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Process-based environmental models tree transpiration: A case study of rubber tree (*Hevea brasiliensis*)

Supat Isarangkool Na Ayutthaya^{1,5*}, Krirk Pannangpetch, Frederic C. Do², Junya Junjittakarn¹, Jean-Luc Maeght¹, Alain Rocheteau¹ and Herve Cochard¹

ABSTRACT: Nowadays, tree transpiration (E_{tree}) limitation is investigated in several plant species especially the commercial trees such as the rubber tree. Exceptional tree physiology responds to droughts, the modeling for prediction of E_{tree} is also interest. The aim of this investigation was to evaluate the environmental model for E_{tree} estimation in all leaf phenology under a wide range of soil water availability and evaporative demand. The results showed that the environmental model called ' $F_{soil} \cdot E_{max}$ ' (which considered only soil water available affect) produced a reduction of estimated E_{tree} the same as the reducing pattern of actual measured in drought conditions. But there was no variability of estimated E_{tree} when evaporative demand changed. The improving of the environmental model by added the reference evapotranspiration (ET_0) which alternated in minimum value between ET_0 and E_{max} , called $F_{soil} \cdot \text{MIN}(E_{max}; ET_0)$ model, produced a reduction in estimated E_{tree} in both soil drought and low evaporative demand conditions at fully mature leaves stage. Therefore, this model was optimum for estimating transpiration under various conditions. Moreover, the annual accumulated E_{tree} of the improved model slightly overestimated the measured value by 20 mm. However, this model produced estimated E_{tree} at fully mature leaves stage better than during leaf shedding-flushing stage.

Keywords: environmental model, rubber tree, *Hevea brasiliensis*, transpiration

Introduction

As demand and competition for water continually increases, the efficiency of water management becomes a critical aspect for sustainable development and food supply. Transpiration (E_{tree}) is a key component of water management, and its rate is dependent on the evaporative demand of the atmosphere, soil water availability, and physiological responses of the

tree. The potential rate of transpiration (E_{max}) at a given time is governed by the atmosphere and radiation. Such a rate can be reached only when there is sufficient soil water to fulfill the demand, i.e. when soil is wet. (Meinzer, 2003; David et al., 2004; Novak et al., 2005; Huang et al., 2009). However in some circumstances when the demand from the atmosphere is extreme, although there is sufficient soil water available, the transport system of the plant may not be able

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to cope with the demanding rate, high tension of soil-plant-atmosphere water continuum would develop, and consequently leads to the closure of stomata. E_{max} is then no longer related to the increases of atmospheric demand. The saturated rate of tree transpiration as limited by the hydraulic properties of the transport system is reported in several trees (Bush et al., 2008; David et al., 2004; Isarangkool Na Ayutthaya et al., 2010b; and Woodruff et al., 2010).

Presently, several empirical models are available to estimate transpiration. However, to further apply model simulation to help optimizing water use and management, it is necessary to use process based models, which would embed key processes that govern tree transpiration under a wide range of environmental conditions, especially under drought conditions. For example, in a mature rubber tree, the combining of hydraulic limitation and evaporative demand model, which obtained by Isarangkool Na Ayutthaya (2010b), produced good estimated E_{Tree} . Nevertheless, all input parameters in hydraulic limited model based more on in tree physiological responses, which some input parameters can change depending on tree size or clone e.g. whole tree hydraulic conductance. Thus, if there is the model that uses the input parameters by environmental conditions, it may be more easy and simple to estimation of tree transpiration.

In a simple approach, transpiration is allowed to vary between 0 and the constant representing the maximum rate E_{max} , according to fraction of soil moisture available in the root zone: F_{soil} (Rodrigues-Iturbe et al., 2001; Mainzer, 2003; Small and McConnell, 2008) given by

$$E_{Tree} = F_{soil} E_{max} \quad (1)$$

F_{soil} is defined by Small and McConnell (2008)

as

$$F_{soil} = \begin{cases} \frac{\theta - \theta_{wilt}}{\theta^* - \theta_{wilt}}, & \theta > \theta^* \\ 1, & \theta > \theta^* \\ 0, & \theta < \theta_{wilt} \end{cases} \quad (2)$$

where θ is current volumetric soil water content, θ_{wilt} volumetric soil water content at which transpiration ceases or permanent wilting point, and θ^* soil water content above which transpiration is not limited by soil water available.

The limitation of the above equation is that it can be applied only to the situation where the variation of the atmosphere is small and can be assumed as constant, hence constant E_{max} . Because of such, E_{max} is replaced by Potential Evaporation (PET), which is based on Penman Equation, as given below

$$E_{Tree} = F_{soil} PET. \quad (3)$$

This allows E_{Tree} to be estimated under the influences from both soil water availability and evaporative demand of the atmosphere (Mahfouf et al., 1996; Feddes et al., 2001; Small and McConnell, 2008).

Isarangkool Na Ayuttaya et al. (2010b) further found with the mature rubber tree that E_{tree} increased linearly with reference evapotranspiration (ET_0) only to the value of ET_0 around 2.0-2.2 mm d⁻¹, beyond which E_{tree} tends to constant. The equation 3 was therefore expanded to include the limitation of hydraulic conductivity of the transport system to E_{tree} , as follows

$$E_{Tree} = F_{soil} \times \text{Min}(E_{max}; ET_0). \quad (4)$$

where *Min* is the alternative in minimum value between E_{max} and ET_0 .

This approach allows the tree transpiration to follow ET_0 only from 0 to critical ET_0 (2.2 mm day⁻¹ for mature rubber tree (Isarangkool Na Ayutthaya et al. 2010b), and E_{Tree} become saturated when exposed at higher ET_0 .

Rubber tree is one of the important economic crops of Thailand. It is a tropical deciduous tree which has leaves shedding and new leaves flushing in the dry season. However, little is known of water use of the rubber tree in Thailand. Also, there had no model validated on the water use of rubber trees in differed leaf phenology. Therefore, the objective of this investigation is to validate if this environmental model can estimate E_{Tree} in all leaf phenology under a wide range of soil water availability and evaporative demand, so that the model can be used to help in optimizing water management in the rubber production system of the country.

Material and Method

Field site and plant material

The experiment was conducted in a plot of clone RRIM600, planted at 2.5m x 7.0m spacing and tapped for 4 years (11 years after planting). The plantation is located at Baan Sila site (N15° 16' 23" E103° 04' 51.3"), Khu-Muang, Buriram province in northeast Thailand. The annual rainfall in 2007 was less than 1,000 mm; the rainy season lasts approximately from April to October. Also, there was an intermittent drought during June–July of this year of experiment. Six representative trees were selected for intensive measurements. Their

trunk girths, measured at 1.50 m height above the soil, varied from 43.3 to 58.3 cm. The average circumference was 52.5 cm, and the maximal leaf area index was estimated around 3.9 in 2007. The field investigation was carried out from January to December 2007.

Climatic measurements

Local microclimate was automatically monitored in an open field, 50 m from any trees. A datalogger (Minimet automatic weather station, Skye Instruments Ltd, U.K.) recorded half hourly values of air temperature, relative humidity, incoming short wave radiation and rainfall. A reference evapotranspiration (ET_0) was calculated according to Allen et al. (1998).

Soil water content measurements

Continuous volumetric soil water content (θ) was measured with a capacitive probe (EnvironSCAN System, Sentek Sensor Technologies, South Australia, Australia). The calibration was done in the experimental soil in the field. For the accurate θ value, the estimated θ values were adjusted by a linear regressions between a capacitive probe and neutron probe (3322, Troxler, Research Triangle Park, North Carolina, USA) for which were installed 12 neutron probe access tubes in the plantation. The 2.0 m in length of neutron probe tubes were set up with six along the rows and six between the rows. The calibration of the neutron probe was also done in the experimental soil with separated calibrations between upper (0-0.2 m) and lower (below 0.2 m) layers.

According to soil water fluctuations, the soil profile was separated between two layers; a top soil (0-0.4 m) and a subsoil (0.4-1.8 m). Average

field capacity and permanent wilting points were equal at 19.8 and 7 cm³/100 cm³ of soil for the top soil, and 25.1 and 10 cm³/100 cm³ of soil for the subsoil, respectively (Isarangkool Na Ayutthaya et al., 2010a).

Xylem sap flux measurements and tree transpiration calculation

The measurements of xylem sap flux density were made using the transient thermal dissipation method (TTD) developed by Do and Rocheteau (2002) which is a modification of the continuous thermal dissipation method of Granier (1985, 1987). The modification avoids the influence of passive temperature gradients. The TTD method is based on the same Granier's probe design and heating power but uses a cyclic schedule of heating and cooling to assess a transient thermal index over 10 minute change. The hourly sap flux density (J_s) was calculated according to the empirical and non species-specific calibration assessed by Isarangkool Na Ayutthaya et al. (2010a):

$$J_s = 12.95K_a \quad (5)$$

where K_a is a transient thermal index (dimensionless), 12.95 is the slope of relationship between J_s and K_a . The unit of J_s is L dm⁻² h⁻¹. An alternate signal (ΔT_a) was defined as:

$$\Delta T_a = \Delta T_{on} - \Delta T_{off} \quad (6)$$

where ΔT_{on} is the temperature difference reached at the end of the 10 minutes heating period and ΔT_{off} is the temperature difference reached after 10 minutes of cooling.

To measure J_s every half hour with a heating period of 10 minutes, a cycle of 10 minutes heating and 20 minutes cooling was applied and the temperature signals were recorded every 10 minutes. ΔT_{off} values were averaged between values before 10 minutes n of heating and after 10 minutes of cooling.

The transient thermal index was calculated as:

$$K_a = (\Delta T_{0a} - \Delta T_{ua}), \quad (7)$$

where ΔT_{0a} is the maximum alternate temperature difference obtained under zero flow conditions and ΔT_{ua} is the measured alternate 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. Probes were inserted into the trunks at a height of 1.8 m above the soil. At this height, average sapwood area was estimated at 1.97 dm². After removal of the bark, 2-cm long probes were inserted into a hole of 2.5 cm deep within the sapwood, in such a way that the whole probe was inside the conductive sapwood. Three probes were inserted into each trunk to take circumferential variability into account. After the probe was inserted, the exposed parts of the needles were coated with silicone. 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, U.K.).

J_s was cumulated over 24 h to calculate daily J_s (J_{s_daily}). For taking care of the variation of sap flux density in the depth of wood, a reduction coefficient of 0.874 was applied to the J_s measured

in the outmost ring of conducting xylem (Isarangkool Na Ayutthaya et al, 2010a). Finally, neglecting tree water storage, E_{Tree} (mm day^{-1}) was estimated according to the equation:

$$E_{Tree} = 0.874 * J_{s_daily} * \text{sapwood area/tree spacing area} \quad (8)$$

Details in input parameters of models

F_{soil} calculation From equation 2, θ_{wilt} is the volumetric soil water content at permanent wilting point of top soil in this plantation ($7 \text{ cm}^3/100 \text{ cm}^3$ of soil; Isarangkool Na Ayutthaya et al., 2010a). θ^* is the volumetric soil water content above which transpiration is not limited, $14 \text{ cm}^3/100 \text{ cm}^3$ of soil, which comparing from relative extractable soil water (REW) at 0.5 that obtained by Isarangkool Na Ayutthaya et al. (2010b).

E_{max} is maximum E_{Tree} , of 2.38 mm day^{-1} , which was a maximum value in our observation in 2007.

Results

Environmental status

Evaporative demand which is expressed by ET_0 normally had a high value (ranged from $1.61\text{-}6.08 \text{ mm day}^{-1}$) in the dry season and had a low value (ranged from $0.43\text{-}4.17 \text{ mm day}^{-1}$) in the rainy season that included an intermittent drought (Figure 1A). Rainfall in this plantation started in the mid April, but there was shortly a lack of rainfall of around 10-15 days at the end April. Also, the rain fall had temporarily stopped again during June – July (Figure 1A). Annual rainfall in this year was less than 1,000 mm, which was lower than optimum value for the rubber tree (1,800 mm), around 45%.

Relatively, volumetric soil water content (θ) in the top soil had the pattern of varying following rainfall, which showed a low value of approximately $7.79 \text{ cm}^3/100 \text{ cm}^3$ of soil in the dry season (January – mid April) and showed a high value of approximately $19.07 \text{ cm}^3/100 \text{ cm}^3$ of soil during August to early November. An intermittent drought during June - July, θ had the lowest value ($7.75 \text{ cm}^3/100 \text{ cm}^3$ of soil) close to the value in the seasonal dry period. However, θ in subsoil had slightly changed; the average value was $11.55 \text{ cm}^3/100 \text{ cm}^3$ of soil. (Figure 1B) This evidence indicated that the top soil θ seemly had more effect on tree transpiration variability than sub soil θ . Therefore, the θ in top soil was focused for F_{soil} calculation.

Expression of top soil water availability in F_{soil} was 1 at mid-end rainy season following rainfall, but there was a reduction of F_{soil} during intermittent drought during June to July and the seasonal dry period (started in mid November). The lowest value of F_{soil} in intermittent drought and seasonal soil drought were 0.11 and 0.10, respectively. (Figure 1C)

Leaf phenology and environments limited tree transpiration

The rubber trees in this plantation had reached full canopy cover stage during mid May to mid November (Figure 2). However, there was no leaf shedding during intermittent drought during the rainy season (June to July), although the lowest value of F_{soil} was during intermittent drought close to seasonal dry period. The seasonal leaf senescence-shedding started in December (Figure 2) after rainfall had ceased for 1.5 month and the F_{soil} was 0.59 (Figure 1A and 1C).

By observation in **Figure 2**, the measured E_{Tree} had following the leaf phenology, which exhibited E_{max} (2.38 mm day^{-1} in mid August) in fully mature leaves period and exhibited a low value close to zero in the leaf senescence-shedding period in seasonal dry period. However, the soil

drought was the main environmental factor limiting E_{Tree} in fully mature leaves period (June to July). Moreover, the E_{Tree} showed a saturating when ET_0 was higher than $2.0\text{-}2.2 \text{ mm day}^{-1}$ (Isarangkool Na Ayutthaya et al. 2010b). Additionally, low ET_0 ($<2.0\text{-}2.2 \text{ mm day}^{-1}$) decreased E_{Tree} .

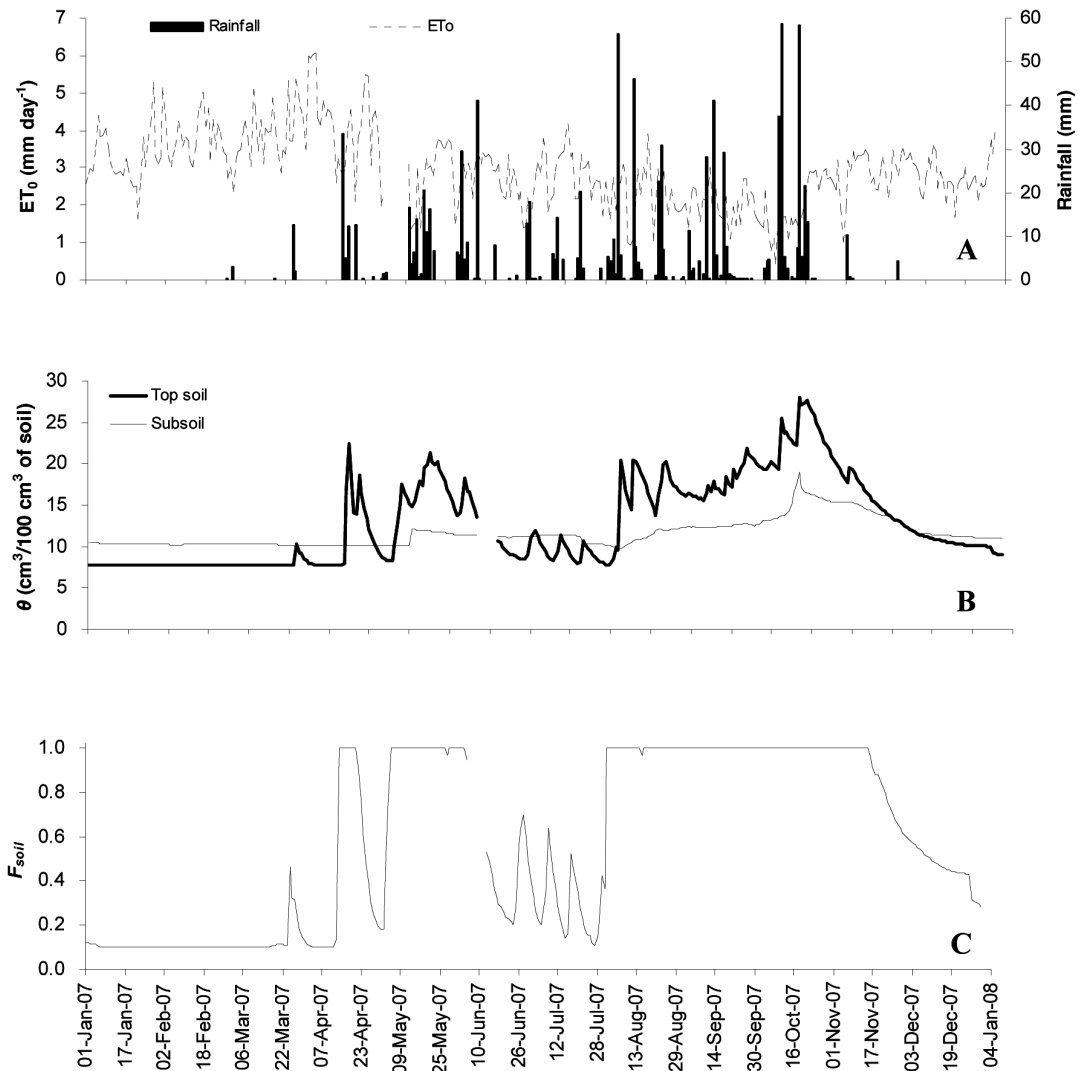


Figure 1 The environmental conditions during January - December 2007: A) rainfall (columns) and reference evapotranspiration (ET_0 ; dotted line), B) volumetric soil water content (θ) in top soil (bold line) and subsoil (thin line) and C) fractional soil moisture (F_{soil}) in top soil.

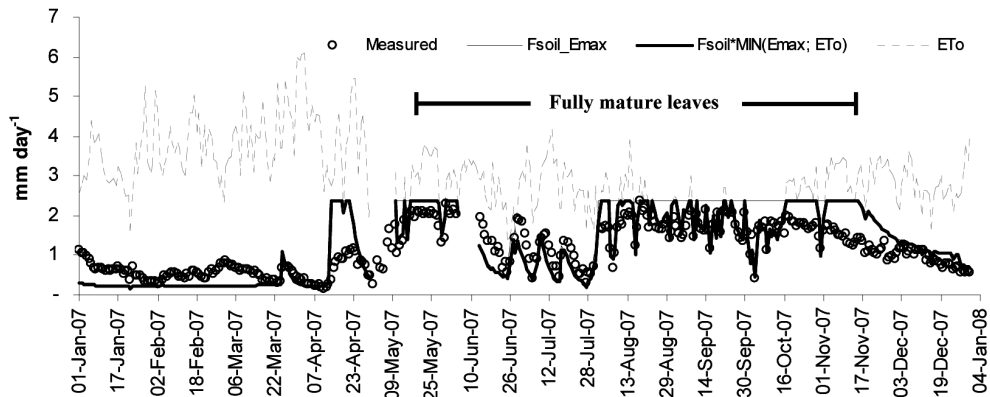


Figure 2 Comparison of measured daily tree transpiration (Measured; opened circle) and estimated daily E_{Tree} of $F_{soil}E_{max}$ model (thin line) and $F_{soil} * MIN(E_{max}; ET_0)$ model (bold line). The gray dotted line indicates the daily ET_0 .

Modeling

' $F_{soil}E_{max}$ model'

The hypothesis of this model is E_{Tree} will express the maximum value when there is no limitation of soil water availability and decreases when soil drought occurs. Therefore, the estimated E_{Tree} values showed maximum value (2.38 mm day^{-1}) when F_{soil} were 1, and decreased when F_{soil} had reduced (Figure 2 and Figure 1C). There was no variability of estimated E_{Tree} according to evaporative demand changing. The accumulated E_{Tree} (annual E_{Tree}), RMSE and R^2 were $462.4 \text{ mm day}^{-1}$, 0.60 and 0.69, respectively (Table 1).

' $F_{soil} * MIN(E_{max}; ET_0)$ model'

The estimated values of this model showed decreases when both soil drought and low evaporative demand occurred (Figure 2). The cumulated E_{Tree} , RMSE and R^2 were $413.2 \text{ mm day}^{-1}$, 0.48 and 0.71, respectively (Table 1).

Additionally, Figure 3 illustrated the pattern of changes of cumulated E_{Tree} in measured E_{Tree} and two environmental models. The $F_{soil} * MIN(E_{max}; ET_0)$ model gave the variable pattern in cumulated E_{Tree}

close to measured E_{Tree} . However, the annual value had slightly overestimated from the measured value by 20 mm. Whereas, the cumulated E_{Tree} from $F_{soil}E_{max}$ model had overestimated by 69.2 mm.

Leaf phenology effect to model estimation

The E_{Tree} estimations from these two models were considerably different in two leaf phenology stages: fully mature leaves period and leaf shedding-flushing period. Firstly in fully mature leaves stage, the $F_{soil}E_{max}$ model had overestimated in the low evaporative demand days ($ET_0 < 2.2 \text{ mm day}^{-1}$; Figure 4A) whereas $F_{soil} * MIN(E_{max}; ET_0)$ model produced good estimated E_{Tree} that was close to 1:1 reference line in both low and high evaporative demand conditions (Figure 4B). The RSME and R^2 confirmed that the E_{Tree} estimation by $F_{soil} * MIN(E_{max}; ET_0)$ model better than for $F_{soil}E_{max}$ model (Table 1). The evaporative demand parameter improved the estimation in low evaporative demand days.

Table 1 Accumulated tree transpiration (Accumulated E_{Tree}), root mean square error (RMSE) and coefficient of variation (R^2) in models which separated in 2 leaf phenology stages.

	Accumulated E_{Tree} (mm)	RMSE	R^2
<u>All periods</u>			
Measured	393.2		
$F_{soil}E_{max}$	462.4	0.60	0.69
$F_{soil} * \text{MIN}(E_{max}; ET_0)$	413.2	0.48	0.71
<u>Fully mature leaves</u>			
Measured	250.0		
$F_{soil}E_{max}$	309.3	0.65	0.45
$F_{soil} * \text{MIN}(E_{max}; ET_0)$	262.0	0.39	0.66
<u>Leaf shedding-flushing</u>			
Measured	143.0		
$F_{soil}E_{max}$	153.1	0.55	0.41
$F_{soil} * \text{MIN}(E_{max}; ET_0)$	151.3	0.54	0.40

With another leaf phenology, leaf shedding and new leaf flushing stage, both $F_{soil}E_{max}$ model and $F_{soil} * \text{MIN}(E_{max}; ET_0)$ model seemly exhibited the same value in estimated E_{Tree} (Figure 4C, 4D and Table 1), which had both over- and under-estimation in E_{Tree} value. Moreover, the comparing of two leaf phenology stages by $F_{soil} * \text{MIN}(E_{max}; ET_0)$ model, produced estimated E_{Tree} in fully mature leaves stage better than leaf shedding-flushing stage (Figure 4B, 4D and Table 1).

Discussion

Comparison between two models

The $F_{soil} * \text{MIN}(E_{max}; ET_0)$ model gave estimated E_{Tree} values better than $F_{soil}E_{max}$ model. Because the $F_{soil}E_{max}$ model produced estimated E_{Tree} at

E_{max} when soil was wet; therefore, estimated E_{Tree} from this model extremely overestimated in low evaporative demand conditions, ET_0 ranged from 0 to 2.2 mm day⁻¹, (Figure 5A). In comparison, the $F_{soil} * \text{MIN}(E_{max}; ET_0)$ model could adjust estimated values close to measured E_{Tree} values in the low evaporative demand conditions. Figure 5B confirmed this evidence in which the estimated E_{Tree} increased following ET_0 during 0 to 2.2 mm day⁻¹, and then exhibited a saturation of estimated E_{Tree} at E_{max} .

The plot between E_{Tree} and θ (Figure 6), the two models showed the estimated E_{Tree} increased following θ increase. It then showed the maximum or E_{max} at 14 cm³/100 cm³ of soil or F_{soil} equaled 1. However, estimated E_{Tree} in $F_{soil}E_{max}$ model (Figure 6A) clearly showed overestimation, especially in low evaporative demand conditions,

because no varying of estimated E_{Tree} in this model in soil wet condition ($\theta > 14 \text{ cm}^3/100 \text{ cm}^3$ of soil). By comparison, $F_{soil} * \text{MIN}(E_{max}; ET_0)$ model could predict in the low evaporative demand conditions, because there was the scatter of estimated E_{Tree} points (Figure 6B).

Affect of leaf phenology on model prediction

Improving the model by added evaporative demand parameter improved the results only in fully mature leaves period (mid May to November; Figure 4B). However, there were the out of scatter points (around one third of total number) from 1:1 reference in the 2 transition of leaf phenology periods for both models (Figure 4C and 4D), which overestimated in April to mid May and mid November to January and underestimated in leafless period during January to March (Figure 2). Moreover, the scatter point in Figure 4B and 4D confirmed that the improved environmental models were more precise in full mature leaves

period than leaf shedding and flushing period (Table 1).

Input parameters

In F_{soil} calculation, θ^* is $14 \text{ cm}^3/100 \text{ cm}^3$ of soil related with REW at 0.5 which is the value that transpiration is not limited (Isarangkool Na Ayutthaya et al., 2010b). Although, field capacity of θ in this field is $19.8 \text{ cm}^3/100 \text{ cm}^3$ of soil. Similarly, Mahfouf et al. (1996) suggested using 0.75 multiply with field capacity of each soil type for θ^* . This way of calculation indicated that the tree would still give maximum transpiration if the value of soil water content is not reducing over 0.5 in REW or 0.75 times from field capacity.

E_{max} equaled 2.38 mm day^{-1} for one input parameter, showed slightly overestimated E_{Tree} if compared with all measured data at saturated tree transpiration (Figure 5 and 6). The E_{max} should slightly reduce to 2.2 mm day^{-1} which is a frequent occurrence value in measured E_{Tree} .

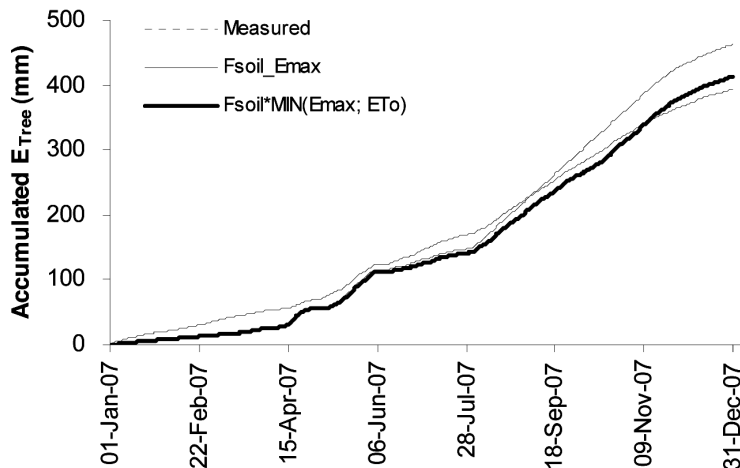


Figure 3 Change of the pattern of accumulated tree transpiration (Accumulated E_{Tree}) in measured E_{Tree} (dotted line), estimated E_{Tree} that predicted by $F_{soil} * E_{max}$ model (thin continuous line) and estimated E_{Tree} that predicted by $F_{soil} * \text{MIN}(E_{max}; ET_0)$ model (bold continuous line) in 2007.

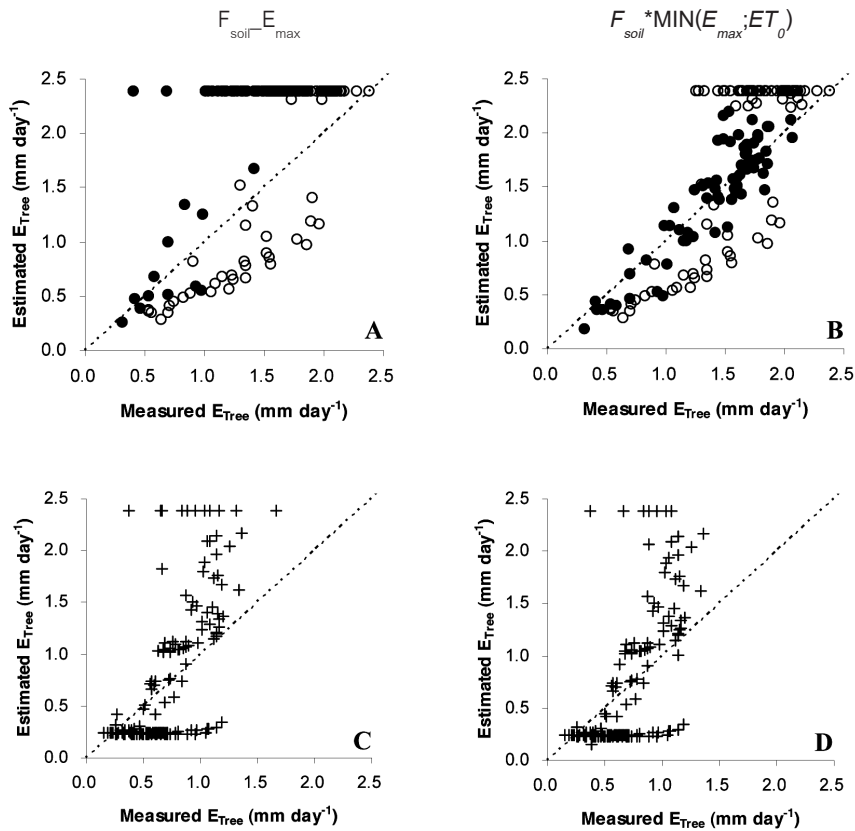


Figure 4 Comparison of estimated tree transpiration (estimated E_{Tree}) and measured tree transpiration (Measured E_{Tree}) in differed phenologies: 1) fully mature leaves period that predicted estimated E_{Tree} by $F_{soil}E_{max}$ model (A) and $F_{soil} * MIN(E_{max}; ET_0)$ model (B), which closed circles and opened circles represented data in low evaporative demand day ($ET_0 < 2.2 \text{ mm day}^{-1}$) and in high evaporative demand day ($ET_0 > 2.2 \text{ mm day}^{-1}$), respectively and 2) leaf shedding and flushing periods that predicted estimated E_{Tree} by $F_{soil}E_{max}$ model (C) and $F_{soil} * MIN(E_{max}; ET_0)$ model (D). The dotted line in each figure is 1:1 reference line.

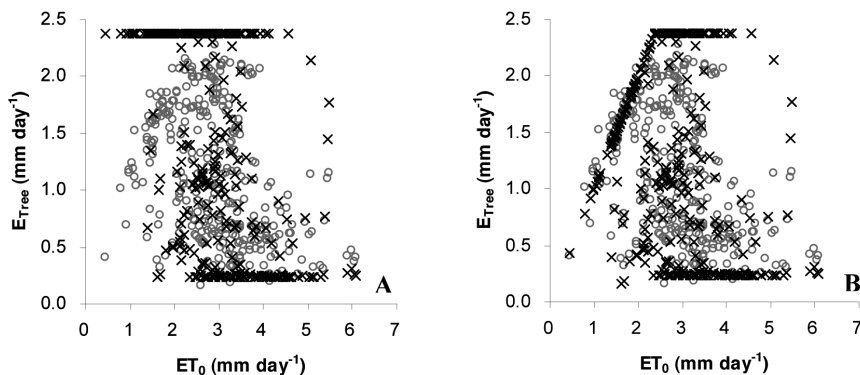


Figure 5 Relationship between tree transpiration (E_{Tree}) and reference evapotranspiration (ET_0) (crosses) by A) $F_{soil}E_{max}$ model and B) $F_{soil} * MIN(E_{max}; ET_0)$ model. The opened grey circles represented the measured E_{Tree} .

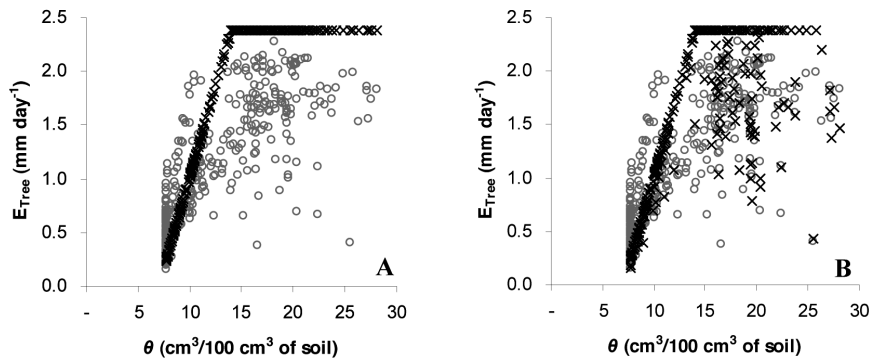


Figure 6 Relationship between tree transpiration (E_{Tree}) and volumetric soil water content (θ) (crosses) by A) $F_{soil}E_{max}$ model and B) $F_{soil} * \text{MIN}(E_{max}; ET_0)$ model. The opened grey circles represented the measured E_{Tree} .

Tree water used

Considering tree water used per tree, which calculated from accumulated E_{Tree} from actual measuring was $6.88 \text{ m}^3 \text{ tree year}^{-1}$. However, tree water used can be higher than this value because 1) in 2007 there was intermittent drought during the rainy season, 2) this plantation is in a non traditional area so the tree has a the leaf area lower than in traditional area and 3) E_{max} of rubber trees planted in traditional areas could be more than our value. Moreover, the new leaf flushing by observation was slower than in the south of Thailand; the early emergence of new mature leaves can increase the water use volume of rubber trees. Therefore, the $F_{soil} * \text{MIN}(E_{max}; ET_0)$ model should be evaluated in other plantations and trees of other size in the future.

Conclusion

The environmental model called ' $F_{soil}E_{max}$ ', which estimated E_{Tree} based on only soil water availability, produced maximum estimated E_{Tree} when the soil was wet and produced low

estimated E_{Tree} when the soil dried, but there was no variability of estimated E_{Tree} when evaporative demand differed.

The improving of environmental model, $F_{soil} * \text{MIN}(E_{max}; ET_0)$ model, by adding the ET_0 , which is alternated in minimum value between ET_0 and E_{max} produced the reduction in estimated E_{Tree} in both soil drought and low evaporative demand conditions. Therefore, this model is better in estimating transpiration under various conditions in fully mature leaf stage. However, it could not improve the estimated value during leaf shedding-flushing stage. Future study should separate E_{max} , which is one input parameter, in each leaf phenological stage for model evaluation.

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