

Four Decades of Progress in Monitoring and Modeling of Processes in the Soil-Plant-  
Atmosphere System: Applications and Challenges

Leaf and soil-plant hydraulic processes in the transpiration of  
tropical forest

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**Abstract**

In order to reveal the control of tree transpiration by the leaf ecophysiological traits and the hydraulic processes from the soil to leaves, transpiration rates of the tree species in tropical seasonal forests were monitored and modeled using independently measured leaf photosynthetic traits. Stand-level transpiration rate was modeled for rubber trees in a plantation and alien and native species in a community forest using a multilayer biophysical model that couples the energy balance and leaf ecophysiological processes. Model simulation was carried out on the assumption that leaf gas exchange was not limited by the hydraulic processes from the root to the leaves, while transpiration rates, which were independently monitored using sap flux measurements, were influenced both by the seasonal trends in leaf ecophysiological traits and the hydraulic processes. The modeled transpiration rate ( $E_{\text{model}}$ ) successfully captured the diurnal trend of the in situ measured one ( $E_{\text{sap}}$ ) in most rainy seasons in rubber plantation and in dry season in community forests, suggesting the absence of hydraulic limitation in soil-plant continuum. The decoupling between the  $E_{\text{model}}$  and  $E_{\text{sap}}$  was observed in mid dry season in rubber plantation and in a native species of the community forest. The daily-scale  $E_{\text{model}}$  overestimated  $E_{\text{sap}}$  by 20-40%, mainly due to the midday depression of  $E_{\text{sap}}$ . On the other hand, in an alien eucalyptus species in community forest, overestimate of  $E_{\text{model}}$  was observed in mid rainy season, suggesting the failure of water uptake by the roots under flooding conditions. The seasonal decreases in daily  $E_{\text{sap}}$  matched the timing of the water transport limitation of soil-plant continuum. Under lowered  $E_{\text{sap}}$  conditions, as high  $E_{\text{model}}$  as other seasons was observed in each species but could not be met due to the water supply, suggesting the leaf ecophysiological traits oriented for high leaf water demand and their imbalance with the seasonally decreasing water supply capacity. In conclusion, seasonal trends in transpiration rate were strongly characterized by the limitation in the process of soil-plant water transport, rather than the seasonal trends in the leaf ecophysiological traits.

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## 1. Introduction

Monsoon Asia experiences seasons of contrasting precipitation, i.e., a rainy season and a dry season with a period of rainless days. In this seasonally changing environment, seasonal trends of transpiration rate are thought to differ among trees and sites because of the site-specific environmental conditions [1-3] and species-specific ecophysiological traits [4-7], especially for avoidance of the risk of excessive water loss and resultant damage in the dry season [8; 9]. Transpiration and its relationship with species and environmental conditions have been intensively investigated in seasonally drought-affected regions owing to the possible threat to local water resources from plantations of fast-growing species [10-14], especially in Monsoon Asia where human society has been influenced by the fluctuating water resources [15].

In central Cambodia, recent research showed the drastic seasonal changes in soil water environments, characterized by the flooding from the mid to the end of rainy season and increased groundwater table depth in late dry season (Miyazawa et al., in submission). In the forest, the sap flux normalized by the evaporative demand (Equilibrium evaporation;  $E_{eq}$ );  $J_s/E_{eq}$  of each species differed in the responses to the changing environments. Some species showed decline in  $J_s/E_{eq}$  under flooding, another species did under soil drought and the other did not show clear decline. Different responses to the changing soil water environments have been observed and were considered due to the differences in depth in root water uptake [16-18], leaf photosynthetic traits [19] and hydraulic properties [20; 21].

Leaf photosynthetic traits and the seasonal trends would partly explain the species-specific responses in  $J_s/E_{eq}$  to the changing groundwater table depth, either as the driver for changing transpiration [22-24] or as the consequence of reduction in canopy transpiration due to other factors. Leaf photosynthetic traits determine the gas exchange rate at the end of soil–plant–atmosphere (SPA) continuum of water flow, and are useful for the prediction of transpiration as long as other SPA processes, such as root water uptake and the control of leaf water potential via stomatal closure do not limit transpiration rate [25]. In other words, comparison of modelled transpiration rate and the measured transpiration rates shows us the existence of limitation in transpiration rate by factors other than the leaf photosynthetic traits. In Indochina Peninsula, researches have been carried out in hill evergreen forests [1] or lowland evergreen forests [26; 27], no researches were, however, carried out for tree species in forests which experience annual cycle of flooding and soil drought in relation to the changing transpiration.

In this study, leaf-level gas exchange traits (the maximum rate of RuBP carboxylation rate;  $V_{cmax25}$  and stomatal control;  $m$ ) of two native and two exotic tree species were periodically measured in a community forest in central Cambodia. Stand-level transpiration rate per leaf area under the ambient environments;  $E$  was modeled based on the obtained leaf photosynthetic traits data in order to examine whether leaf photosynthetic traits could explain the species-specific seasonal trends in  $J_s/E_{eq}$ .

**Nomenclature**

$E_{eq}$	Equilibrium evaporation ( $\text{mm day}^{-1}$ )
$J_s$	Sap flux of a tree species weighed by the sapwood area of the sample trees ( $\text{kg m}^{-2} \text{s}^{-1}$ )
m	A parameter representing the stomatal control in equation [1] (unitless)
$V_{cmax25}$	The maximum rate of RuBP carboxylation by Rubisco ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )
VPD	Atmospheric vapour pressure deficit (kPa)

**2. Materials and methods***2.1. Study site*

The study was carried out at the Svay Bakav water cycle study site ( $11^{\circ}59'20''\text{N}$ ,  $104^{\circ}44'27''\text{E}$ ), Kampong Chhnang province, Cambodia. In March 2008, the site was located in a reforested area, which was established on heavily degraded land 10 years before the onset of the study. The Cambodia government designated the area as ‘community forest’, which is managed by the villagers for the purpose of forest conservation. Community forests are used by villagers for the production of non-timber forest products and timber cutting is forbidden.

The forest is composed of 10 woody species, with basal area  $8.62 \text{ m}^2 \text{ ha}^{-1}$  and mean tree height 10.8 m. We studied a native species, Popel (*Shorea roxburghii* G.Don.), and an artificially introduced alien species, eucalyptus (*Eucalyptus camaldulensis* Dehnh.), which accounted for 27.7 and 25.7 % of the total basal area of the stand, respectively. These species are evergreen broadleaved trees according to the observations of the villagers or Williams et al. [28]. Litter fall data showed a peak in leaf fall occurred in February to April. However, a decline in LAI in these months was not detected by the periodic LAI monitoring (Miyazawa et al., in submission). For each species, seven trees were selected for sap flow measurements.

The climate is a typical Monsoon Asian climate [3], with a distinct dry season for 4–5 months (from the end of November to early-mid April) and a rainy season (from the end of April to November), in which nearly 90% of the annual precipitation falls. The annual average air temperature is  $27.2^{\circ}\text{C}$  and annual precipitation is 1777 mm in 2008–2011 in this study site (Miyazawa et al. in submission)[29]. The daytime air temperature reaches the annual maximum in March and April ( $33.7 \pm 0.7^{\circ}\text{C}$  for the hottest months), and the annual minimum in December and January ( $29.1 \pm 0.9^{\circ}\text{C}$  for the coldest months). The soil of this region is a red-yellow podozol [29], while the soil at the study site was a sandy soil in the 0–3 m soil depth, according to the soil core samples.

A weather station for the study site was newly established in an open site in April 2008 equipped with a pyranometer (LP PYRA 03, Delta Ohm, Padua, Italy), photosynthetically active radiation (PAR) sensor (PAR-02, Prede Co. Ltd, Tokyo, Japan), rainfall gauge (TK-1, Takeda Keiki Co. Ltd, Tokyo, Japan) and air temperature–humidity sensors (HMP45D, Vaisala, Helsinki, Finland). For details about the measurements of environmental conditions in this study site, see Miyazawa et al. (in submission).

*2.2. Sap flow measurements*

Stand mean xylem sap flux over the sapwood area (sap flow rate per xylem area weighed by the sapwood,  $J_s$ ;  $\text{g m}^{-2} \text{s}^{-1}$ ) was monitored using Granier–type sap flux sensors [30] at breast height. Here we

briefly describe the measurement system. Each sensor consists of a pair of probes 20 mm in length (heater probe and reference probe) that are inserted into the stem. The heater probe emits heat of a known power (0.2 W) and measures temperature, whereas the reference probe, which is set 15–20 cm below the heater probe, only measures temperature. Each sensor was connected to a four-line cable. Two of the lines connected the heater in the heater probe to a power board and other two lines connected the thermocouple to the data logger to measure the temperature difference between the probes. To avoid the effects of solar radiation on the temperature data measured by the sensor, each sensor was shielded by an aluminum cover and a heat insulator. Sensors were installed in April 2008 on the selected trees of the four species.

The difference in temperature between the heater probe and reference probe ( $\Delta T$ ) was monitored and used for calculation of sap flux and sap flux weighed by the sapwood:  $J_s$  of the selected trees following Kumagai et al. [31]. Two data loggers (CR1000, Campbell Scientific) with attached multiplexers (AM16/32, Campbell Scientific) scanned  $\Delta T$  at 10 s intervals and the average was recorded at 30 min intervals.

For each tree,  $J_s$  was converted to water uptake per tree  $y$  multiplying sapwood area, and leaf-level transpiration rate based on sap flux measurements;  $E_{\text{sap}}$  was estimated by dividing the total leaf area of each tree. Total leaf area and sapwood area of the trees were non-destructively estimated using the allometric equations, which were established using destructive measurements of the nearby trees for each species.

### 2.3. Leaf photosynthesis measurements

Leaf-level photosynthetic traits were periodically measured since September 2008. Using an Li-6400 portable photosynthesis system (Li-cor, Lincoln, NE, USA), the relationship between net photosynthetic rate ( $A$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and intercellular  $\text{CO}_2$  concentration ( $C_i$ ,  $\mu\text{mol mol}^{-1}$ ) ( $A$ – $C_i$  relationship) was obtained using excised leaves of the trees selected for sap flow measurements. Although excision is thought to have influences on the gas exchange, preliminary research showed that impacts of excision on gas exchange or on the model simulation of leaf gas exchange were small within an hour following the procedure of Miyazawa et al. [32]. For each species, three trees were selected and six leaves on excised branches for each species were used for the measurements of  $A$ – $C_i$  relationship.

After photosynthesis measurements, leaves were kept in the dark for more than 20 minutes to measure the dark respiration rate at leaf temperature 28–30°C ( $R_d$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).

In rainy season 2009 and dry season 2010, diurnal course of leaf gas exchange rates was monitored at 1–3 minute intervals in order to construct the model of stomatal control for each leaves in rainy season and dry season, respectively (six leaves per species). The environmental conditions in the cuvette were maintained as the same as the ambient ones using the ambient light through the transparent cuvette top and the temperature controller of Li-6400. Because of the high transpiration rate, cuvette vapor pressure was higher than the inlet ones, so the vapor pressure of the inlet air was reduced using the attached tube with desiccant. After the leaf gas exchange rate reached stable, the leaf gas exchange rates and the cuvette environmental conditions were recorded.

Stomatal control of the leaves was expressed using the parameter  $m$  in equation of Ball et al. [33] as follows:

$$g_{\text{sw}} = m A h_s C_s^{-1} + b \quad (1)$$

where  $h_s$  is the leaf surface relative humidity,  $C_s$  is the  $\text{CO}_2$  concentration at leaf surface ( $\mu\text{mol mol}^{-1}$ ) and  $b$  is the intercept of  $g_{\text{sw}}$  at  $A = 0$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).

## 2.4. Model simulation of leaf gas exchange within a canopy

Stand-level transpiration rates based on model simulation ( $E_{\text{model}}$ ) of leaves in different positions of the canopy were simulated using an ecophysiological-meteorological model. The model is basically the same as that in Leuning et al. [34], which integrates the carbon assimilation, stomatal conductance, transpiration and energy exchange at 5 layers of different depth from the top canopy using numerical methods. The model take into consideration of (1) radiation absorption by sunlit and shaded leaves based on the profile of related factors with canopy depth, (2) coupled submodel for the carbon assimilation and stomatal conductance [35], (3) leaf surface energy balance equations as the function of transpiration in 2, isothermal net radiation, leaf surface conductance for heat and vapor and leaf temperature, and (4) effects of leaf temperature on 2, for each layer. In each layer, the model simulated the microenvironments (absorbed radiation by sunlit and shaded leaves and wind speed) and the leaf photosynthetic traits as the function of LAI cumulated from the top canopy.

The two estimates of stand-level transpiration rates;  $E_{\text{model}}$  and  $E_{\text{sap}}$  were compared to examine whether the model could well model the absolute values of  $E_{\text{sap}}$  and capture the diurnal trends. The existence of limitation in transpiration due to SPA factors unconsidered in the model was examined by the coincidence of  $E_{\text{model}}$  and  $E_{\text{sap}}$ .

Table 1. Gas exchange data of the alien species, eucalyptus and native species, Popel.

		Rainy season		Dry season	
$V_{\text{cmax25}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Popel	47.16	$\pm$ 6.92	58.75	$\pm$ 23.32
	Eucalyptus	60.66	$\pm$ 20.14	59.07	$\pm$ 8.95
Dark respiration rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	Popel	1.29	$\pm$ 0.56	1.71	$\pm$ 0.35
	Eucalyptus	1.83	$\pm$ 0.45	2.43	$\pm$ 0.72
$m$	Popel	31.29		18.99	
	Eucalyptus	15.34		11.22	
$J_s/E_{\text{eq}}$	Popel	1.61	$\pm$ 0.7	1.685	$\pm$ 0.775
	Eucalyptus	1.25	$\pm$ 0.253	1.724	$\pm$ 0.252

## 3. Results and discussion

### 3.1. Photosynthetic traits and the seasonal trends

The seasonal trends in  $V_{\text{cmax25}}$  were less clear in both Popel and eucalyptus (Table 1). Obtained  $V_{\text{cmax25}}$  were higher than those in late successional tree species in Central Cambodia [27] and those in other Monsoon Indochina Peninsula [26; 36; 37] and were similar to plantation trees in this region (*Hevea brasiliensis*, [38-40]) The high  $V_{\text{cmax25}}$  reflects the successional status of the species measured in this study. Eucalyptus was planted here as fast growing species (Forestry Administration of Cambodia, unpublished data) and Tbeng and Popel successfully survive in this study site under frequent disturbance by human activities and wild fires, through resprouting from the stumps.

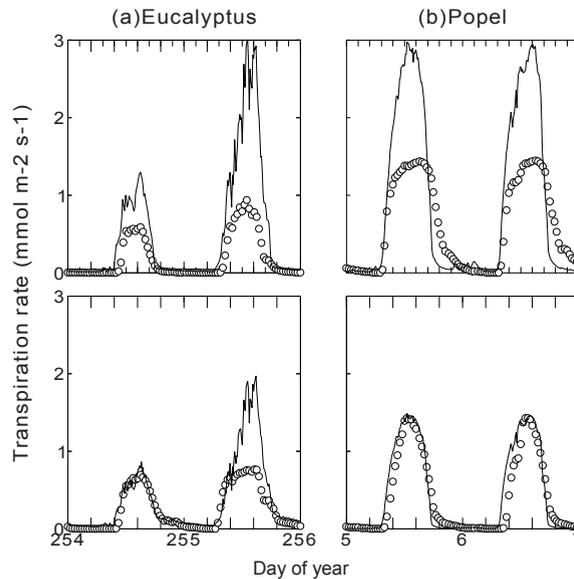


Fig. 1. Transpiration rate per leaf area of an individual tree calculated based on sap flux measurements (circles) and multi-layer model simulation (lines) for Popel and eucalyptus.

Stomatal control expressed by  $m$  in equation [1] was high in Popel and leaves had high  $g_{sw}$  supported by the unlimited water availability from the shallow ground water (Miyazawa et al., in submission). Because of the high stomatal conductance and the broad leaf blade of Popel, the modelled transpiration rate at sun-exposed leaves was not different between the two species despite the large differences in the stomatal conductance.

The seasonal trends in  $V_{cmax25}$  did not coincided with that of  $J_s/E_{cq}$  in each species (Table 1). In rainy season, eucalyptus showed decline in  $J_s/E_{cq}$  to 70% of that of the dry season, but did not show reduced  $V_{cmax25}$ . Popel kept high  $V_{cmax25}$  level in dry season 2010 when  $J_s/E_{cq}$  was 70% of the rainy season. In Popel, leaf water potential did not show clear decrease in dry season both in midday and predawn (data not shown), and the decreased  $J_s/E_{cq}$  was not due to the seasonal changes in photosynthetic traits or the gradual decrease in the soil water environments. It should be noted that clear decrease in  $J_s/E_{cq}$  was observed just after the field measurements and our measurements might have failed to capture the photosynthetic traits under the drought conditions in Popel.

### 3.2. Comparison of estimates of transpiration rates based on sap flux and model simulation

Modelled transpiration rate per leaf area ( $E_{model}$ ) reached a peak in midday and captured the diurnal trends in  $E_{sap}$  but differences in the trends were observed and the absolute values were not similar in eucalyptus (Fig. 1). In Popel,  $E_{model}$  showed diurnal trends similar to  $E_{sap}$  in dry season, suggesting that transpiration of Popel was mainly determined by the factors considered in the model; leaf photosynthetic traits and the radiation and the atmospheric environments. Both  $E_{sap}$  and  $E_{model}$  reached a daily peak earlier than the timing of peak atmospheric vapor pressure deficit (VPD), due to the decoupling between the atmosphere and the leaf surface [41]. On the other hand,  $E_{sap}$  reached before noon and did not show further increase with the increase in VPD. The absence of increase in  $E_{sap}$  despite the increasing

evaporative demand suggested by the increasing  $E_{\text{model}}$  suggested processes in SPA from root water uptake to water transport to the leaves. Because leaf water potential kept low levels both in predawn and midday, water transport from the roots to the leaves was not thought responsible for the absence of increasing  $E_{\text{sap}}$  in the afternoon. Because the ground was flooded during rainy seasons, the flooding might have influenced the root water uptake, although flooding did not show clear influences on leaf-level photosynthetic traits or the  $J_s/E_{\text{eq}}$ .

Eucalyptus showed nighttime transpiration rate in dry season, behaviour typical in trees in drought conditions [41]. The leaf water potential in midday showed low levels, which was observed in the same species in drought conditions in saline regions in Australia [42], suggesting that eucalyptus had difficulties in the access to the groundwater table in dry season. Although previous studies about trees under dry conditions showed reduced photosynthetic capacity, eucalyptus did not show such decrease (Table 1). Despite the difficulties in the access to the groundwater, daily transpiration rate in dry season was higher than that in rainy season due to the increased evaporative demand.

As like the case for Popel,  $E_{\text{sap}}$  of eucalyptus reached a daily peak in the morning before the peak of  $E_{\text{model}}$  in rainy season, suggesting the existence of limitation on transpiration by factors unconsidered in this study. The reduced  $J_s/E_{\text{eq}}$  in rainy season in eucalyptus was not due to the changes in photosynthetic traits (and  $E_{\text{model}}$ ), but to the limitation of transpiration by other factors such as flooding effects on root water uptake [43-45]. Flooding is known to cause reduced photosynthetic traits and decreased leaf water potential, but such effects were not observed in this study. Detailed analysis of the SPA components other than the leaves should be investigated in further studies.

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