenology may correspond to particular changes of root dynamics and proliferation; decay and growth in soil layers according to soil water availability. These processes influence to water relations and whole tree hydraulic conductance, particularly the leaf and root which contribute to more than 70% of the total hydraulic resistance. Because leaf senescence and shedding induce the decrease of total leaf hydraulic conductance. The contribution by soil water deficit, the decrease of soil to root conductance and root conductance. At last, leaf flushing involves with increase of hydraulic conductance at leaf scale (Isarangkool Na Ayutthaya *et al.*, 2010).

4.2 Phenology of rubber in seasonal dry period

In northeast Thailand, the period of leaf yellowing-shedding-bud bursting-leaf flushing normally takes around five months, from December to April. Hence, such period of relatively low green leaf area should markedly reduce whole tree transpiration. The dry season generally lasts from November to April (Isarangkool Na Ayutthaya, 2010). But in Southern Thailand leaf shedding always occurs in the end of January until February. Bud bursting-leaf flushing occurs around one month during March and the earlier of April.

Gonkhamdee *et al.* (2009) had followed growth dynamics of fine roots of rubber trees down to 450 cm. They found that in tropical dry area the onset of the dry season (November) corresponded to a period of active growth in the subsoil from 100 to 400 cm depth. After a rest period, root growth appeared again in the very deep soil between 300 and 400 cm around the time of massive leaf flushing in March. The onset of the rainy season (May) corresponded to an active growth in the top soil above 100 cm. The higher root length density was found above 50 cm. Root decay was observed above 100 cm at the end of the rainy season in September-October. Guardiola-Claramonte *et al.* (2008) also stress up for rubber tree the importance of including leaf phenology in soil water balance model to correctly predict the trend of water uptake in dry season to subsoil at the end of the dry season when leaf flushing occurring.

5. BILJOU: a daily water balance model

The water budget for a soil profile refers to the water additions, subtractions, and the amount of water stored or remained in the soil, equation [3]. The hydrologic cycle component which adds water to the soil is infiltration, and evapotranspiration processes are components of water removal. Within a particular volume of soil in root zone, the available soil water holding capacity refers to the amount of water which the soil can hold, available for plants evapotranspiration purposes. Any excess water which infiltrates, and which cannot be retained as the soil water becomes the percolation to deep soil layer, the water that moves downward through the soil profile below the root zone; or if the downward movement is restricted, it's subject to interflow, the horizontal movement of water out of the soil volume. The interflow and deep percolation components produce the seepage flow.

In this study we focused on the simple water model; BILJOU99, daily water balance model (Granier *et al.*, 1999) (Figure 2). The main purpose of this model is to quantify the intensity and duration of drought in the stands. It requires the daily potential evapotranspiration and rainfall as input climatic data. Required site and stand parameters are only maximum extractable soil water and leaf area index, the latter controlling (i) stand transpiration; (ii) under canopy floor evapotranspiration; and (iii) rainfall interception. The other information like root distribution and soil porosity can be used if available for improving the simulation of short term soil water recharge.

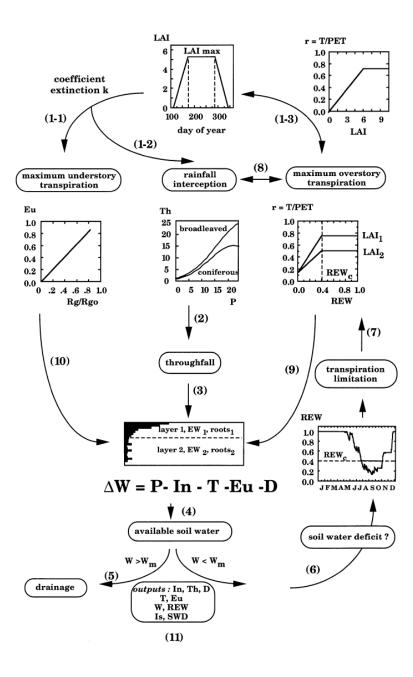


Figure 2 Flow chart of the daily water balance model: BILJOU. The model is iterative and the presented loop is run day after day. The successive steps are: (1) *LAI* defines understorey evapotranspiration (1–1), rainfall interception (1–2) and overstory transpiration (1–3); (2) throughfall is calculated according to forest type, *LAI* and incident rainfall; (3) throughfall is added to the available soil water of the previous day n-1. The new available soil water is calculated and compared to maximum soil water to define drainage (5) or soil water deficit (6). If soil water deficit occurs (7) or if the canopy is wet (8), the r ratio (rm) is reduced. Overstory transpiration (9) and understorey evapotranspiration (10) are then subtracted to soil water content. Daily water fluxes and drought indices are finally computed (11).

Source: Granier et al. (1999)

Water stress occurs when relative extractable soil water (*REW*) drops below a threshold of 0.4 under which transpiration is gradually reduced due to stomatal closure. Transpiration strongly depends on evaporative demand under non limiting soil moisture. The relationship can indicate as the ratio of transpiration to potential evapotranspiration; represent as rm. The ratio is driven as a function of stand *LAI*. However, under water stress condition rm decreases linearly as soon as *REW* to below a threshold (*REW*_c) (Figure 3). This is the situation when soil water becomes limiting for transpiration. In several species *REW*_c was found constant around 0.4 (Granier *et al.*, 1999; Sinclair *et al.*, 2005). The equation of relative extractable soil water is showed as following equation:

$$REW = \frac{EW}{EW_m} = \frac{W - W_m}{W_F - W_m}$$
[11]

where EW is extractable soil water as $W - W_m$; W is available soil water, W_m is minimum soil water or soil water at wilting point, and EW_m is maximum extractable water as $W_f - W_m$; W_f is soil water content at field capacity.

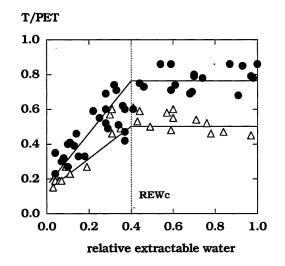


Figure 3 Ratio T/PET or *rm* calculated from sap flow measurements in an oak stand as a function of relative extractable water (*REW*) calculated from neutron probe measurements. Two data sets are reported: *LAI*=6 (black circles) and *LAI*=4.5 (open triangles). The dotted line shows the critical *REW* (*REW*_c=0.4).

Source: Granier et al. (1999)

Run off was neglected in present study. It is assumed that the model applied in areas covered by rubber trees on gentle slopes. Finally, this model is the tool to indicate soil water content including amount of soil water deficit. Normally, it approaches water stress conditions when *REW* drop below 0.4; as indicating soil water deficit (*SWD* in millimeters) is therefore calculated daily against this threshold as reported by Granier *et al.* (1999) as the following equation;

$$SWD = 0.4EW_m - EW$$
[12]

If REW < 0.4, two stress indices are calculated: firstly, the number of days of water stress i.e. the number of days during which $EW < 0.4EW_m$ and secondly, water stress index (I_s) which cumulates the difference between REW and REW_c as the following equation:

$$I_{s} = \sum SWD / EW_{m}$$
[13]

6. General description of study sites

The present study was conducted with the experimental plots from three sites. Two sites based in southern part of northeast Thailand where the subtropical climate (Aw; Tropical Savannah) has been influenced by Mekong basin. And one plot based in Southern Thailand where the tropical monsoon climate (Am; Tropical Monsoon) has been influenced by gulf of Thailand and Andaman sea (Figure 4 and 5). We proposed to evaluate the effect of climatic regimes along the gradient line of rainfall distributions. The considerations were performed by the bucket water balance model. The mature rubber plantations have been selected with the same clone; RRIM 600. The analysis and predictions over 1971 to 2100 by Thai Meteorological Department with Climate scenario A2 reported that the increase of rainfall over three sites will not be evident for future, but the increase in maximum and minimum temperature is promised around 4-5 and 2-3 °C at Northeastern and Southern Thailand, respectively.

First site (Buri Ram; BRR) was located at Baan Sila site (N15° 16′ E103° 04′), Khu-Muang, Buri Ram province, Northeastern Thailand. The trees were planted by 2.5 x 7.0 m spacing (571 trees ha⁻¹) and tapped for 4 years or age 11 years old from planting. The soil is deep loamy sand. Mean contents of clay, loam, and organic matter varied from 9.9, 24.2 and 0.78% in the top soil (0-20 m) to 20.2, 23.6 and 0.34% at a depth of 1.5 m, respectively. In this nontraditional rubber tree plantation area, the environmental conditions are water limited for rubber. The dry season lasts six months, from November to April, and average annual rainfall is 1176 mm.

Second site (Chachoengsao; CCS) was located at the Chachoengsao Rubber Research Center (N13° 41′ E101° 04′), Chachoengsao province, Eastern Thailand. The plot has been planted in 1994 with 2.5×7.0 m spacing. Tapping began when the trees were 9 years old in 2003. The soils in this plot belong to the Kabin Buri series with 50% sand, 15% silt, and 35% clay. The soil depth is limited at 1-1.5 m by a compact layer of ferralitic concretions. The mean annual air temperature and cumulative rainfall were 28.1 °C and 1328 mm, respectively, with a strict dry season between November and April.

Third site (Songkhla; SKL) was located at Baan Rai Ooi (N6° 59', E100° 22'), Chalung, Hat Yai, Songkhla province, Southern Thailand. The trees were planted by $3.0 \ge 7.0 \text{ m}$ spacing (476 trees ha⁻¹). It was 14 year old and the rubber trees have been tapped for 6 years. The soil is clay loam. Mean contents of clay, silt, and sand varied from 37.9, 37.7 and 24.3 % at depth of 0-0.3 m and 40.6, 37.5 and 21.8 % at depth of 0.6-1.0 m, respectively. The wet season is in June to December and dry season for three months, from February to April. Average annual rainfall is 1955 mm (1979-2008).

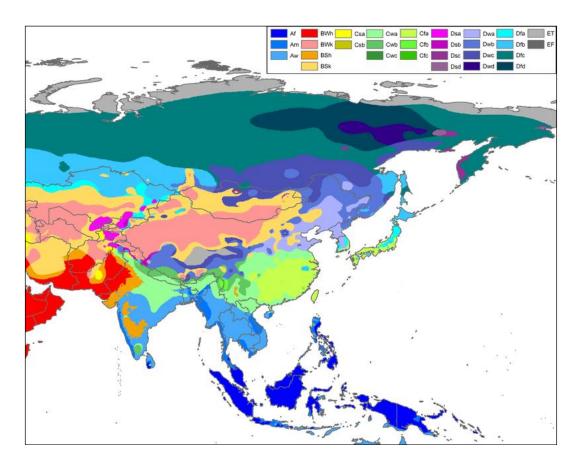


Figure 4 Köppen-Geiger climate type map of Asia. The area in north and northeast of Thailand is classified as Aw; Tropical Savannah and Southern Thailand is Am; Tropical monsoon. Source: Peel *et al.* (2007)

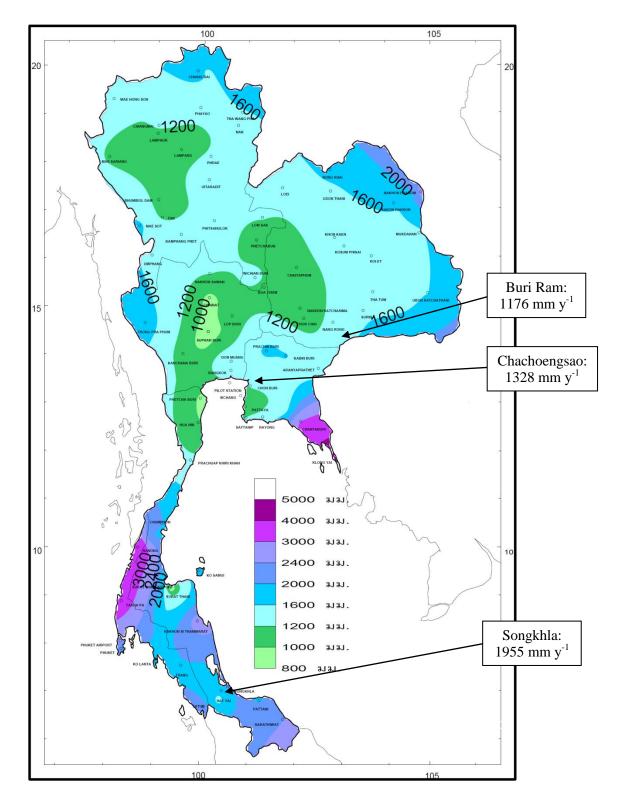


Figure 5 The map of rainfall distributions in Thailand: the analysis based from 2001 to 2008 Source: Thai Meteorological Department (Accessed year 2015)

Chapter 3

A simple framework to analyze water constraints on seasonal transpiration in rubber tree plantations

Abstract

Climate change and fast extension in climatically suboptimal areas threaten the sustainability of rubber tree cultivation. A simple framework based on reduction factors of potential transpiration was tested to evaluate the water constraints on seasonal transpiration in tropical sub-humid climates, according pedoclimatic conditions. We selected a representative, mature stand in a drought-prone area. Tree transpiration, evaporative demand and soil water availability were measured every day over 15 months. The results showed that basic relationships with evaporative demand, leaf area index and soil water availability were globally supported. However the implementation of a regulation of transpiration at high evaporative demand whatever soil water availability was necessary to avoid large overestimates of transpiration. The details of regulation were confirmed by the analysis of canopy conductance response to vapour pressure deficit. The final objective of providing hierarchy between the main regulation factors of seasonal and annual transpiration was achieved. In the tested environmental conditions, the impact of atmospheric drought appeared larger importance than soil drought contrary to expectations. Our results support the interest in simple models to provide a first diagnosis of water constraints on transpiration with limited data, and to help decision making towards more sustainable rubber plantations.

1. Introduction

Almost 30 years, the rubber plantations have largely expanded into climatically sub-optimal areas in the north and northeast of Thailand. The dynamic of land use is similar to that in other rubber producing countries, with expansions also recorded in northeast India, the highlands and coastal areas of Vietnam, Southern China and the southern plateau of Brazil (Priyadarshan *et al.*, 2005). In such areas, rubber can be constrained by drought, low temperature and high altitude or conversely by periodic heavy rainfall. Moreover, with climate change, higher frequencies of extreme events (flooding, drought) in the rainy season and an increase in temperature and evaporative demand in the dry season are expected in both traditional and new areas (Masaki *et al.*, 2011). In addition, despite the large extension of land covered by rubber plantation, little is known of its environmental impacts and particularly about carbon and water balances (Guardiola-Claramonte *et al.*, 2010, Kumagai *et al.*, 2013). To address the sustainability of rubber plantations and to choose appropriate plant material and management practices, it is necessary to forecast rubber tree behavior on a large scale and over long periods of time. Hence the availability of simple models with limited data to analyze water constraints on tree transpiration and consequences on growth, production and soil water balance is a key issue (Boithias *et al.*, 2012; Carr, 2012; Guardiola-Claramonte *et al.*, 2010).

Our final objective is to evaluate, on an annual basis, the relative contributions of soil water shortage and atmospheric drought to the regulation of maximal transpiration in rubber tree stands under various pedoclimatic conditions. The use of a robust and simple model based on reduction factors of potential transpiration simulation appeared as a reasonable first approach to schematically separate the main controls. Granier et al. (1999) proposed such a model of daily water balance called BILJOU to evaluate water constraints in forest stands. It has been successfully used in temperate and tropical humid forests (Granier et al., 1999, Wagner et al., 2011). Transpiration models based on canopy conductance regulation have been also assessed and used (Jarvis, 1976; Stewart, 1988; Granier et al., 2000; Granier et al., 2007). However they require an hourly step, more parameters and input data. As a first approach we chose to use the framework of BILJOU99 (Granier et al., 1999). The model assumes, under non limiting soil water, a linear response of maximal transpiration (T_{max}) versus potential evapotranspiration (PET) for a leaf area index (LAI) inferior to 6, the slope being the ratio "rm" depending on the LAI. The model assumes that under a soil water shortage, rm decreases linearly below a threshold of relative extractable water (*REW*) of 0.4. Like many models, it does not consider direct constraint due to atmospheric drought (Boote et al., 2013). However, Isarangkool Na Ayutthaya et al. (2011) have shown that transpiration in mature rubber trees was strongly regulated above a threshold of evaporative demand, whatever the soil water availability. Such a regulation was

related to an isohydric behavior expressed by stability of minimum leaf water potential and maximum whole-tree hydraulic conductance. The idea was to add a reduction factor above a critical climatic demand.

To test our modeling approach based on BILJOU99 framework, we selected a representative mature stand where trees faced the full range of soil and atmospheric drought conditions over a complete annual cycle. Tree transpiration, the evaporative demand and the soil water availability were measured every day over 15 months. The first objective was to test simplified controls of transpiration through evaporative demand, leaf area index and relative extractable water. We hypothesized that the basic relationships hold, except when the evaporative demand becomes too high. The second objective was to test an evolution of the model including sensitivity to atmospheric drought. We assumed that it would provide a reasonable indication of the trend in seasonal transpiration. The third objective was to assess by modeling the hierarchy between soil water and atmospheric constraints on transpiration on an annual basis. We assumed a predominant control by soil drought according to common thinking.

2. Materials and method

Study site

The plantation was located at Baan Sila (N15° 16′ 23′′ E103° 04′ 51.3′′), Khu-Muang, Buri Ram province in northeast Thailand. The experiments were conducted in a monoclonal plot (clone RRIM 600), planted at 2.5 x 7.0 m spacing (571 trees ha⁻¹). The trees were 11 years old and had been tapped for 4 years for latex harvesting. The soil is deep with a loamy sand texture. The mean contents of clay, loam and organic matter varied from 9.9, 24.2 and 0.78% in the surface layer (0 - 0.2 m) to 20.2, 23.6 and 0.34% at a depth of 1.5 m, respectively. In this non-traditional rubber tree plantation area, the environmental conditions are water limiting for *H. brasiliensis*. The dry season lasts 6 months, from November to April, and average annual rainfall is 1,176 mm. Canopy yellowing and defoliation occurred between December and March. In a sample of 237 trees, canopy fullness was assessed every 2 weeks for each tree according to seven categories of the percentage of green leaves (100, 90, 75, 50, 25, 10 and 0%). When the defoliation was almost complete, the maximum leaf area index (LAI_{max}) was estimated from leaves collected in nine 1 m² litter traps. A schematic change in the *LAI* over the year was deduced from observations of canopy fullness and litter fall measurements.

Climatic measurements

The local microclimate was monitored automatically in an open field at a distance of 50 m from any trees. An automatic weather station (Minimet automatic weather station, Skye Instruments Ltd, Llandrindod Wells, UK) recorded half-hourly values of air temperature, relative humidity, incoming short wave radiation, wind speed and rainfall. The reference evapotranspiration was calculated according to the FAO 56 formula in Allen *et al.* (1998).

Soil water content measurements

Volumetric soil water content (θ) was measured with a neutron probe (3322, Troxler, Research Triangle Park, NC, USA) calibrated for the experimental soil with separate calibrations for the upper (0 - 0.2 m) and lower (below 0.2 m) layers. Twelve 2 m-long tubes were set up in pairs; in each pair, one tube was located in the planting line between two trees, and the other in the middle of the inter-row. Measurements were made every 0.2 m, from a depth of 0.1 to 1.5 m every 2 weeks. Based on observed fluctuations in soil water, the soil profile was separated into two layers: topsoil (0 - 0.6 m) and subsoil (0.6 - 1.6 m). The average field capacity and permanent wilting points were measured as 0.21 and 0.07 m³ m⁻³ for the topsoil, and 0.25 and 0.10 m³ m⁻³ for the subsoil, respectively (Isarangkool Na Ayuthaya *et al.*, 2010). Additionally, θ was measured continuously with a capacitance probe (EnvironSCAN System, Sentek Sensor Technologies, Adelaide, SA, Australia). The vertical probe included nine sensors located every 0.2 m at the same level as the neutron probe measurements. For each sensor, θ was estimated from cross-calibration with the neutron probe measurements over the whole seasonal range. Relative extractable water was calculated for each layer according to Granier *et al.* (1999):

$$REW_i = (W - W_m) / (W_f - W_m)$$
[14]

where REW_i is the relative extractable water in each soil layer *i*, W_m is the minimum soil water content, W_f is the soil water content at field capacity and W is the actual soil water content. To calculate the total *REW* for the sensitive root zone, REW_i was weighted by the percentage of fine root length within each layer. As the soil profiles showed low soil water availability and little change in the subsoil (Figure 1B), for modeling purpose the total *REW* was calculated for the top soil (0 - 0.6 m). In this site, the top soil contained 83% of the fine root length accumulated down to 1.6 m (Gonkhamdee *et al.*, 2009). The fraction of fine root length used for weighting the *REW* in the top soil was 0.63, 0.32 and 0.05 for the layers 0 - 0.2, 0.2 - 0.4 and 0.4 - 0.6 m, respectively.

Transpiration measurement

The xylem sap flow density was measured using the transient thermal dissipation method (TTD, Isarangkool Na Ayutthaya *et al.*, 2010). The TTD method is based on using the same Granier probe design and heating power but uses a cyclic schedule of heating and cooling to assess a transient thermal index over a 10-min rise in temperature. The hourly sap flux density $(J_s; \text{ kg m}^2 \text{ h}^{-1})$ was calculated according to the non-species-specific calibration assessed by Isarangkool Na Ayutthaya *et al.* (2010):

$$J_{\rm s} = 12.95 \times K_{\rm a} \times 10^2$$
^[15]

where K_a is the transient thermal index. A temperature signal (ΔT_a) was defined as:

$$\Delta T_{\rm a} = \Delta T_{\rm on} - \Delta T_{\rm off} \tag{16}$$

where ΔT_{on} is the temperature difference reached at the end of the 10-min heating period and ΔT_{off} is the temperature difference before heating. To measure J_s every half hour with a heating period of 10 min, a cycle of 10 min heating and 20 min cooling was applied and the temperature

signals were recorded every 10 min. ΔT_{off} was interpolated at the time of ΔT_{on} from ΔT_{off} surrounding measurements. The transient thermal index was calculated as:

$$K_{\rm a} = \left(\Delta T_{\rm 0a} - \Delta T_{\rm ua}\right) / \Delta T_{\rm ua}$$
^[17]

where ΔT_{0a} is the maximum temperature difference obtained under zero flow conditions and ΔT_{ua} is the measured signal at a given J_s . the zero flux signal was determined every night assuming that sap flow was negligible at the end of the night.

This assumption was strongly supported by slight change of daily ΔT_{0a} over the study period and minimum nocturnal *VPD* always lower than 0.3 kPa (Donovan *et al.*, 2001). The probes were inserted into the trunks at a height of 1.8 m above the soil. At this height, average sapwood area was estimated to be 1.97×10^{-2} m². After removal of the bark, the 2-cm-long probes were inserted to a depth of 2.5 cm into the sapwood, in such a way that the whole probe was fully inside the conductive sapwood. Three probes were inserted into each trunk to account for circumferential variability. The trunk area containing the probes was protected from direct solar radiation and rainfall by a deflector. Probes were connected to a data logger (CR10X, Campbell Scientific, Leicester, UK). Hourly sap flow density (J_s) , measured in the outermost ring of the sapwood, was accumulated over 24 h to calculate daily J_s (J_{out_day} expressed in kg m⁻² d⁻¹). To account for radial variation in the sap flux density in the deep sapwood, a reduction coefficient of 0.874 was applied to the J_s measured in the outermost ring of conducting xylem (Isarangkool Na Ayutthaya *et al.*, 2010). Finally, neglecting tree water storage, transpiration (T; mm d⁻¹) was estimated according to the equation:

$$T = 0.874 \times 10^{-2} \times J_{out day} \times (\text{sapwood area/tree spacing area})$$
 [18]

Canopy conductance calculation

The canopy conductance $(G_c; \text{ mm s}^{-1})$ was calculated by inverting an approximate of the Penman-Monteith equation. The approximation assumes that tree stand transpiration is well coupled to the atmosphere, i.e. decoupling coefficient (Ω) close to 0 (Jarvis and McNaughton, 1986; Phillips and Oren, 1998):

$$G_{c} = \frac{\gamma \cdot \lambda \cdot T}{C_{p} \cdot \rho \cdot VPD}$$
[19]

where γ is the psychrometric constant (Pa K⁻¹), λ is the latent heat of water vaporization (J kg⁻¹), T is transpiration, C_p is the specific heat of dry air at constant pressure (J kg⁻¹ K⁻¹), ρ is the atmospheric density (kg m⁻³) and *VPD* is the air vapour pressure deficit (kPa). G_c was calculated at midday (G_{c_md}) from the maximum vapour pressure deficit (*VPD*_{max}) and the daily maximum transpiration estimated from the sap flow (T_{max} ; mm s⁻¹).

Modeling

Basic relationships

The main relationships of BILJOU99 framework have been described in the introduction and more details are provided in Granier *et al.* (1999). The model inputs are daily data of leaf area index, rainfall and Penman potential evapotranspiration (*PET*). Instead of *PET* we used the FAO reference evapotranspiration *ETo* (Allen *et al.*, 1998) which is currently available in world weather networks. The model can simulate the soil water balance by daily tipping buckets if runoff is negligible, which was not the case here. The present study was focused on transpiration controls and for the sake of accuracy we used only measured soil water availability.

Details of calculation

Potential, climatic or maximal transpiration was first calculated from the following equation:

$$T_{\max} = rm * ETo$$
^[20]

where rm depends on LAI_{max} ;

Second, $T_{\rm max}$ could be decreased according to the LAI pattern by the following reduction coefficient:

$$rLAI = (LAI / LAI_{max})$$
^[21]

The effect of soil water shortage was simulated by the calculation of a reduction coefficient (*rREWc*) as:

$$rREWc = rLAI \qquad \text{if } REW > REWc$$
$$rREWc = (rLAI / REWc) * REW \qquad \text{if } REW \le REWc \qquad [22]$$

where REWc is the critical value of relative soil water content.

Hence the transpiration was calculated according to the following formula:

$$T_{\rm mod} = rREWc * T_{\rm max}$$
[23]

The expected saturation of transpiration at high evaporative demand was introduced in the BILJOU99 framework by applying a reduction coefficient above a critical value of *ETo*:

$$T_{\text{mod}_\text{ETOc}} = min \ (rREWc \ ; \ rEToc) \ * \ T_{\text{max}}$$
[24]

For simplicity of writing we could have included the negative effect of high *ETo* in equation [20]. But we have preferred to separate the effects because of functional reasons. Equation [20] represents a general climatic driving effect (positive) on transpiration whatever plant species. While *rEToc* in equation [24] expresses a negative effect which varies according species and which is attributed to plant hydraulic limitations (Oren and Pataki, 2001; Bush *et al.*, 2008; Isarangkool na Ayutthaya *et al.*, 2011; Ocheltree *et al.*, 2014).

Diagnosis of hierarchy between water constraints

The approach was to use the calibrated framework to simulate independently or in combination the factors that control the regulation of transpiration on an annual basis and to separate the rainy season and dry season. The regulations of transpiration was expressed as the ratio between the cumulated potential transpiration, driven by evaporative demand and stand characteristics under full canopy conditions (LAI_{max}), and the cumulated actual transpiration possibly reduced by defoliation, soil water availability or sensitivity to air dryness. Such a calculation assumes that reduction factors act independently which is certainly not true in the details. The annual cycle of transpiration was considered from January 1 to December 31, and the rainy season from May 1 to October 31. The few gaps in the daily transpiration were interpolated from *ETo* using an average ratio T/ETo measured on surrounding data (at least 4 days).

Data analysis

Statistics were performed using the XLSTAT software (Addinsoft, Paris, France). The agreement between measured and simulated data was quantified by using the coefficient of determination (R^2), root mean square error (*RMSE*) and relative root mean square error (*RRMSE*). Absolute and relative root mean square errors were calculated according to the following formulas:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n} (x_{mea,i} - x_{mod,i})^{2}}{n}} , RRMSE = \sqrt{\frac{\sum_{i=1}^{n} (x_{mea,i} - x_{mod,i} / x_{mea,i})^{2}}{n}}$$

where $x_{mea,i}$ is the measured value, $x_{mod,i}$ is the simulated value at place *i* and *n* is the number of values.

3. Results

Seasonal variations of environmental water constraints, LAI and transpiration

The evaporative demand as expressed by *ETo* largely fluctuated between 1 and 9 mm d⁻¹ with a cumulative value of 1,247 mm year⁻¹ (Figure 6A), 23% above the cumulative rainfall (965 mm) in 2007. *ETo* values were particularly high during the six months of the dry season, from 3 mm d⁻¹ in November up to 9 mm d⁻¹ in March, corresponding to a *VPD* value above 1.0 kPa. The evaporative demand remained relatively high in the first part of the rainy season (from May to July) and decreased markedly in August, September and October, with *ETo* and *VPD* values below 2.0 mm d⁻¹ and 0.7 kPa, respectively.

The water availability of the bulk soil or *REW* logically followed the rain occurrence (Figure 6B), with values close to 1.0 at the start of the rainy season in the topsoil (0 - 0.6 m). The availability decreased sharply to 0.2 in July, in the middle of the rainy season. The *REW* again reached high values (above 0.5) from August to October. *REW* values above 1 at the end of October suggested temporary water logging in the topsoil which was confirmed by observations. The *REW* quickly decreased in the dry season, reaching 0.2 in January. In the deep soil (0.6 - 1.6 m), the *REW* value indicated low water availability with little change over the year (maximum 0.26).

As represented by the schematic change in the *LAI* (Figure 6C), leaf shedding occurred in January and February, immediately followed by leaf flushing, with the latter occurring when the evaporative demand was the highest. The maximum *LAI* deduced from litter fall measurements averaged 3.9 at the end of 2007 (n = 9, SD = 0.7). The period with full canopy included approximately the period of highest soil water availability and lowest evaporative demand.

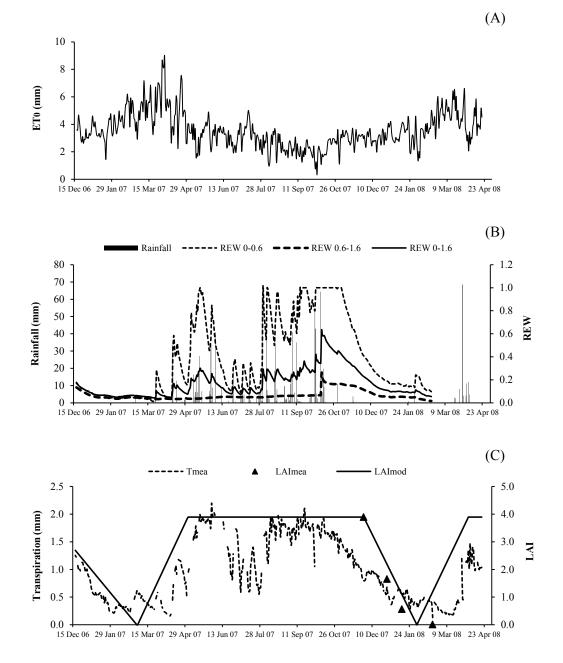


Figure 6 Seasonal course of: (A) reference evapotranspiration (ETo); (B) rainfall (solid bar) and relative extractable water of bulk soil (*REW*) for layers 0 - 0.6 m (*REW* 0-0.6), 0.6 - 1.6 m (*REW* 0.6-1.6) and 0 - 1.6 m (*REW* 0-1.6); and (C) measured transpiration (T_{mea} , dotted line) and leaf area index estimated from litter fall (*LAI*_{mea}, triangles) and schematic shape (*LAI*_{mod}, solid line).

The maximum transpirations estimated by sap flow measurements (T_{mea}) were steady (approximately 2.0 mm d⁻¹) throughout the period with full canopy (Figure 6C). The intermittent decreases evident in June and July related to the evolution of the *REW* in the topsoil (Figure 6B). The lowest transpiration corresponded to the time of leaf shed. However it never reached zero values despite almost complete defoliation. However, the sap flow measurement using the TTD method has low accuracy at very low flow rates (Isarangkool na Ayutthaya *et al.*, 2010). The minimum recorded transpiration was 0.1 mm d⁻¹ on April 11, 2007 and the maximum value was 2.2 mm d⁻¹ on May 31, 2007.

Transpiration versus ETO, REW and LAI

ETo

Under conditions of full canopy and non-limiting soil water (REW > 0.5), transpiration plotted versus ET_0 showed a linear response at low evaporative demand but it exhibited a pseudo-plateau above approximately 2.3 mm d⁻¹ (Figure 7A). The average slope of the linear section crossing the origin was estimated as 0.9 (\pm 0.052). Such a slope corresponds to rm, the T_{max}/ET_0 ratio, in the model framework (Equation 20). Several values of T_{max}/ET_0 were above 1.0 at low ET_0 . First, ET_0 is a reference value which does not necessarily represent the maximum ET for this particular stand. Second, transpiration could have been overestimated by sap flow measurement, particularly for rainy days and low flow rates. In Figure 7B, T_{max}/ET_0 was plotted versus ET_0 discarding y values above 1. The relationship fitted well a Lohammar's function ($y = -0.585\ln(x) + 1.2492$; $R^2 = 0.87$). The R^2 has little meaning here because the variables were directly related by ET_0 in the calculation. However Lohammar's function provided better results of $T_{mod_ET0_0}$ than a linear adjustment. The plot of midday canopy conductance (G_{c_md}) versus VPD_{max} confirmed the underlying mechanism of stomatal regulation at increasing VPD (Figure 8). According to the fitted Lohammar's function (Lohammar *et al.*, 1980), the reference G_e at 1 KPa and the sensitivity term equal 4.74 mm s⁻¹ and 7.6, respectively.

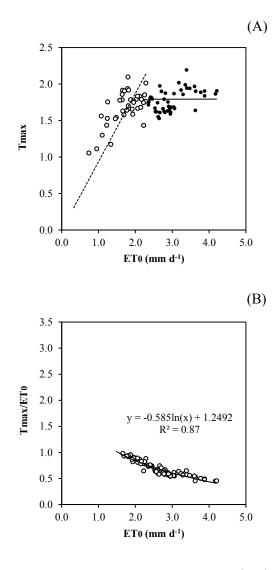


Figure 7 Daily transpiration versus reference evapotranspiration (ETo): (A) measured maximum transpiration (T_{max}) in the absence of soil water stress (*REW* 0-0.6 \geq 0.5), closed circles indicate $ETo > 2.3 \text{ mm d}^{-1}$, open circles indicate $ETo < 2.3 \text{ mm d}^{-1}$, dotted line represents the linear regression below 2.3 *ETo* and crossing origin; (B) relative transpiration (T_{max}/ETo) .

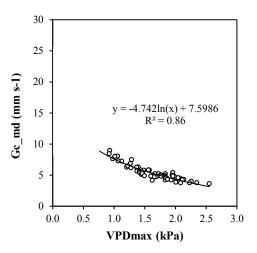


Figure 8 Midday canopy conductance (G_{c_md}) versus maximum vapour pressure deficit (VPD_{max}) at full canopy period and in the absence of soil water stress (*REW* 0-0.6 \geq 0.5).

LAI

Transpiration estimated by sap flow measurements (T_{mea}) followed in the expected manner the *LAI* seasonal pattern (Figure 6C) which supports a strong control of transpiration by the *LAI*. However, the soil water availability decreased at the same time in the dry season.

REW

The plot of T/ET_0 versus REW showed scatters of points consistent with the assumption of a threshold around REW = 0.4 (Figure 9). Above a threshold between 0.4 and 0.5, T/ET_0 exhibited a pseudo-plateau averaging 1.0, with large variability. Below the critical REW, a linear decrease toward 0:0 crossed the scatter of points. However, the assessment of the value critical REW was approximate due to the lack of soil data between 0.4 and 0.5 REW.

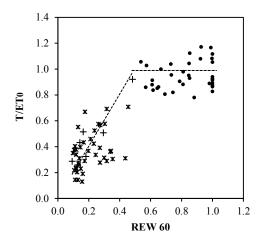


Figure 9 Relative transpiration (*T/ET0*) versus relative extractable soil water (*REW*) in top soil (0 - 0.6 m) during full canopy period (*LAI*_{max}), closed circles indicate $REW \ge 0.5 \& ET0 < 2.3 \text{ mm d}^{-1}$, asterisks indicate $REW < 0.5 \& ET0 < 2.3 \text{ mm d}^{-1}$. Trends are shown as dotted lines, averaged as 1.0 for $REW \ge 0.5$ and as a reduction coefficient for REW < 0.5.

Simulation of transpiration

Conditions of simulation

For the calculations described in paragraph of Material and Methods :

- *rm* was tested between 0.9 and 1.0 according to Figure 7A and Figure 9, and finally 1.0 was kept.
- LAI_{max} was taken equal to 3.9 as measured.
- *REW* was calculated for the top soil (0 0.6 m) with weighting by percentage of fine root length distribution as described in paragraph 2.3.
- The active soil depth and weighting by root distribution were kept constant over the annual cycle.
- *REWc* was taken equal to 0.4 according to BILJOU99 framework and Figure 9.
- *rEToc* was calculated according the function deduced from Figure 2B:

If $ETo \leq EToc$, rEToc = 1If ETo > EToc, $rEToc = a *\ln(ETo) + b$ with $EToc = 2.3 \text{ mm d}^{-1}$, a = -0.585 and b = 1.2492.

Simulated transpiration

The transpirations simulated with the original framework of BILJOU99 (T_{mod}), largely overestimated during the full canopy period, particularly in April, May, June, August and November, during periods of high evaporative demand (Figure 10). The values simulated with regulation at high *ETo* (T_{mod_ET0c}) logically better expressed the seasonal change of transpiration; however substantial inaccuracy remained in the dry season with overestimates in November and underestimates in other periods (Figure 10). Table 1 summarizes the previous observations: large errors with T_{mod} and the substantial improvement with regulation at high evaporative demand in the rainy season (*RRMSE* < 35%). In the dry season, the errors were substantial (*RRMSE* > 60%); however they are emphasized by the relative expression versus the low absolute values.

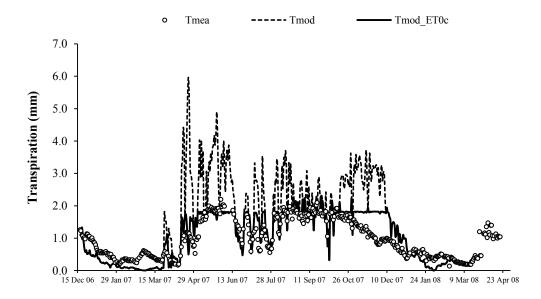


Figure 10 Seasonal change of transpiration from measurement (T_{mea}) , simulation with original BILJOU99 framework (T_{mod}) and with evolution including threshold of ETo $(T_{mod ET0c})$.

Model	Observation No.	R ²	Whole year <i>RMSE (RRMSE</i>) (mm.d ⁻¹)	Wet season <i>RMSE(RRMSE)</i> (mm.d ⁻¹)	Dry season <i>RMSE(RRMSE)</i> (mm.d ⁻¹)
$T_{\rm mod}$	379	0.56	1.06 (1.01)	1.00 (0.67)	1.10 (1.19)
$T_{\rm mod_ET0c}$	379	0.77	0.39 (0.56)	0.30 (0.31)	0.45 (0.68)

Table 1 Evaluation metrics of simulations of transpiration according to two frameworks: originalBILJOU (T_{mod}), simulation with reduction coefficient of ETo ($T_{mod ET0c}$).

RMSE; root mean square error and *RRMSE*; relative root mean square. Wet season from May 1 to October 31, 2007 and Dry season from December 18, 2006 to April 4, 2007 and November 1, 2007 to February 22, 2008.

Hierarchy between reduction factors of annual transpiration

On an annual basis, the cumulative measured transpiration (430 mm) was 66% lower than the potential annual transpiration (1,247 mm). The regulation was substantial in the rainy season (-39%) and twofold higher in the dry season (-81%). The simulated data provided close estimates of transpiration reduction (-64.5%) when all constraints were considered (*LAI* x *REWc* x *EToc* in Figure 11). When considering only one reduction factor, the *LAI* variation induced the lowest reduction, logically located in the dry season, at the time of defoliation. The impacts of *REWc* and *EToc* were similar with substantial reduction around -45%, slightly higher for *EToc* (-50.1%). The *EToc* constraint was significantly higher than the *REWc* constraint in the rainy season (Figure 11B). It was noteworthy that the overall effect of the *EToc* constraint alone already represented 76% of the total reduction with the combination of the three factors of constraint. The combination with two factors of constraints supported the proposal that *EToc* had a larger impact than *REWc*. The small difference in the simulation between *REWc* and *REWc* x *LAI* suggested that the *REWc* constraint included already the *LAI* effect. The *REWc* x *EToc* interaction equivalent to the reduction with three factors, which confirmed the previous suggestion.

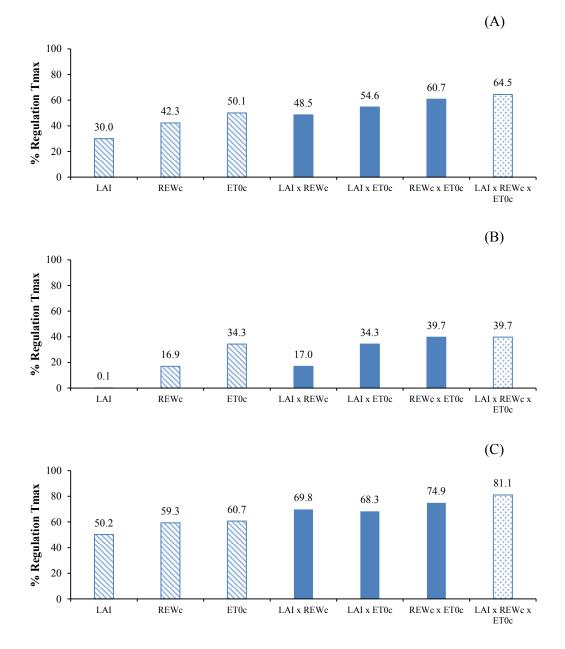


Figure 11 Regulation of seasonal transpiration (simulated with constraints/maxima) for: (A) the annual cycle; (B) the rainy season; and (C) the dry season, according to reduction factors issued from the *LAI* change, critical relative extractable water (*REWc*) and critical potential evapotranspiration (*EToc*). For details of simulation see paragraphs 2.6 and 3.3.

4. Discussion

Basic relationships of BILJOU99 framework

Our results confirmed that the basic relationships of the original framework (Granier *et al.*, 1999) hold except that the regulation of transpiration at high evaporative demand was not well simulated.

ETO_

Experimental data showed a strong regulation of transpiration under nonlimiting soil water at high evaporative demand, when the ETo was approximately above 2.3 mm d⁻¹. The analysis of the corresponding canopy conductance confirmed a dramatic decrease above VPD values equal to 1 kPa. This result supports the previous analysis of Isarangkool Na Ayutthaya *et al.* (2011) where such a response was related to isohydric behavior with a stable maximal value of the whole tree hydraulic conductance and a stable minimum value of the leaf water potential. Such regulation of transpiration versus high evaporative demand is known for several species (David *et al.*, 2004; Ocheltree *et al.*, 2014; Pataki and Oren, 2003). However, the sensitivity of this response appears dependent on wood anatomy and hydraulic conductivity. *Hevea brasiliensis* is a diffuse-porous species (Richter and Dallwitz, 2000). And our results follow the general trend that stomatal control versus high evaporative demand is stricter in diffuse-porous species than in ring-porous species. (Oren and Pataki, 2001; McCulloh and Woodruff, 2012).

 $T_{\rm max}/ETo$

Below the threshold of critical evaporative demand, the simple and common concept of a stable rm ratio between maximal transpiration and reference evapotranspiration under non limiting conditions held with our data, as rm ranged around 1.0 for a maximum *LAI* estimated at 3.89. These values appear relatively high compared to the range of 0.70 - 0.80 quoted by Granier *et al.*, (1999). However the latter quotation concerned the ratio versus *PET* (Potential Evapotranspiration with the Penman equation) which should be higher than *ETo*, the reference

evapotranspiration using the Penman-Monteith formula and FAO56 coefficients (Allen *et al.*, 1998). Moreover the accuracy on absolute value of transpiration by sap flow measurement including scaling from tree to stand level is estimated around 20% (Isarangkool Na Ayutthaya *et al.*, 2010).

REWc

Our data supported the general assumption of a linear decrease of T_{max}/ETo below a critical value around 0.4 for the *REW* (Granier *et al.*, 1999, Bréda *et al.*, 2006). This threshold of 0.4 was also quoted for other classical expressions of soil water availability, i.e. the plant available soil moisture or PAW (Sadras and Milroy, 1996) or the fraction of transpirable soil water or FTSW (Sinclair *et al.*, 2005).

LAI

The seasonal pattern of transpiration followed remarkably the main trend in the *LAI*. However, this observation did not confirm here the well-known control of transpiration by the *LAI* because the *REW* was also decreasing in the dry season. Moreover, simulations in paragraph 3.3 have shown that the decrease in the *REW* was already sufficient to reduce transpiration.

Simulation of transpiration with model evolution

Transpiration

Our results confirmed that including regulation by high evaporative demand in the model largely improved the accuracy in simulation of transpiration. However, substantial errors remained and particularly in the dry season. Besides inaccuracy on estimate of absolute transpiration by sap flow measurement, several points could explain this result with such a simple model. The model relationships were mainly tested in the rainy season and under full canopy conditions and they were applied on the annual cycle. The change in the *LAI* was estimated roughly from litter fall measurements and canopy fullness observations. Temporary water logging could have decreased transpiration in November. Also, stomatal regulation could change with leaf age, particularly during senescence and refoliation (Kositsup *et al.*, 2010). Moreover, the profile of fine root length activity changes in the dry season as shown by Gonkhamdee *et al.* (2009) while in the simulation, the *REW* calculation used the same soil depth and root profile for weighting. However at the end, the simulation provided a reasonable indication of trends in seasonal regulation of transpiration which was the objective of the tested framework.

Several models of water balance previously used for rubber tree did not consider atmospheric constraints on transpiration: CROPWAT (Allen *et al.*, 1998), WANULCAS (Boithias *et al.*, 2012; Guardiola-Claramonte *et al.*, 2010; VanNoordwich and Lusiana, 1999). The consequences could be (1) an overestimate of transpiration and root water uptake and (2) a further underestimation of stomatal regulation and consequently an overestimation of C assimilation. In a recent review, Boote *et al.* (2013) included this process as a current limitation of many crop models. Bregaglio *et al.* (2014) reported the good performance of a simple approach in arid environments based on transpiration use efficiency that explicitly accounts for the negative impact of vapour pressure deficit on photosynthesis.

A limitation of the reduction factor based on *EToc* is likely the generality of the relationship and value of *EToc* which has to be tested in different experimental conditions.

Diagnosis of the hierarchy between water constraints

The simple framework of simulation has allowed comparing the relative impact of the different constraints on annual and seasonal transpiration. The soil water shortage did not appear as the major water constraint on transpiration in the studied area. High evaporative demand, as expressed by *ETo*, appeared at least of similar importance, if not higher, than soil water shortage. The provided hierarchy is contrary to expectations in this growing area known as climatically under-optimal due to the low amount and variability of rainfall. Clermont-Dauphin *et al.* (2013) recently provided evidence that soil water shortage was not the main cause of low growth rates in young rubber plantations of North East Thailand and they suggested the importance of high evaporative demand and temporary water logging.

The results from the simulation are directly due to the fact that the sensitivity to air dryness was taken into account in the model. Such a type of response is dependent on the species or variety. We studied the most-planted clone in Thailand (RRIM 600) and the response may change with other varieties of *Hevea brasiliensis*. But the recent of work of Kobayashi *et al.* (2014) in Cambodia confirmed the sensitivity of canopy stomatal conductance to *VPD* for mature rubber trees of another clone (RRIC 100). However the details of the response may likely change according to the clone, age and stand characteristics, root development (Devakumar *et al.*, 1999), spatiotemporal acclimation and root proliferation (Liu *et al.*, 2014). We doubt in the generality of the relationship and critical *ETo* used in the framework to simulate sensitivity to air dryness. The results of Sangsing *et al.* (2004) on young plants of RRIM 600 and RRIT 251 did not show isohydric behavior under water constraints as observed in mature trees. The variability of water relations and sensitivity to air dryness certainly deserves more study.

On the other end, the lower influence of soil water shortage versus evaporative demand cannot be attributed to a relatively low soil water constraint in the experiment. The growing area of Buri Ram (south of Northeastern Thailand) is known as soil water limited with an average annual rainfall of around 1,150 mm, which is far below the recommended threshold of 1,500 mm. Moreover, the year of study was particularly dry with a rainfall amount of 965 mm. The measurements of soil water availability confirmed the severity of water shortage in both the top soil and deep soil, in the dry season as in the rainy season (Figure 12B).

Defoliation is usually limited to one or two months, with the defoliation peak between mid-January and mid-February. However, in dry years such as in the year of study, the period of defoliation could last over three months, from January to March. In addition to internal controls, canopy phenology can be influenced by both soil and atmospheric droughts (Eamus and Prior 2001, Do *et al.*, 2005). These relationships were not taken explicitly into account in the model. It is likely that such inclusions could have changed the results of simulation in the details. However it is doubtful that they could change completely the conclusion and particularly the fact that impact of atmospheric drought on transpiration regulation was at least of similar importance than soil drought.

5. Conclusions

In conclusion, the adapted framework of BILJOU99 had allowed analyzing the relative contribution of soil water shortage and atmospheric drought to the regulation of transpiration on a seasonal scale. This paper provides two main insights. The first stresses the importance of taking into account the direct regulation of transpiration versus high evaporative demand which often is omitted in simple agro-climatic models. According species, water constraint due to evaporative demand could have been underestimated in previous studies in the sub-humid tropics. The second relies on the interest in simple agro-climatic models to provide a first diagnosis of water constraints on transpiration, in order to help the evolution of cultural choices and practices toward greater sustainability.

Chapter 4

Water balance modeling of rubber tree plantations under tropical conditions: locally and regionally different parameterizations

Abstract

The expansion in climatically suboptimal areas and impact of climate change has been the big challenge to rubber tree cultivation. It threatens the sustainability of rubber cultivation and may cause to hydro-ecological impacts. The general objectives were to develop the water balance model to evaluate the annual basis of environmental constraints on tree transpiration of rubber and be able for the long term estimation of transpiration and ecophysiology. We selected the three representative mature stands in drought-prone and traditional areas. Sap flow, evaporative demand and soil water availability were evaluated to characterize the canopy transpiration. The transpiration and water balance model dealt with the general framework of agro-climatic model; BILJOU. The classical concept of regulation regarding to climate, leaf area index and soil moisture has been proved. But the saturation of transpiration at high evaporative demand was regionally different. The implementation of modeling particularly in sub-tropical climate and drought prone area required a threshold of high evaporative demand. In addition the distribution of deep roots would play an action as buffer to drought in those contexts. Our results provide a simple water balance model as a tool to evaluate the annual basis of environmental constraints on tree transpiration and enable for ecophysiology of rubber tree plantations.

1. Introduction

Rubber tree is an important crop, the only commercial source of natural rubber. At present, more than 9.82 million hectares (UNCTAD, 2013) in about 40 countries are devoted to rubber tree cultivation with a production of about 12.5 million tons of dry rubber each year.

Hevea is native from rain forests of the equatorial region in the Amazon basin (Priyadarshan *et al.*, 2005). The equatorial belt and humid zones of tropical and monsoonal climate are traditional plantation areas (Raj *et al.*, 2005). Increased world rubber consumption and pleasing prices have been the driving forces behind the current boom in rubber markets in Asia, (China, India and the ASEAN Countries) that has resulted in the rapid expansion of rubber plantation areas (Nhoybouakong *et al.*, 2009). Consequently, plantations have expanded in new or non-traditional areas where rubber can be constrained by drought, low temperature, high altitude or conversely by periodic heavy rainfall (Priyadarshan *et al.*, 2005).

Moreover, climate change poses significant uncertainties and risks to the environment and development in many countries. Thailand and Indonesia, respectively the first producer and the biggest plantation area of rubber tree are forecasted to be areas prone to climate changes. The main risk factors are higher temperatures, changes in rainfall patterns, shift of seasons and increasing number of extreme climatic events. The primary economic sector, particularly agriculture, is under uncertainties (Thomas, 2008; Ketsomboon and von der Dellen, 2013). A higher frequency of extreme events (flooding, drought) in rainy season and an increase of temperature and evaporative demand in dry season are likely in traditional as in new plantation areas (Ketsomboon and von der Dellen, 2013, Thavorntam and Tantemsapya, 2013). Consequently, rubber trees will have to cope with varying and unpredictable levels of constraints requesting appropriate strategies to foster sustainability of the plantations. Moreover, the expansion of plantation areas in suboptimal areas may have the environmental impacts (Chantuma *et al.*, 2012), for example if they change the water balances (Guardiola-Claramonte *et al.*, 2010) or soil organic matter (Li *et al.*, 2012; Yang *et al.*, 2004).

Regarding water use, rubber (at least the most common clone, RRIM 600) is an isohydric species (Sangsing *et al.*, 2004; Cochard *et al.*, 1996; Isarangkool Na Ayutthaya *et al.*, 2011). It means that the control of stomatal aperture prevents excessive desiccation and xylem

cavitation and maintains high minimum leaf water potential. The effects of soil moisture and atmospheric drought on soil water and on tree transpiration have been reported by Guardiola-Claramonte *et al.* (2010) and Isarangkool Na Ayutthaya *et al.* (2011). The later showed that, in a relatively dry area of NE Thailand, whole tree conductivity limits the transpiration under high evaporative demand, even if water is available in the soil. Our previous work showed that such behavior can be modeled through a climatic water balance model, such as BILJOU modified to include limitation of tree transpiration above a threshold of evaporative demand (Sopharat *et al.*, 2015). Such climatic models are useful for forecasting the consequences on growth, production and soil water balance on the long term as they require easily accessible parameters conversely to more functional models (Boithias *et al.*, 2012, Carr, 2012).

However the effects of different climatic conditions and consequently soil and atmospheric drought on response of transpiration have not been yet practically studied on rubber. Will the behavior of the trees be similar in less constraining areas? The ability of a climatic water balance model to analyze the constraints on tree transpiration is hence a key issue.

Our general objective of this study was to test the daily water balance model BILJOU (Granier *et al.*, 1999) and to evaluate the seasonal constraints on rubber tree transpiration for long term estimations. We selected three representative mature stands where the trees faced a large range of climatic regime. The specific objectives were to compare the annual variations of transpiration and soil moisture and to evaluate the constraint variables between traditional and new plantation areas. We hypothesized that the soil water availability along the climatic gradient was the prior factor of constraint, compared to evaporative demand. We also tested if the isohydric regulation of rubber tree could be hold under variable climatic conditions.

2. Materials and method

Study site

This study was conducted in experimental plots from three sites along a gradient of rainfall. Mature (already tapped for latex production) rubber plantations have been selected with the most common clone; RRIM 600. Two plots were located in southern part of Northeastern Thailand where the tropical dry or subtropical climate is influenced by the Mekong basin. The third plot was in Southern Thailand where the tropical monsoon climate is under marine influence from both the gulf of Thailand and the Andaman Sea. Specifications of the sites are shown in Table 2.

First plot (Buri Ram; BRR) was located in Buri Ram province, Northeastern Thailand. In this non-traditional rubber tree plantation area water is limiting for *H. brasiliensis* (Isarangkool Na Ayutthaya *et al.*, 2011). The dry season lasts six months, from November to April, and average annual rainfall is 1176 mm. The soil was deep loamy sand. Mean contents of clay, loam, and organic matter varied from 9.9, 24.2 and 0.78% in the top soil (0 - 20) to 20.2, 23.6 and 0.34% at a depth of 1.5 m, respectively.

Second plot (Chachoengsao; CCS) was located at the Chachoengsao Rubber Research Center, Chachoengsao province, Eastern Thailand. The area is non-traditional with 1328 mm cumulative rainfall, with a strict dry season between November and April. The soils belong to the Kabin Buri series with 50% sand, 15% silt and 35% clay. The soil depth is limited at 1.0-1.5 m by a compact layer of ferralitic concretions.

Third plot (Songkhla; SKL) was located in Songkhla province, Southern Thailand. This is a traditional rubber cultivation area. The wet season lasts from June to December and the dry season lasts three months, from February to April. Average annual rainfall is 1955 mm (1979-2008). The soil is clay loam. Mean contents of clay, silt, and sand varied from 37.9, 37.7 and 24.3 % at depth of 0-0.3 m and 40.6, 37.5 and 21.8 % at depth of 0.6-1.0 m, respectively.

Climatic measurements

The local microclimate at BRR was monitored automatically in an open field, at a distance of 50 m from any trees with an automatic weather station (Minimet automatic weather station, Skye Instruments Ltd, Llandrindod Wells, UK). At CCS, it was measured in the center of the observation plot, at the top of a 25 m-high tower setup with a built-in weather station connected to a data logger (CR1000, Campbell Scientific, UK). At SKL, it was recorded automatically in an open field, at a distance of 1025 m from experimental plot with an automatic weather station (Wireless Vantage Pro2TM Plus including UV & Solar Radiation Sensors; Davis Instruments Corp. USA). Half-hourly values of air temperature, relative humidity, solar radiation, wind speed and rainfall were recorded and the reference evapotranspiration (*ET* θ) was calculated according to Allen *et al.* (1998).

Table 2 The summary of parameters of the experimental plot at Buri Ram (BRR), Chachoengsao

 (CCS) and Songkhla (SKL) province.

Parameter	Buri Ram	Chachoengsao	Songkhla
Age (years)	13	14	14
Plant density (tree ha ⁻¹)	571 (spacing7 x 2.5 m)	571 (spacing7 x 2.5 m)	476 (spacing7 x 3 m)
Height (m)	12	22	22
Sapwood area ^a (dm^2)	1.97	2.73	2.43
Maximum LAI	3.89 ^b	4.38 [°]	3.27 [°]
Relative sapwood area ^d	1.97	1.60	1.35
Specific sapwood area ^e	0.50	0.62	0.74
Measurement period	18 Dec 06 – 20 Apr 08	16 Mar 07 – 24 Sep 09	1 Jan 11 – 31 Dec 12
Maximum soil water ^f (% Vol.)	0.20	0.35	0.32
Minimum soil water ^g (% Vol.)	0.07	0.09	0.25
Soil texture	Loamy Sand	Sandy clay loam	Clay loam
Determined root zone (cm)	160	80	120
Average annual rainfall (mm)	1176	1328	1955

^a average sapwood area at 1.7 m from ground level, ^b measured by litter traps (December 2007, January - February 2008), (SD = 0.7), ^c measured by hemispherical photography, ^d ratio of maximum LAI and sapwood area, ^e ratio of sapwood area and LAI, ^f soil water content at pF 2.2, ^g soil water content at pF 4.2.

Soil water measurements

BRR plot. Volumetric soil water content (θ) was measured with a neutron probe (3322, Troxler, Research Triangle Park, NC, USA) calibrated for the experimental soil with separate calibrations for upper (0-0.2 m) and lower (below 0.2 m) layers. Measurements were made every 0.2 m, from a depth of 0.1 to 1.5 m every 2 weeks. Based on observed fluctuations in soil water, the soil profile was separated into two layers, topsoil (0-0.6 m) and subsoil (0.6-1.6

m). Average field capacity and permanent wilting points were measured at 0.21 and 0.07 m³ m⁻³ for the topsoil, and 0.25 and 0.10 m³ m⁻³ for the subsoil, respectively (Isarangkool Na Ayutthaya et al., 2010). Additionally θ was measured continuously with a capacitance probe (EnvironSCAN System, Sentek Sensor Technologies, Adelaide, South Australia, Australia). The R^2 of linear regressions of top soil and sub soil was 0.92 and 0.87, respectively.

CCS plot. Every month during the observation period, soil samples at 20, 40, and 60 cm were collected in three locations within the plot; the samples were used to determine the water content after oven drying for 24 h at 105 °C. In June 2008, manual tensiometers (Raindrop, Eastern Agritek Co., Rayong, Thailand) were installed at soil depths of 30 and 60 cm at three locations close to each selected trees. The soil matric potential (ψ_{θ}) was recorded once every 2 days from July 3, 2008 to October 21, 2009 except between January 1, 2009 and June 14, 2009 because the soil was too dry during this period to measure ψ_{θ} with the tensiometers.

SKL plot. In June 2011, manual tensiometers (Raindrop, Eastern Agritek Co., Rayong, Thailand) were installed at soil depths of 10, 30, 60, 100 and 200 cm. Three sets of all depths were installed transversely in the area of selected trees. ψ_{θ} was recorded once every 2 days from June 4, 2011 to November 13, 2011.

Relative extractable water (REW)

Relative extractable water was calculated for each layer according to Granier *et al.* (1999):

$$REW_i = (W - W_m) / (W_f - W_m)$$
 [25]

where W_m is the minimum soil water content, W_f is the soil water content at field capacity and W is the actual soil water content.

To calculate the total REW for the total root zone, the REW_i per layer was weighted by the percent of fine root length inside each layer (as detailed by Gonkhamdee *et al.* (2009) and Chairungsee (2014)). At BRR, to validate the model, the REW at 0-0.6 m was used, because REW at topsoil accounted for most the transpiration and whole tree hydraulic conductance of this rubber plantation (Isarangkool Na Ayutthaya *et al.*, 2011, Sopharat *et al.*, 2015) and soil water below 0.6 m showed little changes (Figure 12C). Soil water at CCS and SKL was considered over the depth of 0-0.8 m and 0-1.2 m, respectively. Because soil depth at CCS is limited at 1-1.5 m by a compact layer of ferralitic concretions (Chairungsee *et al.*, 2013) and soil water table at SKL interpreted by tensiometer was around 1 m from soil surface over rainy season and 2 m in dry season. The drainage was modeled with the concept that when soil filled up by rainfall was over the field capacity in a given layer, water flowed to the next layers of the soil. The macroporosity and the infiltration parameters were not considered in this study.

Transpiration measurement

Sap flow density at BRR was measured by the transient thermal dissipation method (TTD, Isarangkool Na Ayuthaya *et al.*, 2010). The measurement was conducted over 15 months from December 2006 to April 2008. The probes were connected with a data logger (CR10X, Campbell Scientific, Leicester, U.K.). The hourly sap flux density $(J_s; \text{ kg m}^{-2} \text{ h}^{-1})$ was calculated according to the empirical and non-species-specific calibration assessed by Isarangkool Na Ayutthaya *et al.* (2010). At CCS and SKL, the measurement was conducted by the thermal dissipation method (Granier, 1987). The temperature difference between two probes was inversely correlated with sap flux density (J_s) according to Granier (1987). The measurement at CCS was done from 2007 to 2009 while the measurement at SKL was done in 2011 year round. Sap flow signals were recorded on a data logger (CR1000, Campbell Scientific, Leicester, U.K.). The six experimental trees were selected for the study each plot.

Hourly J_s was cumulated over a 24h period to calculate daily SFD and multiplied by sapwood area. Average daily total flow of the representative trees was divided by the soil surface theoretically available for a tree (17.5m² in BRR and CCS; 21 m³ in SKL) in order to estimate the observed tree water uptake in mm. Finally, neglecting tree water storage, transpiration (*T*; mm d⁻¹) was estimated according to the equation;

$$T = 0.874 \times 10^{-2} \times J_s \times \text{(sapwood area/tree spacing area)}$$
 [26]

where 0.874 is a reduction coefficient to compromise the reduction of sap flux density by the depth of sap wood (Isarangkool Na Ayutthaya *et al.*, 2011).

To remove the possible discrepancies between SKL and CCS in the absolute values of transpiration linked to the natural thermal gradient, the analysis was considered by relative value (T/T_{max}) .

Canopy dynamics

The canopy greenness and fullness at BRR was recorded over 100 trees every two weeks at the time of defoliation-refoliation, from December to April. The leaf shedding was almost complete at a short time and the maximum leaf area index was estimated by litter fall collection at 3.89 in 2007 (n = 9, SD = 0.7). A schematic change of leaf area index (*LAI*) over the year was deduced from observations of canopy fullness and litter fall measurements. The effective *LAI* at stand level of CCS and SKL was measured with hemispherical photography (Jonckheere *et al.*, 2004; Sopharat and Sdoodee, 2008; Chairungsee *et al.*, 2013). All pictures were analyzed using the GLA software (Institute of Ecosystem Studies, Simon Fraser University, Burnaby, Canada).

Root distribution

Gonkhamdee *et al.* (2009) reported that the majority of fine roots (83%) at BRR was within the upper 60 cm (accompanied with our observations in different sites with core sampling and minirhizotron technique and group discussions, data not shown). In modeling we proposed that root distribution index (*RDI*) of soil depth 0-15, 15-35, 35-55, 55-65 and 65-75 cm deduced by observations was 0.53, 0.26, 0.04, 0.09 and 0.08, respectively. It was assumed that no soil water contributing to transpiration below 160 cm in calculations. Similarly, we proposed *RDI* of CCS through soil depth 0-15, 15-35, 35-55, 55-70 and 70-80 as 0.53, 0.26, 0.04, 0.09 and 0.08, respectively. Soil depth was limited at 1-1.5 m by a compact layer of ferralitic concretions

(Chairungsee et al., 2013). Root distribution at SKL was assumed as 0.53, 0.26, 0.04, 0.09 and 0.08 corresponding to depth of 0-20, 20-40, 40-60, 60-80 and 80-120 cm, respectively.

Run off was neglected in present study. It was assumed that the study sites covered by rubber trees on horizontal and gentle slopes. However, the discussion of water loss due to runoff was included. Particularly, runoff has observed at BRR and annual flooding was observed at SKL.

Understorey and soil evapotranspiration

Understorey and soil evapotranspiration (E_u) was assumed that is proportional to the available energy reaching this level (Diawara *et al.*, 1991) when water is not limiting. Available energy below trees is proportional to global radiation above the canopy, and dependent on *LAI* of the tree layer. In the model, available energy below the canopy is calculated from the Beer-Lambert function and a light coefficient of extinction (k). It was assumed that an average value of k is 0.5 (Jarvis and Leverentz, 1983). Soil evaporation plus understorey transpiration were assumed to absorb water from the upper soil layer. We assumed that it was linearly decreasing with *REW* in the upper soil layer.

Rainfall interception and throughfall

Rainfall interception (In) and throughfall (Th) was estimated by the implementation of those studies by Yusop *et al.* (2003), Jiang and Wang (2003), and Oludare (2008). When rainfall higher than 1 mm and less than 50 mm, the interception (In) was calculated as following;

$$In = P * P_i * (LAI/LAI_{max})$$
^[27]

where *P* is rainfall (mm), P_i is coefficient of interception; $P_i = 0.14$ for P < 50 and $P_i = 50$ for P > 50, and *LAI* and *LAI*_{max} is leaf area index and its maximum, respectively. Then throughfall is the difference between rainfall and interception of rainfall.

Modeling

Basic relationships

The main relationships of BILJOU99 framework have been described in the introduction and more details are provided in Granier *et al.* (1999). The model inputs are daily data of leaf area index, rainfall and Penman potential evapotranspiration (*PET*). Instead of *PET* we used the FAO reference evapotranspiration ETo (Allen et al., 1998) which is currently available in world weather networks. The model can simulate the soil water balance by daily tipping buckets if runoff is negligible, which was not the case here. The present study was focused on transpiration control and for the sake of accuracy only measurement of soil water availability was used.

Conditions of modeling:

According original BILJOU framework; BILJOU99, maximal transpiration was first calculated from the following equation:

$$T_{\max} = rm * ETo$$
[28]

where rm depends on LAI_{max} . It was taken as 1.0 for BRR. It was also taken as 1.0 for CCS and SKL as pseudo-slope in full canopy conditions (Figure 15).

Second, T_{max} could be decreased according *LAI* pattern by the following reduction coefficient:

$$rLAI = (LAI/LAI_{max})$$
^[29]

where LAI_{max} is maximum leaf area index.

To simulate the effect of soil water shortage, the critical relative extractable water (*REWc*) in response to *LAI* was taken as 0.4 as in original BILJOU. It allowed calculating a reduction coefficient as following:

$$rREWc = rLAI \qquad \text{if} \qquad REW > REWc$$
$$rREWc = (rLAI / 0.4) * REW \quad \text{if} \qquad REW \leq REWc \qquad [30]$$

The same percentage of fine root length distribution was considered to weight *REWi* per soil layer over the annual cycle as the common method.

To include the regulation of transpiration at high evaporative demand in BILJOU framework (Isarangkool Na Ayutthaya *et al.*, 2011), a reduction coefficient of *ETo* was calculated. The coefficient was given by the function;

$$rEToc = a*ln(x) + b$$
[31]

where rEToc is the reduction coefficient by ETo, x is ETo, a and b is coefficient of relationship as Lohammar's equation (Lohammar *et al.*, 1980).

Then the transpiration was hence calculated according to the following formula:

$$T_{\text{mod ET0c}} = min \left(rREWc: rEToc \right) * T_{\text{max}}$$
[32]

Data analysis

Statistics were performed with XLSTAT (Addinsoft, Paris, France). The agreement between measured and simulated data was quantified by using coefficient of determination (R^2), root mean square error (*RMSE*) and relative root mean square error (*RRMSE*). Absolute and relative root mean square errors were calculated according to the following formulas:

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n} (x_{mea,i} - x_{mod,i})^{2}}{n}} , RRMSE = \sqrt{\frac{\sum_{i=1}^{n} (x_{mea,i} - x_{mod,i} / x_{mea,i})^{2}}{n}}$$

where $x_{mea,i}$ is measured value, $x_{mod,i}$ is simulated value at place *i* and *n* is the number of values.

3. Results

Seasonal variations of environmental water constraints, LAI and transpiration

BRR

The evaporative demand, *ETo* largely fluctuated between 1 and 9 mm d⁻¹ with a cumulated value of 1247 mm (Figure 12A), 29% above the cumulated rainfall, 965 mm, in 2007. *ETo* values were particularly high over the six months of dry season, from 3 mm d⁻¹ in November up to 9 mm d⁻¹ in March, corresponding to a daily maximum *VPD* (*VPD*_{max}) above 2.2 kPa. The evaporative demand remained relatively high in the first part of the rainy season, from May to July, and decreased markedly in August, September and October, with *ETo* and *VPD*_{max} below 2.0 mm d⁻¹ and 2.0 kPa, respectively.

The water availability of bulk soil or *REW*, logically followed the rain occurrence (Figure 12B), with values close to 1.0 at the start of the rainy season when the surface layers (0-0.6 m) were considered. *REW* sharply decreased down to 0.2 in July, in the middle of the rainy season. It reached again high values (above 0.5) from August to October. *REW* of the topsoil quickly decreased at the start of the dry season, down to 0.2 in January. *REW* considered in the deep soil (0.6-1.6 m) showed low water availability with little change over the year (maximum 0.26).

The schematic change of *LAI* (Figure 12B) showed that leaf shedding occurred between mid-January and mid-March, immediately followed by flushing of new leaves, occurring thereby when the evaporative demand was the highest. The maximum *LAI* deduced from litter fall measurements averaged 3.9 at the end of 2007. The period with full canopy included approximately the period of highest soil water availability and lowest evaporative demand.

Transpiration estimated by sap flow measurements (T_{mea}) was steady around 2.0 mm d⁻¹ during full canopy period (Figure 12B). There were intermittent decreases in June and July related to the evolution of *REW* in the topsoil (Figure 12A). The lowest transpiration corresponded to the time of leaf shed. The minimum recorded transpiration was 0.1 mm d⁻¹ on April 11, 2007 and the maximum value was 2.2 mm d⁻¹ on May 31, 2007.

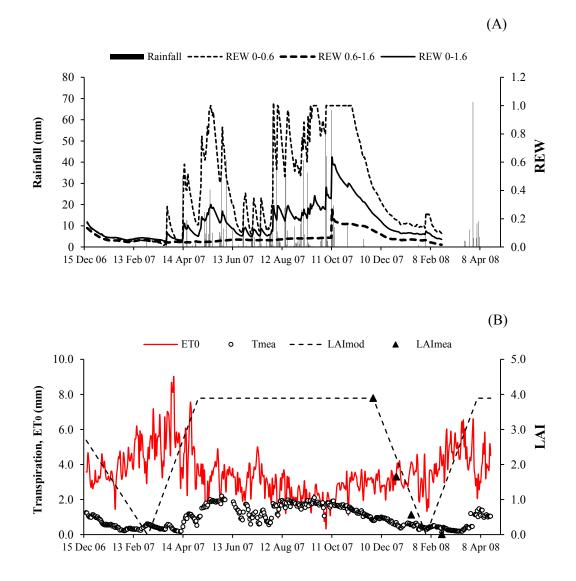


Figure 12 Seasonal course of transpiration and environments of Buri Ram site; (A) relative extractable water of bulk soil (*REW*) for layers 0-0.6 m (*REW* 0-0.6), 0.6-1.6 m (*REW* 0.6-1.6) and 0-1.6 m (*REW* 0-1.6), and rainfall (solid bar) and (B) reference evapotranspiration (*ETo*), measured transpiration (T_{mea} , open circle), leaf area index estimated from litter fall (*LAI_{mea}*, triangle) and schematic shape (*LAI_{mod}*, dot line).

CCS

Overall image the variation of evaporative demand at CCS represented according with BRR. *ETo* fluctuated between 1 and 8.8 mm d⁻¹ with a cumulated value of 3760 mm, 13% above a cumulated rainfall of 3316 mm over 30 months. And it was 1463 mm (Figure 13), 1% above a cumulated rainfall of 1451 mm over the year 2008. *ETo* values were annually high over the six months of dry season, from 4 mm d⁻¹ in November and 8 mm d⁻¹ in March, corresponding to *VPD* daily averages above 1.2 kPa. However, over three years *ETo* were suddenly decreased by summer rainfall in April annually.

REW of CCS was directly calculated with the difference of pressure head from tensiometers. The maximum and minimum pressure head was considered in the rank of 0 and -10 m, respectively. *REW* of surface soil followed logically the rain occurrences (Figure 13A). At surface layer 0-40 cm, the minimum value closed to 0.3 in January 2008. It stayed between 0.6 and 1.0 during the occurrence of rainy season from June till October. Five months of dry period was started in October until last February. *REW* of the topsoil rapidly decreased at the start of the dry season in November, down to 0.3 and 0.4 in January 2008 and February 2009, respectively.

Rapid decrease of *LAI* by shedding represented annually last December 2007 and last January 2009. The shedding events were in the same time with peak of *ETo*. And rapid expansion of new leaves resulted increase of *LAI* in the consecutively couple weeks. During growing season it stayed around 2.7 to 3.2, and maximum *LAI* was 4.27 in April 2008.

The relative transpiration variations of CCS showed the same common pattern with the site of BRR. It started to decrease sharply in early dry season, December. The relative transpiration was steady around 0.89, 0.78 and 0.97 mm d^{-1} during the full canopy period of 2007, 2008 and 2009, respectively. The annual decline of transpiration corresponded to the time of defoliation and decrease of soil moisture, during January and February.

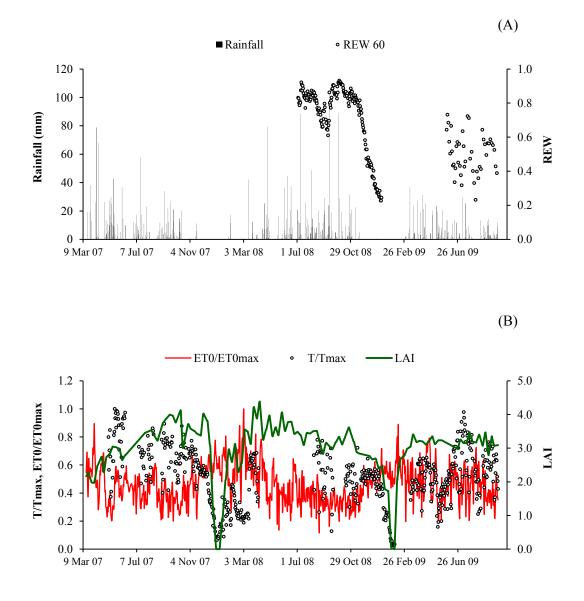


Figure 13 Seasonal course of transpiration and environments of Chachoengsao site: (A) rainfall (solid bar) and measured extractable soil water at soil depth 0.6 m (*REW*; open circle) and (B) relative value of reference evapotranspiration (ETo/ETo_{max} , red line), relative transpiration (T/T_{max} , open circle), leaf area index estimated by hemispherical photography (*LAI*, thick line).

ETo fluctuated between 0.3 and 4.8 mm d⁻¹ according to dense and low rainfall, respectively. A cumulated *ETo* of 784 mm (Figure 14) 64% lower the cumulated rainfall, 2213 mm. *ETo* were particularly lower compare to BRR and CCS. Low *ETo* corresponded to dense rainfall events, particularly rainy season during August and December. It was steady around 4.0 mm d⁻¹ when intermittent drought evidenced in July. The slight increase of *ETo* during shedding and refoliation was different with sharp increase at BRR and CCS. However, the interruption by summer rainfall at SKL was consistent with CCS. Moreover, averaged thirty year of rainfall distribution around SKL (1979-2008, data from Kho Hong Agromet, Songkhla, Thailand) showed the rainy event 160 day per year (201 day per year by observation in 2011) higher than 147 day per year of observation at CCS during 2007 to 2009.

REW at SKL was also directly calculated with the difference of pressure head from tensiometers. The intermittent drought of topsoil (0.3 m) was developed where *REW* down to 0.4 in July and August (Figure 14B). But the subsoil at 0.6 m stayed above the stress over the rainy season from July to December. *REW* of the deep soil (2 m) expressed high water availability (*REW* > 0.8) with little change.

Rapid defoliation by shedding occurred between last January and last February (Figure 14B). Maximum *LAI* of the growing season in 2011 was 3.27, slightly lower than 3.47 before shedding in previous season. The defoliation was approximately 1 month later the occurrences at CCS. And the slight decrease of *LAI* in July was consistent with topsoil water stress and high *ETo*.

The relative transpiration estimated by sap flow measurements followed the seasonal pattern of *LAI* (Figure 14B). It was steady around 0.99 during full canopy period. The lowest transpiration corresponded to the time of defoliation. It was on March 3, 2011 with the same time of lowest *LAI*.

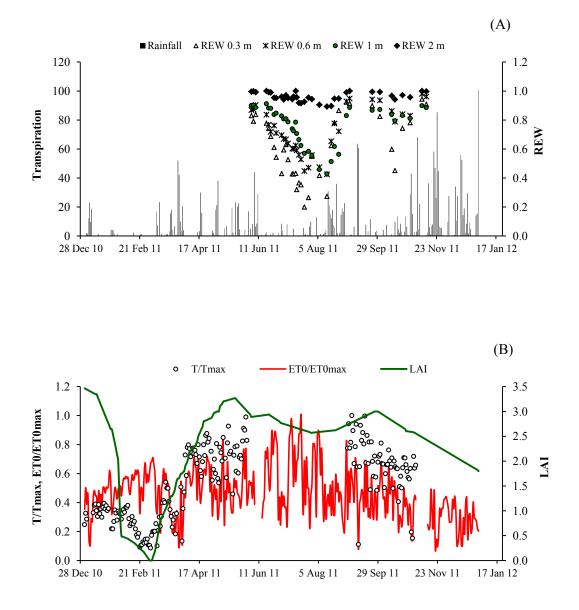


Figure 14 Seasonal course of transpiration and environments of Songkhla site; (A) relative extractable water of bulk soil (*REW*) for layers 0.3 m (*REW* 0.3 m), 0.6 m (*REW* 0.6 m), 1 m (*REW* 1 m), 2 m (*REW* 2 m), and rainfall (solid bar) and (B) relative value of reference evapotranspiration (ETo/ETo_{max} , red line), relative transpiration (T/T_{max} , open circle), leaf area index estimated by hemispherical photography (*LAI*, thick line).

Transpiration versus LAI, ET0 and REW

In conditions of full canopy and non-limiting soil water (*REW*>0.5), transpiration at BRR plotted versus *ETo* showed a linear response at low evaporative demand but it exhibited a plateau above approximately 2.3 mm d⁻¹ (Figure 15A). The average slope of the linear section was 0.9 (\pm 0.052). The expression of CCS was similar with BRR. But with the limited data of soil moisture, we could not analyze such a relationship with the data of CCS and SKL, particularly low soil moisture (Figure 15C, 15D). However, seasonal response between transpiration and *ETo* at both sites was represented evidently. The response of transpiration to *ETo* during full canopy period was obviously similar with BRR. The analysis with relative transpiration showed that threshold of *ETo* induced saturation of transpiration at CCS was higher than BRR (Figure 15B, 15D). It was around 3.5 mm d⁻¹ at CCS, while it was around 2.3 mm d⁻¹ at BRR. The different response between full canopy period and off season was also evident at SKL. However, the plateau of transpiration was by *ETo* above 2.2 mm d⁻¹. However, we assumed that pseudo-slope between the absolute transpiration and *ETo* in response of CCS and SKL was approximately 1.0, consequently brought to the transpiration modeling.

The simulation of transpiration and soil water

The transpiration of BRR simulated with the original framework of BILJOU99 (T_{mod}) , was largely overestimated over the full canopy period, particularly in April, May, June and November, at periods of high evaporative demand (Figure 16A, Table 3). The simulation with regulation of high ETo (T_{mod_ET0c}) improved the seasonal change of transpiration; however inaccuracy remained in dry season with underestimations. Meanwhile, the transpiration of CCS and SKL were well explained by original framework of BILJOU99 (Figure 16B, 16C, Table 3). It was classical that *REWc* as 0.4 well explained the transpiration of SKL, but it was 1.0 for CCS. The interest was the expressions of underestimate during dry season were consistent among three sites. The transpiration estimation of CCS was evidently accurate in senescence period, November and December (Figure 16B).

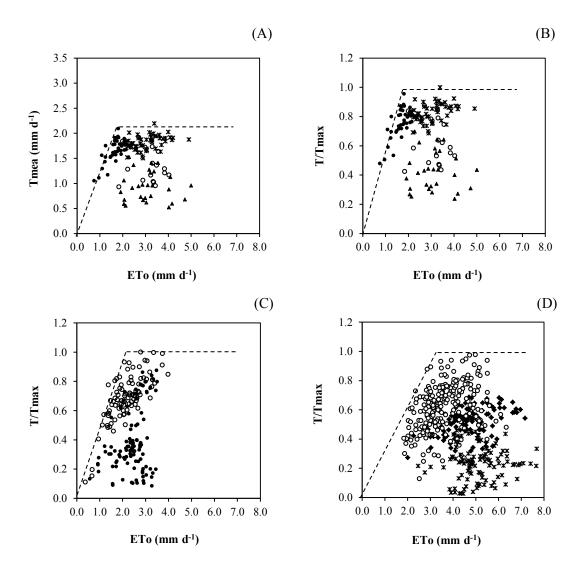


Figure 15 Daily reference evapotranspiration (*ETo*) versus (A) measured transpiration (T_{mea}) of Buri Ram site in full canopy; May – October (asterisk; *REW* > 0.5 & *ETo* \geq 2.2, closed circle; *REW* > 0.5 & *ETo* < 2.2, open circle; *REW* \geq 0.2 & < 0.5, triangle; *REW* < 0.2), (B) relative transpiration (T/T_{max}) of Buri Ram site in full canopy; May – October (asterisk; *REW* > 0.5 & *ETo* \geq 2.2, closed circle; *REW* > 0.5 & *ETo* < 2.2, open circle; *REW* \geq 0.2 & < 0.5, triangle; *REW* > 0.5 & *ETo* \geq 2.2, closed circle; *REW* > 0.5 & *ETo* < 2.2, open circle; *REW* \geq 0.2 & < 0.5, triangle; *REW* < 0.2), (C) relative transpiration (T/T_{max}) of Songkhla site (open circle; May – October, close circle; November – April) and (D) relative transpiration (T/T_{max}) of Chachoengsao site (open circle; full canopy during May – November, asterisk; December, March & April, trapezoid; January – February). Dot line is a pseudo-plateau line and pseudo-slope. Solid line is a slope with observed data.

Without address of rEToc but it was sufficient to estimate REW for SKL; R^2 equaled to 0.80, 0.81, 0.48 and 0.37 for soil depth at 0.3, 0.6, 1.0 and 2.0 m, respectively. However, it allowed the moderate accuracy for CCS. It was contrast with BRR that the accuracy of simulated *REW* was poor (Table 3).

The interest for BRR was the simulation with coefficient of interception; $P_i = 0.141$ when P < 50, resulted the lower accuracy of transpiration ($R^2 = 0.64$, RMSE = 0.46) and REW ($R^2 = 0.22$, RMSE = 0.31). But the randomly adjusted $P_i = 0.5$ allowed higher accuracy of transpiration ($R^2 = 0.70$, RMSE = 0.39) and REW ($R^2 = 0.53$, RMSE = 0.29). The difference of P_i as 0.395 was hence implied to water loss by runoff or/and drainage. This implementation was also done with modeling of CCS, $P_i = 0.3$ improved the estimation.

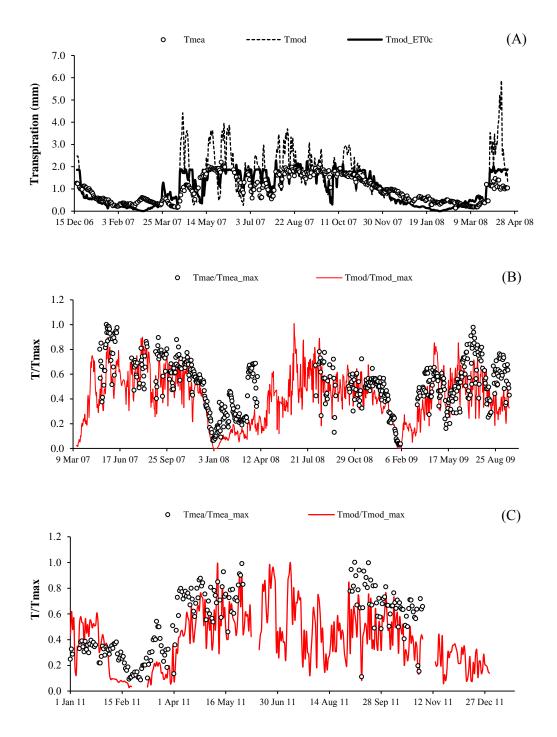


Figure 16 Seasonal change of simulated results at (A) Buri Ram site; transpiration from measurement (T_{mea}) , simulation with original BILJOU (T_{mod}) and BILJOU evolution with threshold of *ETo* (T_{mod_ET0c}) , (B) Chachoengsao site; relative transpiration from measurement (T/T_{max}) , simulation with *REWc* 1.0 $(T_{mod_REWc \ 1.0})$ and (C) Songkhla site; relative transpiration from measurement (T_{mea}/T_{mea_max}) , simulation with original BILJOU (T_{mod}/T_{mod_max}) .

Model	Site	Comparison	Observation	\mathbf{R}^2	RMSE	RRMSE
			No.			
Original	BRR	Transpiration	432	0.51	0.79	0.84
		REW	431	0.54	0.31	0.97
Evolution		Transpiration	432	0.70	0.39	0.63
		REW	431	0.53	0.29	0.96
Original	CCS	Transpiration	572	0.47	0.75	0.47
		REW	231	0.56	0.20	0.34
Evolution		Transpiration	572	0.39	0.70	0.47
& 0.4 <i>REWc</i>		REW	231	0.62	0.19	0.33
Original		Transpiration	572	0.58	0.61	0.39
& 1.0 REWc		REW	231	0.66	0.16	0.35
Original	SKL	Transpiration	202	0.59	0.57	0.59
		REW^{a}	36	0.81	0.15	0.25

Table 3 Evaluation metrics of simulations of transpiration according to three models: original
 BILJOU, simulation with evolution model by reduction coefficient of *ETo*.

RMSE; root mean square error is to indicate global accuracy and stability, *RRMSE*; relative root mean square error is to indicate accuracy and stability in individual dimension. ^{*a*} relationship between measured *REW* at depth of 0.6 m and simulate *REW* at 1.2 m with logarithm.

4. Discussion

The regulation of high evaporative demand

It was proved that under well-watered soil conditions of subtropical climate, transpiration was tightly regulated in response to high evaporative demand (Isarangkool Na Ayutthaya et al., 2011). Our modeling confirmed that transpiration in subtropical climate; BRR, exhibited saturation at high evaporative demand with the threshold of ETo 2.3 mm d⁻¹ (Figure 15). Although data analysis showed the tendency of such response in CCS and SKL, implementation with modeling induced underestimation of transpiration in both sites. The major factors responsible on decrease of transpiration at both sites were classical; LAI, climate and soil moisture (Granier et al., 2000; Small et al., 2008; Sommer et al., 2002). Despite seasonal response between transpiration and evaporative demand of three sites was consistent. It is suggested that the rubber (clone RRIM 600) served the adaptations to the difference of climate regimes. However, the physical property of xylem vessels in preventing cavitation of the same clone would not be different by environments (Pammenter and Vander Willigen, 1998). Hence the isohydric behavior of RRIM 600 (Isarangkool Na Ayutthaya et al., 2011) has to be additionally redefined which may focus to leaf scale (Ocheltree et al., 2014). We suggested that response with high evaporative demand is the priority of safety margins to prevent cavitation for rubber, particularly in drought prone areas where is higher risk to cavitation.

It was suggested that driving by difference of climatic regimes, despite RRIM 600 could be adaptable to hold maximum transpiration; *rm* as 1.0 or higher when soil water and evaporative demand is not limiting. However, the leaf scale response to climatic drought would be different and suggested by the adaptation of leaf hydraulic conductivity regardless of stem hydraulic conductivity or sapwood permeability (Maherali and DeLucia, 2000).

Within a species, trees grown in climates with high evaporative demand will have low ratio of leaf and sapwood area (A_L/A_S) (Whitehead *et al.*, 1984). It is a common concept that A_L/A_S declines with increase of tree height, and declines along gradients of low to high evaporative demand (McDowell *et al.*, 2002). Low A_L/A_S and high sapwood permeability provides the way to increase hydraulic conductivity in response to high evaporative demand and prevent xylem tensions from reaching values that cause catastrophic cavitation (Maherali and DeLucia, 2000). However, the relative sapwood area in Table 2 deduced by *LAI* and sapwood area showed that it increased positively with the gradients evaporative demand. It was contradictory with common concepts. Despite it decreased with increase of tree height. We suggested that higher A_L/A_s in BRR caused the susceptibility in loss of canopy conductivity when evaporative demand increasing. In this case high evaporative demand played a substantial regulation on transpiration in subtropical area. This suggestion is regardless of vulnerability of xylem to cavitation, isohydric property still maintained. According to Darcy's law and basis with the same clone, sapwood permeability and soil-leaf water potential would not be diverged (McDowell *et al.*, 2002; Mencuccini and Grace, 1995).

Moreover, with regardless of long term of climatic factors it could be in several reasons cause rubber has different responses; the sensitivity of root stock to variations of soil water content (Atkinson *et al.*, 2000; Chen *et al.*, 1997), the sensitivity of root xylem to cavitation and stomatal closure, daily loss of root conductivity (Domec *et al.*, 2004 and 2006), development of root in soils and the plasticity of root cavitation resistance (Feddes *et al.*, 2001), the effect of soil texture regardless of soil moisture regime (Jackson *et al.*, 2000).

Simulation of transpiration and soil water availability with BILJOU evolution

Our modeling lacked the dynamics of fine root distribution, particularly deep root during dry season (Alsina *et al.*, 2010; Guardiola-Claramonte *et al.*, 2010). Consequently, to explain water uptake which detected by sap flow measurements in conditions of low leaf area and dry season by modeling was insufficient. The interest of underestimation of transpiration at CCS; hard pan against penetration of deep root, is the ability of its proliferation and soil water uptake during dry season (Weaver and Crist, 1922). To account the threshold of evaporative demand in modeling caused the underestimate of transpiration in CCS and SKL.

Transpiration

The transpiration modeling of BRR was reasonable to explain by the regulation of high evaporative demand over the course of full canopy. However, only *LAI* based on agroclimatic model was sufficient to estimate transpiration in CCS and SKL. To account threshold of evaporative demand resulted the underestimation for CCS and SKL. It was suggested that the empirical implementation to model transpiration could be different, even the same clone. The local and regional parameterizations have to be concerned (Feddes *et al.*, 2001).

REWc as 1.0 rather than 0.4 well explained the transpiration of CCS. It means the transpiration decreased linearly when soil moisture started decreasing from higher value. It is suggested that the limitation at 1-1.5 m by a compact layer of ferralitic concretions (Chairungsee *et al.*, 2013), might be a factor limited transpiration response at this site and related root proliferation. Therefore the limitation of root zone might be a major factor in contribution.

The underestimation of CCS was a great number during dry season in 2008. It was consistent with BRR and SKL, but it was slightly lower in BRR and SKL. The difference between measured and simulated transpiration during dry season could deduce the ability of deep root to redistribute hydraulic conductivity to the soil surface.

The results from model suggested that it requires the dynamics of fine root distribution in modeling. And the definition of soil depth at soil surface which corresponded with fine root distribution was very sensitive to transpiration estimation, as we defined 15 cm soil surface at CCS rather than thicker, corresponded with fine root distribution in this sites (Chairungsee, 2014).

The annual transpiration of three sites was a common pattern. The transpiration decreased evidently during dry season; around January in BRR and CCS and February in SKL. And the sap flow measurement and estimation of water uptake increased rapidly after start of flushing. However, it would be suggested that the stomata of newly flushed leaves might remain closure until the onset of the first rains (Rojas-Jiménez *et al.*, 2007). Accordingly, the *LAI* analysis with logistic growth curve with the data set of SKL showed that it took around 77 days to approach full canopy. And maximum increasing rate of *LAI* was around day 26 after flushing. Consequently, the hydraulic capacity of new leaves may not link to hydraulic conductivity in the stem and roots. The soil water discharge by recovery of stem water potential (Guardiola-

Claramonte *et al.*, 2010) is suggested a limit of our model, resulting underestimation in dry season. However, our modeling implied that during flushing the climatic-independent water uptake was around 60 % by deep roots.

In addition, it was surprised that even with or without drought but the transpiration of three sites decreased annually during mid-year. It was also consistent with study at other sites (Guardiola-Claramonte *et al.*, 2010; Kobayashi *et al.*, 2014).

REW

The calibration with measured *REW* of CCS and SKL stated that soil matric potential provided more realistic *REW* than those based on soil water content. It could be suggested that the available soil water sensitive to transpiration response played role in a rank between field capacity and -100 kPa, in active root zone. Modeling based on soil water content could lead to unrealistic *REW*, and hence transpiration reduction function (Verhoef and Egea, 2014). Thus we propose that modeling with climatic model in the different soil properties, soil water potential rather than water content would be considered for eliminating the effect of soil texture and locations. Because it relates directly to the concept of soil-plant-atmosphere continuum through the hydraulic pull (Sperry *et al.*, 1998). However, soil water retention curve is still required for water balance.

The defined root zone of BRR, CCS and SKL (Table 2) were reasonable to explain water discharge by active fine roots. The calibration by *REW* by those fractions of root distribution supported the results of transpiration estimation. The underestimation of transpiration during dry season emphasized the hypothesis of deep root water uptake (Gonkhamdee *et al.*, 2009; Guardiola-Claramonte *et al.*, 2010) and the contribution of hydraulic redistribution (Burgess *et al.*, 1998; Dawson, 1993; Domec *et al.*, 2004; Emerman and Dawson, 1996; Lee *et al.*, 2005).

5. Conclusions

The classical concept of transpiration regulation by climate, leaf area index and soil moisture is approved. But the saturation of transpiration by high evaporative demand showed the regional differences. The implementation of modeling, including threshold of high evaporative demand is required locally in sub-tropical climate and drought prone area. However, such framework induces underestimation in mildly drought prone and optimal area. Our results provide a simple water balance model as a tool to evaluate the annual basis of environmental constraints on tree transpiration and enable for ecophysiology of rubber tree plantations.

Chapter 5

Leaf area index and latex yield: a comprehensive link understand the direction of C-assimilation and carbohydrate reserve in rubber tree

Abstract

Tapping in rubber trees induces a strong additional sink related to carbohydrate reserve and latex production. However, the timing from the CO₂ assimilation till latex flow is poorly answered. Therefore, a response at canopy scale between rubber yield production and leaf area index (*LAI*) with supplement of climatic factors was studied. The representation of the mature rubber plantations were selected in traditional area, southern Thailand. It showed that the variations of *LAI* were the prior factor influence on the latex yield production. The variations of dry rubber weight lagged behind *LAI* pattern and percent of dry rubber content (%DRC) around 80 (R^2 =0.65, *RMSE*=6.83) and 53 (R^2 =0.32, *RMSE*=9.70) days, respectively. And the maximum temperature above 25 °C influenced on %DRC later 81 days (R^2 =0.36, *RMSE*=2.13). However, there was poor correlation between rubber yield and climatic factors in this study. The results support the hypothesis that the majority of latex yield initiated from the carbohydrate reserve. It is suggested that around three months after photosynthesis; the carbon assimilation at canopy is spent to metabolize latex.

1. Introduction

The relationship between latex yield and environmental factors, with consequence on growth has been described in many studies: the assessment of the potential of rubber yield in dry sub-optimal conditions (Priyadarshan *et al.*, 2005), the relationship between latex yield and antecedent meteorological parameters (Rao *et al.*, 1998), the influence of soil and meteorological factors on water relations and latex yield (Rao *et al.*, 1990; Raj *et al.*, 2005), the potential to increase rubber production by matching tapping intensity to leaf area index (Righi

and Bernardes, 2008), the ecophysiological factors to underpin productivity of rubber (Rodrigo *et al.*, 2001).

In general low vapour pressure deficit (*VPD*) and higher soil moisture is favorable for latex yield. Latex vessel pressure potential or turgor pressure controlling latex flow is directly affected by *VPD*. Air temperature above 35 °C induces stomatal closure and reduction of photosynthetic rates. It is quite clear that the rubber yield production is influenced antecedently by the climatic factors e.g. rainfall, maximum and minimum temperature, sunshine duration, *VPD*, and evapotranspiration. A 10 day mean minimum temperature of over 22 °C is favorable to latex regeneration but unfavorable for latex flow. The ambient temperature 18-24 °C is ideal for latex flow. The significant positive correlation has been observed between prior a month rainfall and the latex yield of rubber (Rao *et al.*, 1990, 1998). Soil water availability 3 days prior to tapping was reported as the prior factor affecting latex yield. And the responses of yield with environmental factors of rubber varies depend on clonal character (Raj *et al.*, 2005). Rubber is produced when photo-assimilate compounds are channeled to rubber synthesis (Righi and Bernardes, 2008). It could be concluded that rubber yield and latex flow variability associate with prevailing and antecedent weather and climatic conditions.

Moreover, it is well known that tapping the rubber trees for latex harvest induces a strong artificial carbon sink to regenerate the exported latex (Lacote *et al.*, 2004 and 2010, Silpi *et al.*, 2007). Therefore, carbon allocation to the laticifer cells is known the key-point of rubber tree productivity (d'Auzac *et al.*, 1989; Lacote *et al.*, 2010). It was reported that photosynthesis correlated with girth increment but not with latex yield (Samsuddin *et al.*, 1978). In addition, it was reported that photosynthesis traits is related with planting density (Samsuddin and Impens, 1979), adaptation to shade (Senevirathna *et al.*, 2003) and canopy profile and depth (Kumagai *et al.*, 2013). Kositsup *et al.* (2009) showed that photosynthetic parameters of rubber leaf vary a lot according to their position within the canopy.

Although those studies provided the relevant information of latex yield production, practically the canopy scale has been rarely studied and linked to the variations of latex yield production. The study by Righi and Bernardes (2008) highlighted that *LAI* and its longevity are the most important factors influence to dry matter production and thus resulting growth and productivity. Rubber production decreases during re-foliation when photosynthesis is

restricted and has then a positive correlation with *LAI*. It was also suggested that the use of *LAI* can be supplementary to understand the carbon allocation and availability latex harvesting management in rubber field, and then to optimize latex productivity. Therefore understanding the ecophysiological response in principles of latex yield and phenological factors, particularly changes of *LAI*, would be promising to increase latex productivity in a sustainable way.

To clarify those requirements, understanding the main factors and timing which influence rubber yield production is primarily important. However, the timing and the beginning of the pathway from CO_2 assimilation at canopy scale to latex flow by tapping is poorly understood and answered. The first objective was to quantify the basic relationship between climatic factors and latex yield production, particularly antecedent correlations. In order to give the explanation of the relationship between phenological variations of rubber tree and production, the second objective was to consider the correlation of *LAI* and rubber yield production. It was hypothesized that *LAI* plays significant role on latex yield under climatic changes.

2. Materials and method

Study site

The study was conducted in Hat Yai, Songkhla Province, southern Thailand; the traditional cultivation area for rubber in Thailand. The climate is tropical monsoon, annually dominated by the south-west and north-east monsoons, in May-October and November-January, respectively. Mean precipitation is 1955 mm (1979-2008). Rainfall is strongly seasonal with 58% of annual precipitation during September to December. Maximum precipitation is 396 mm in November, whereas the driest month is February (29 mm) (Figure 17). Annual maximum and minimum temperature is 32.3 °C and 23.9 °C, respectively. The predominant vegetations in the area are tropical evergreen forest and rubber trees plantations.

The plot-scale study

The plot-scale study took place in a farmer's rubber plantation located at 6° 59' N, 100° 22' E. The plantation was 14 years old and has been tapped for 6 years. The area is 1.5 hectare. The clone is RRIM 600, planted with 7 x 3 m² spacing, i.e. 476 trees per hectare. The average tree girth at 1.70 m from ground level was 64.0 cm. The soil texture is clay. Soil moisture and transpiration in this plot were estimated by a simple water balance: BILJOU99 (Granier *et al.*, 1999).

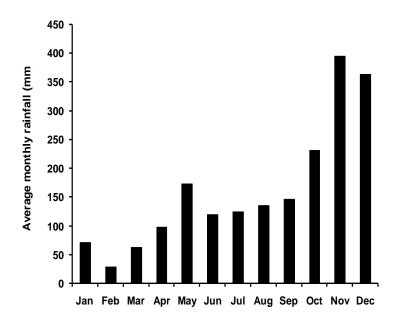


Figure 17 The average monthly rainfall during 1979-2008. Data from Kho Hong Agrometeorological Station, Kho Hong, Hat Yai district, Thailand.

Leaf area index measurement

Leaf area index (*LAI*) variations were measured from hemispherical canopy photography (Nikon Coolpix 8400 digital camera mounted with Nikon Fisheye Converter FC-E8 lens, Delta-T Devices Ltd). The calibration curve of *LAI* was obtained from leaf collection by litter traps (detail by Jonckheere *et al.*, 2004, Sopharat and Sdoodee, 2008). The photographs were recorded every two days during shedding and flushing period, and every two weeks or monthly during vegetative season. All pictures were analyzed using the GLA software (Institute of Ecosystem Studies, Simon Fraser University, Burnaby, Canada; Frazer *et al.*, 1999). *LAI* data were gap filed to daily data by linear interpolation which was the differentiate rate of two points data.

Latex yield measurement

The theoretical tapping system used by the farmer in the experimental plot was S/3 2d/3, i.e. tapping on one third of spiral around the trunk in downward direction; tapping two days with one day rest. However, the actual tapping frequency was more irregular. The trees could not be tapped during the rainy days and the lost days were compensated by tapping "every possible day". This corresponds to the actual tapping systems used by the farmers in this area. There was no tapping rest during the leaf-shedding-refoliation period. The latex yield components *e.g.* fresh latex weight (Kg), dry rubber content (%) and the calculated dry rubber weight (Kg) were collected every tapping day from 16 February 2010 to 29 September 2012. The data were collected from the cooperative where the production was delivered. After delivery, the total latex weight (Kg) from the 1.5 hectare plot was measured by a digital balance. About 10 cc of mixed latex was then put into a ceramic cup and the wet weight (g) recorded. After fast drying in a microwave oven, the dry sample was weighted (g) and recorded.

The percent of dry rubber content (%DRC) was calculated as;

$$\% DRC = \frac{Dry \ weight}{Wet \ weight} \times 100$$
[33]

Daily total weight of dry rubber (Kg) has been consequently calculated as following;

$$Total dry rubber = \% DRC \times Total latex weight$$
[34]

The district scale study

In order to validate the study in plot scale, we reconsidered the data which observed in 2007 to 2008 in a small district, namely Namom, Songkhla province, 6° 58' N, 100[°] 33' E. The total area is 14,328 ha, and was including 8,011 ha of rubber plantations in 2007. The soil texture is mainly sandy-loam. The yield data derived from the cooperatives. The records of six smallholders regularly tapping were selected for this study. At the cooperatives, the %DRC was measured by Latexometer; specific gravity measurement (Reji Kumar and Jacob, 2009). *LAI* was measured with the same hemispherical photograph method. Twenty plots from small, mature and old rubber plantations within the district were selected for this part (Sopharat and Sdoodee, 2008). The sampling area for hemispherical photography was from 40 x 40 m² in each plot. The tree girths were also systematically measured from those plots. They were measured at 1.70 m above ground level; each plot was randomly selected in the area of 1600 m². The measurements were conducted in April 2007, October 2007 and February 2008.

Correlations between latex yield, LAI and climatic factors

The statistical analysis was performed with XLSTAT (Addinsoft, Paris, France). The correlations analysis between antecedent factors; *LAI* and climatic factors, and latex yield has been conducted to consider the influence of antecedent factors on latex yield. The hourly climatic data of plot scale study were derived from the automatic weather station (Wireless Vantage Pro2TM Plus including UV and Solar Radiation Sensors; Davis Instruments Corp. USA) installed 1.0 Km from the experimental plot. And the district scale study, the daily climatic data were derived from Khoa Hong Agro-meteorological Station, 7.0 Km from study sites.

Growth analysis

Variations of *LAI* and of the latex yield components were fitted to logistic functions after the start of refoliation (Brown and Rothery, 1993).

$$y = \frac{a}{(1+be^{-cx})}$$
[35]

The value of a is first estimated by the maximal value of y. The values of b and c are then estimated using a straight-line fit to a linearized model.

3. Results

Seasonal dynamics of LAI and latex yield

The daily records of latex yield and variations of *LAI* are showed in Figure 18. *LAI* showed clearly the brevi-deciduous behavior, leaf shedding began in early January and was completed at the end of February in both years 2011 and 2012. *LAI* started to increase sharply again after shedding, there was no dormancy period. After flushing and fast expansion of new leaves, LAI reached the maximum on May 11 in 2011, around 3.2. Again *LAI* started to decrease in late season of 2011. A slower decreasing rate began from September to the end of December 2011, caused *LAI* down to 1.8. But in the same time of previous season, *LAI* was still high. During December 2010 and January 2011 *LAI* was maintained at 3.4. However and consistently, in 2011 and 2012 the canopy has annually completed shedding in the beginning of March.

In 2010, the yield increased gradually from May to the end of October, and then heavy rainfall forced the farmer to stop tapping until the end of November. Tapping was recorded as erratic yield in December 2010. From 2011 to 2012, the peak of latex yield production occurred in January, following the rainy season during. Then it declined while synchronized with defoliation (the beginning of February). The sharp decrease of latex yield occurred suddenly when *LAI* closed to zero, during high temperature and dry soil. The latex yield variations appeared synchronized with *LAI*, with a gap of (how many) weeks after the beginning of defoliation. In 2011 latex yield peaked again at the beginning of August. It was around three months after *LAI* peaked in May. Then there was a decreasing trend until mid-December, despite high daily fluctuations and then a new peak in February 2012. Hence, delay was observed between the two parameters: yield and *LAI*. The decrease in yield followed up the previous decrease in *LAI*. Then the latex increased again, but in beginning of August 2011, after *LAI*

getting at maximum at the end of April 2011. It was reproducible in January 2012 but with a less effect during august 2012.

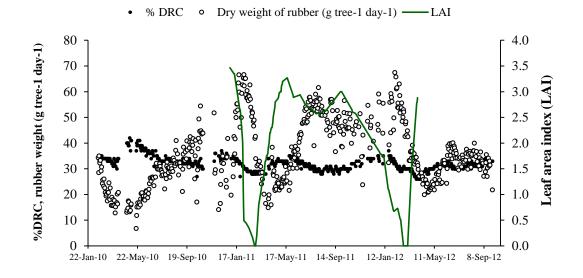


Figure 18 Variations of leaf area index (*LAI*), dry weight of rubber (g tree-1 day-1) and percent of dry rubber content (%DRC) of plot scale study.

The correlation of LAI, environmental factors, %DRC and latex yield

The significant correlation was found between dry rubber weight and *LAI*. The highest correlation occurred when dry rubber weight lagged 80 days behind *LAI* (R^2 =0.65, RMSE=6.83), with interception at 21.58 (g tree⁻¹ day⁻¹) (Figure 19). However, the results showed little correlation between other variables. The dry weight of rubber lagged 53 days behind variations of %DRC (R^2 =0.32, RMSE=9.70) (Figure 20). And %DRC lagged 81 days behind maximum temperature (R^2 =0.36, RMSE=2.13), when maximum temperature above 25 °C and without consideration of maximum temperature from March 25 – August 27, 2011 or during full canopy period. However, the correlation between latex yield and other climatic factors; reference evapotranspiration (*ETo*), *VPD* and minimum temperature were very poor (R^2 < 0.1). The correlation between estimated transpiration and soil moisture by water balance model (BILJOU; Granier *et al.*, 1999), showed that it seemed the dry rubber weight followed the variation of transpiration later around 33 days (R^2 = 0.14).

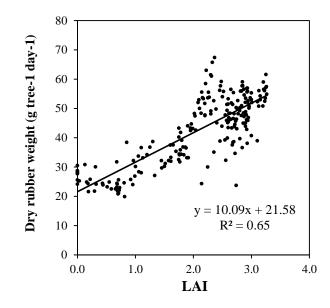


Figure 19 The correlation between leaf area index (*LAI*) and dry rubber weight; dry rubber weight lagged 80 days behind *LAI*.

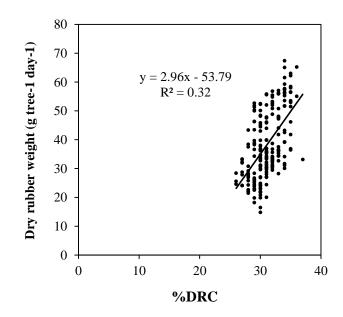


Figure 20 The correlation between percent of dry rubber content (%DRC) and dry rubber weight; dry rubber weight lagged 53 days behind %DRC.

The increase in LAI and latex yield after recovery

The analysis based on logistic growth equation, LAI and dry weight of rubber (g tree⁻¹ day⁻¹) can be showed with the time after the recovery day as following equations;

Recovery of LAI =
$$\frac{3.28}{(1+10.10Exp(-0.09x))}$$
 (R² = 0.93) [36]
Dry weight of rubber = $\frac{81.02}{(1+3.28Exp(-0.02x))}$ (R² = 0.95) [37]

where x is the day after *LAI* and dry weight of rubber start to recovery, remarkably after it raise up from minimum.

The recovery time of *LAI* and dry weight of rubber started on March 4, 2011 and April 20, 2011, respectively (Figure 21). The maximum dry weight of rubber from prediction (81.02 g tree⁻¹ day⁻¹) was far above the observed data (61.59 g tree⁻¹ day⁻¹). The observed data showed that *LAI* exhibited the maximum in day 78 (May 20, 2011). Theoretically with prediction, *LAI* reached its maximum 98 days after recovery (June 9, 2011). And the prediction showed that the increasing rate of *LAI* and dry weight of rubber exhibited the maximum (inflection point) in 27 (March 29, 2011) and 59 (June 17, 2011) days after recovery, respectively.

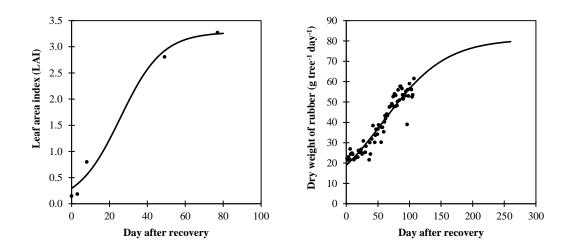


Figure 21 Modeling of leaf area index (*LAI*) and dry weight of rubber based on logistic growth curve (black circle is the observed data and solid line is the model).

The variations of district scale

Figure 22 showed the evolution of the relative latex yield over six farms at a district level, together with the average *LAI* over twenty plots in the same area. Although the measurements were done during the previous years (2007-2008), the trends of *LAI* and latex yield were consistent with the study in the plot scale. *LAI* increased from the start of measurements (mid-April 2007) and reached the maximum at the end of May, while the minimum latex yield was around the mid to end-April and a plateau stage was in August. The lag between *LAI* and latex yield was confirmed as plot scale, despite high daily variability and a high inter-farm variability.

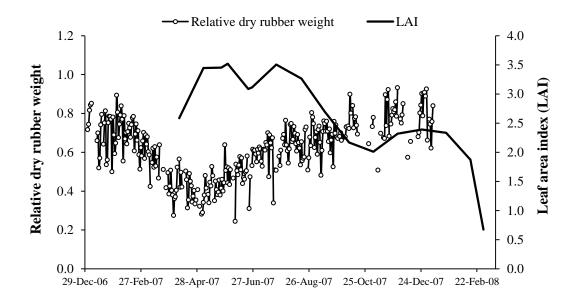


Figure 22 Variations of average leaf area index (*LAI*) of mature plantations (averaged from 20 plots) and the relative dry rubber weight in district scale.

4. Discussion

The variation and response between LAI and latex yield

The abrupt increase of LAI by flushing and expansion of new leaves could indicate with equation [36]. During growing season of 2011 the highest increasing rate of LAI was 0.084 (LAI unit per day) on day 27 after bud burst. In the same time latex yield approached the lowest level. It indicated that it may relate with the partition and mobilization of assimilates to the competing sinks; new shoots, deep roots and laticifers (Rojas-Jiménez *et al.*, 2007; Silpi *et al.*, 2007; Chantuma *et al.*, 2009). During leaf flushing and dry period, preparing new shoots ready for photosynthesis and deep roots for water uptake to increase stem water potential above a certain threshold consequently allowing bud break and flushing, could be much higher important than to produce latex (Guardiola-Claramonte *et al.*, 2008). And normally the leaves exhibit a full rate of photosynthesis 50 to 60 days after emergence (Samsuddin and Impens, 1979). It supports that carbohydrate reserve (Silpi *et al.*, 2007; Chantuma *et al.*, 2009) plays role as the major source for latex production, particularly during shedding. It is suggested that around three months after photosynthesis; the carbon assimilation at canopy is spent to metabolize latex.

Our study showed that *LAI* is a good indicator of the canopy to predict variation of latex yield. In this study it was the primary factor influence to the variations of latex yield. The correlations between climatic factors and latex yield in our study were antecedently and directly poor. However, in previous studies the environmental factors, particularly *VPD* and temperature (Rao *et al.*, 1990, 1998), and soil water ability (Raj *et al.*, 2005) showed high correlation with latex yield. *VPD* and soil water showed the significant negative and positive correlation with latex yield, respectively (Raj *et al.*, 2005; Rao *et al.*, 1998). Maximum temperature experienced during 1 day, 7 days and 30 days prior to the tapping explains about 32%, 42% and 64%, respectively, of the day-to-day variability in latex yields (Rao *et al.*, 1998). In our study *LAI* showed the positive correlation with latex yield of RRIM 600. And it was consistent between district and plot scale.

Our finding could highlight that the sources important to latex production have been already generated long time before it turn to latex synthesis. We would conclude that *LAI* plays role as the prior factor in the canopy scale to generate the source for carbohydrate reserve in tapped trees (Annamalainathan *et al.*, 2013). The prevailing or short antecedent period of climatic factors might be just only the factors favorable to latex biosynthesis in laticiferous cells, which related to latex flow (Raj *et al.*, 2005), and utilizing assimilates derived from leaf photosynthesis and other sources (Jacob *et al.*, 1998; Chantuma *et al.*, 2009).

Our study lacked the full set of climatic data and details of latex flow. Thus the relevant relationship between latex yield and climate was less evident comparing to previous studies. However, seven day moving average of *VPD* versus latex yield showed a tendency of positive correlation during 6 December 2010 and 19 November 2011, and off this period with negative correlation ($R^2 \approx 0.1$).

The consistency between plot scale and district scale

District scale study confirmed that *LAI* is the primary factor controlling latex yield production. It was consistent between plot scale and district scale study. The variations of latex yield were primarily controlled by *LAI* from canopy component as we consider defoliation and refoliation periods specifically. Moreover, in district scale, the yield also dropped to lower level during dry season, the same time when *LAI* exhibited the maximum (in May 2007). The statistic correlation between *LAI* and latex yield could not be represented because of the limitation of data set. But the variations of *LAI* and latex yield were according with the study in plot scale. It supported the idea that carbohydrate synthesized at canopy scale is not directly and instantaneously transported to latex synthesis. But it is reserved before synthesize latex in the laticiferous cells. And this reserve is stimulated by tapping implementations and environments (Annamalainathan *et al.*, 2013).

The role of LAI in carbohydrate reserve and sink demand

LAI is a dimensionless variable and was first defined as the total one-sided area of photosynthetic tissue per unit ground surface area (Jonckheere *et al.*, 2004). Thus we propose that the canopy architecture which characterized by gap fraction could be the parameter to primarily indicate the difference in clonal latex production. The study by Gunasekera *et al.*, 2013

showed that CO_2 assimilation rates could be higher even *LAI* lower than other clones. And the efficiency of photosynthesis depends on depth of the canopy (Kumagai *et al.*, 2013). However, in drought prone area, the effect of high evaporative demand (Isarangkool Na Ayutthaya *et al.*, 2011; Kobayashi *et al.*, 2014) to stomatal conductance and CO_2 assimilation has to be further detailed.

The relationship in Figure 19 showed the interception was 21.58 (g tree⁻¹ day⁻¹). It indicated that although the leaves were shed until *LAI* close to zero, the latex still produced. And the lag around 80 days between *LAI* and latex yield, may confirm the concept of carbohydrate reserve (Silpi *et al.*, 2007; Chantuma *et al.*, 2009). Therefore, the carbohydrate synthesized at canopy scale may not be directly and instantaneously transported to latex synthesis. But it is reserved before synthesize latex in the laticiferous cells. And it is additionally stimulated and acquired by tapping (Annamalainathan *et al.*, 2013).

However, how long from CO_2 diffusion until metabolizing to latex yield has not been yet clearly answered and remains poorly understood. Our finding clues that the process to generate latex would be longer than two months. Lagging behind *LAI* around 80 days of latex yield showed that the canopy is the key related to carbohydrate reserve (Annamalainathan *et al.*, 2013; Silpi *et al.*, 2007). However, the detail of assimilation process before turn to latex must be further studied, particularly the pathway and the direction of assimilation.

The importance of phenology on the tapping method

The study by our colleagues (data not show) reported that rainy day in Southern Thailand tends to increase (Sdoodee and Rongsawat, 2012). The occurrence of this event may disturb and decrease the annual tapping days. Such mention was evident in Figure 18 and 22. The big gap of the untapped days, October and November occurred during heavy rainfall events. In addition, the increase of rubber price of the resent years induced the farmer tapped unusually as normal tapping system. The farmers tapped "every possible day" in order to compensate the lost days from rainy days and try to achieve the high income. There was no tapping rest during the leaf-shedding-refoliation period. Consequently, a higher tapping frequency appeared in dry season until the beginning of rainy season. To alter the tapping method base on phenological stage and environmental factors would be promising to keep the sufficient and efficient latex production as its optimum potential (Soumahin *et al.*, 2010; Traoré *et al.*, 2011).

5. Conclusions

Our study showed that *LAI* pattern was the prior factor influence on the latex yield production. The variations of latex yield lagged behind *LAI* pattern and percent of dry rubber content. It supports the hypothesis that the majority of latex yield initiated from the reserved carbohydrate.

Chapter 6

General Conclusions

This study was conducted in three different sites in order to study the effects of climatic regimes particularly climatic and soil drought on particular transpiration of rubber tree, most generally planted clone: RRIM 600. The considerations were performed by the bucket water balance model; BILJOU99. The mature rubber plantations have been selected with the same clone. Two sites located in southern part of Northeastern Thailand where is influenced by subtropical climate (Aw; tropical savannah). And one site located in Southern Thailand where is influenced by tropical monsoon climate (Am; tropical monsoon).

The results confirm that the basic relationships of the original framework of agro-climatic and water balance model; BILJOU99 hold except that the regulation of transpiration at high evaporative demand was not well simulated. The adapted framework of BILJOU99 has allowed analyzing the relative contribution of soil water shortage and atmospheric drought to the regulation of transpiration on a seasonal scale. It stresses the importance of taking into account the direct regulation of transpiration versus high evaporative demand in particular tropical subhumid climates. It provides a first diagnosis of water constraints on transpiration. The transpiration in subtropical climate; BRR exhibited saturation at high evaporative demand. Such response, however, represented different levels in higher rainfall distribution areas, CCS and SKL. The major factors responsible for decrease in transpiration at both sites were classical; LAI, climate and soil moisture. The constraint by high evaporative demand in conditions of high rainfall distribution is likely lower compare to the areas of severe drought. It is suggested that the response with high evaporative demand is the priority of safety margins to prevent cavitation for rubber, particularly in drought prone areas where is higher risk to cavitation. It may relate to the acclimation of leaf and sapwood area and the susceptibility in loss of canopy conductivity when evaporative demand increasing in condition of higher ratio of leaf and sapwood area. And the acclimation could hold the survival of rubber tree; however the consequence of growth and production certainly deserves more study.

The adapted framework of BILJOU99 explained well the constraints and seasonal dynamics of transpiration in subtropical climate area; BRR. However, such framework induces underestimation in mildly drought prone area; CCS and optimal area; SKL. The dynamics of fine root distribution, particularly deep root during dry season was not included in this study. Consequently, to explain water uptake which detected by sap flow measurement during conditions of low leaf area and dry season by modeling is hence insufficient. The underestimation of transpiration at mildly drought prone area, CCS; hard pan against penetration of deep root, suggested the relevant root proliferation and deep soil water uptake during dry season. Accounting a threshold of evaporative demand induced the underestimate of transpiration in CCS and SKL. Thus, the reduction factor due to stress of high evaporative demand and generality of this relationship are not accepted for RRIM 600 in this condition of simulation.

The BILJOU99 is likely sufficient to simulate transpiration and soil water availability of rubber tree plantations. However, the implementation in particular transpiration estimation is slightly different depend on climatic zone and the ratio of leaf and root area. The generality of modeling is sufficient to explain seasonal transpiration of rubber tree. However, modeling with threshold of evaporative demand is important to eliminate overestimation of transpiration in severe drought areas. Whatever to estimate transpiration and soil availability, BILJOU99 could be used as the tool for diagnosis of the constraints on transpiration of rubber tree plantations.

In addition, the study with preliminary results from BILJOU99 and the relationship between *LAI* and latex yield production could help to support the idea of carbohydrate reserve in rubber tree. *LAI* pattern was the prior factor influence on the latex yield production. It supports the hypothesis that the majority of latex yield initiated from the carbohydrate reserve. It took around three months after photosynthesis that the assimilated carbon is spent to metabolize latex. However, the framework of hourly modeling is required in particular latex flow diagnosis.

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List of Publication and Proceedings

- Sopharat, J., Gay, F., Thaler, P., Sdoodee, S., Isarangkool Na Ayutthaya, S., Tanavud, C., Hammecker, C. and Do, F.C. 2015. A simple framework to analyze water constraints on seasonal transpiration in rubber tree (*Hevea brasiliensis*) plantations. Front. Plant Sci. 5: 1-11.
- Minirhizotron camera (Thai patent): The mini-camera for fine root study through transparent tube which buried under the soil and root zone. (Patent number 8518)

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