

# Implications of leaf-scale physiology for whole tree transpiration under seasonal flooding and drought in central Cambodia



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## ABSTRACT

In central Cambodia, rapidly growing non-endemic species are often planted for timber production. The introduction of non-endemic species into stands with native species has been found to alter the forest transpiration characteristics in this region with distinct dry and rainy seasons defined by the different rainfall patterns. However, less is understood about the underlying processes, especially the ecophysiological characteristics of native species that are adapted to the highly seasonal environments and the non-endemic species that acclimate to those environments. Leaf ecophysiological traits were measured for two native and two representative non-endemic tree species in central Cambodia to examine whether species-specific seasonal trends in transpiration could be explained by leaf ecophysiological traits. Photosynthetic capacity as represented by the maximum carboxylation rate ( $V_{cmax25}$ ) of each species remained constant in the rainy and dry seasons. Native species had high stomatal conductance ( $g_{sw}$ ) and the parameter for its response to the environments ( $m$ ) in the rainy season and lower levels in the dry season. Additionally, the seasonal change in  $g_{sw}$  for non-endemic species was less clear despite the seasonality in the tree-level transpiration. A multi-layer model that incorporated the measured data related to the leaf ecophysiological traits and their seasonal changes successfully reproduced the daily canopy-scale transpiration rate ( $E_{canopy}$ ). The modeled  $E_{canopy}$  successfully reproduced most of the seasonal and day-to-day changes in measured  $E_{canopy}$  using sap flux measurements and showed the strong control of leaf ecophysiological traits over  $E_{canopy}$  and the species-specific seasonal trends. Two reduction events in measured  $E_{canopy}$  were, however, not explained by the simulation, possibly as a result of species-specific factors that were not considered in this study, i.e., the reduction in water uptake by a native species caused by drought and the hypoxic effects of flooding on the roots of a non-endemic species.

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## 1. Introduction

The Southeast Asian Monsoon creates seasons of contrasting precipitation, i.e., a rainy season as well as a dry season with

periods of days without rain. In this seasonally changing environment, transpiration rates are thought to differ among trees and sites because of the site-specific environmental conditions (Pinker et al., 1980; Tanaka et al., 2003, 2008) and species-specific ecophysiological traits (Eamus et al., 2001; Kelliher et al., 1995; Kunert et al., 2010; O'Grady et al., 2009). Transpiration and its relationship with species and environmental conditions have been intensively investigated in regions experiencing seasonal droughts because the water demands of fast-growing plantation species can pose a threat to local water resources (Bruijnzeel, 2004; Calder et al., 1993; Mielke et al., 2000; Whitehead and Beadle, 2004).

Our previous work demonstrated the presence of drastic seasonal changes in soil water environments, characterized by flooding

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**Table 1**  
List of abbreviations.

Abbreviations	Units	
$A$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Net photosynthetic rate
$A_G$	$\text{m}^2$	Surface area of the stand
$A_s$	$\text{m}^2$	Sapwood area
$b$	$\text{mol m}^{-2} \text{s}^{-1}$	Intercept of Eq. (3)
$C_i$	$\mu\text{mol mol}^{-1}$	Intercellular $\text{CO}_2$ concentration
$C_i/C_a$	–	$C_i$ relative to the air $\text{CO}_2$ concentration
$E_{\text{canopy}}$	$\text{mm day}^{-1}$	Daily canopy-scale transpiration rate
$E_{i,\text{mod}}$	$\text{mm day}^{-1}$	Modeled leaf-scale transpiration rates
$E_{i,\text{sap}}$	$\text{mm day}^{-1}$	Measured leaf-scale transpiration rates
$F_d$	$\text{g m}^{-2} \text{s}^{-1}$	Sap flux measured by a sensor
$g_{\text{sc}}$	$\text{mol m}^{-2} \text{s}^{-1}$	Leaf-scale stomatal conductance for $\text{CO}_2$
$G_{\text{sw}}$	$\text{mol m}^{-2} \text{s}^{-1}$	Leaf-scale stomatal conductance for water vapor calculated based on $J_s$
$g_{\text{sw}}$	$\text{mol m}^{-2} \text{s}^{-1}$	Leaf-scale stomatal conductance for water vapor
$\Gamma^*$	$\mu\text{mol mol}^{-1}$	$\text{CO}_2$ compensation point (40 at 25 °C)
$J_s$	$\text{g m}^{-2} \text{s}^{-1}$	Stand mean xylem sap flux over the total stand sapwood area
$K_c$	$\mu\text{mol mol}^{-1}$	Michaelis–Menten constant for $\text{CO}_2$ (404 at 25 °C)
$K_o$	$\text{mmol mol}^{-1}$	Michaelis–Menten constant for $\text{O}_2$ (248 at 25 °C)
LAI	$\text{m}^2 \text{m}^{-2}$	Leaf area density
$m$	–	Slope of Eq. (3)
$SF_n$	–	Sap flux normalized based on the equilibrium evaporation
$V_{\text{cmax}25}$	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Maximum rate of ribulose-1,5-bisphosphate carboxylation normalized at 25 °C
VPD	kPa	Air vapor pressure deficit
$\psi_{\text{leaf}}$	MPa	Leaf water potential

from the middle to the end of the rainy season and a lowered groundwater table late in the dry season in central Cambodia (Miyazawa et al., 2014). In the studied forest, sap flux was normalized based on the equilibrium evaporation (Jarvis and McNaughton, 1986) of each species that differed for each species in terms of the responses to the changing groundwater table. One species, eucalyptus (*Eucalyptus camaldulensis* Dehnh.) exhibited a decline in the ratio of sap flux to the equilibrium evaporation ( $SF_n$ , Table 1) under flooding in the rainy season. Another species, Popel (*Shorea roxburghii* G. Don.) did so in dry season with the progression of lowering of the water table and a third species, Tbeng (*Dipterocarpus obtusifolius*) did not show clear decline. Such varied responses to changing soil water environments have been observed in previous studies and were considered to have been caused by differences in the depth in root water uptake (Becker, 1996; Cleverly et al., 2006; Kume et al., 2007), leaf photosynthetic traits (Herbst et al., 2008) and hydraulic properties (Katul et al., 2003; Williams et al., 1996, 1998).

Information related to the leaf ecophysiological traits and their seasonal trends would provide insight into the basis underlying the species-specific responses in transpiration that occur in response to changes in the groundwater table. Leaf ecophysiological traits are known to change as the driver for changing transpiration (Baldocchi, 1997; Law et al., 2000; Wilson et al., 2001; Xu and Baldocchi, 2004). Stomatal conductance for water vapor ( $g_{\text{sw}}$ ) changes in response to the atmospheric evaporative demand and the soil water content especially in the presence of drought to balance canopy transpiration and root water uptake (Katul et al., 2003). Many species in regions with pronounced rainy and dry seasons are known to reduce leaf gas exchange rates during the dry season (Aranda et al., 2012; Ishida et al., 2006; Liu et al., 2004; Pereira et al., 1987). These studies imply that species in central Cambodia should show similar seasonal trends in leaf ecophysiological traits, such as in the photosynthetic capacity  $V_{\text{cmax}25}$  (maximum rate

of ribulose-1,5-bisphosphate carboxylation normalized at 25 °C, Farquhar et al., 1980), and a parameter for stomatal control ( $m$ , the slope of stomatal conductance and the function of photosynthetic rate and leaf surface environments, Ball et al., 1987). Results for some species, however, did not show the expected remarkable reduction in these leaf ecophysiological traits during dry season because of the species-specific ecophysiological traits (Ferrio et al., 2003; Martinez-Ferri et al., 2000) and/or site-specific edaphic conditions (Prior et al., 2004; Tanaka et al., 2003), making it difficult to predict transpiration rates of forests with clear seasonality in rainfall without in situ measurements. In the Indochina Peninsula, research studies have been conducted related to leaf ecophysiological traits in hill evergreen forests (Tanaka et al., 2003) and lowland evergreen forests (Ishida et al., 2006; Kenzo et al., 2012; Norisada and Kojima, 2005); these showed variations in their seasonal trends among species and sites. However, no research studies have been conducted for co-occurring tree species in forests whose productivity and water use are affected by seasonal flooding and drought.

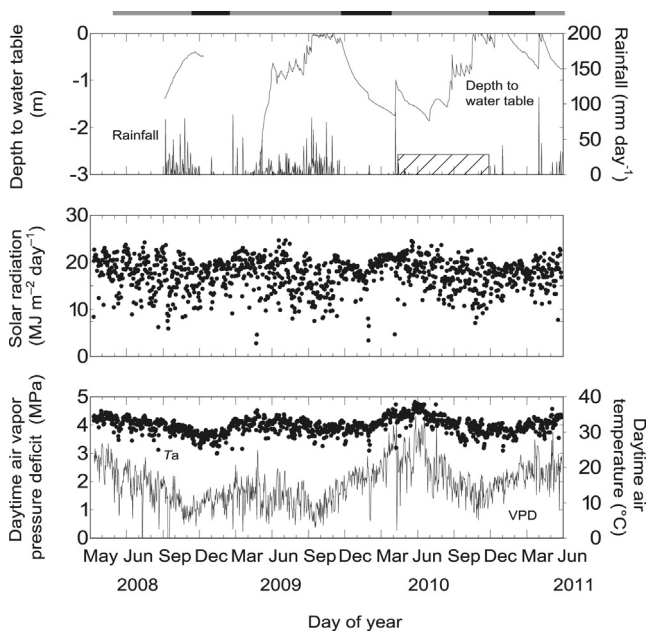
The goal of this study is to investigate the leaf ecophysiological traits of the co-occurring tree species and to clarify how the seasonality in transpiration of each species is controlled by species-specific leaf ecophysiological traits. Toward that goal, field measurements were conducted in a community forest in central Cambodia, which had been established as a conservation area under the non-timber producing management by nearby villagers. The community forest is composed of various naturally regenerated Popel, Tbeng and other native tree species and non-endemic eucalyptus and acacia (*Acacia auriculiformis*) that had been planted for timber production. Interspecific variation in the canopy-scale transpiration rate ( $E_{\text{canopy}}$ ) and its response to the changing environments is thought to be caused by variations in  $g_{\text{sw}}$  and its seasonality specific to the species. Therefore, among leaf ecophysiological traits with a close relationship to  $g_{\text{sw}}$ ,  $V_{\text{cmax}25}$  and  $m$  of two native and two non-endemic tree species were periodically measured. Canopy-scale transpiration rate ( $E_{\text{canopy}}$ ) was computed using a multilayer model (Leuning et al., 1995). This model was used both as a tool for scaling up the observed leaf-scale gas exchange rates and as a way to investigate the role of seasonal changes in the leaf ecophysiological parameters on  $E_{\text{canopy}}$  in rainy and dry seasons. For these purposes, we examine whether the modeled  $E_{\text{canopy}}$  successfully captures the patterns of seasonal and day-to-day changes in measured  $E_{\text{canopy}}$  by taking seasonal changes in leaf ecophysiological traits into consideration.

We examine the following hypotheses. First,  $V_{\text{cmax}25}$  and  $m$  of each species are high during the rainy seasons and are low under drought conditions during the dry season, which effectively reduces  $E_{\text{canopy}}$ . Additionally,  $V_{\text{cmax}25}$  and  $m$  show species-specific seasonal trends corresponding to those in the  $SF_n$ . Finally, seasonal changes in  $V_{\text{cmax}25}$  and  $m$  strongly influence  $E_{\text{canopy}}$ , i.e., input of data obtained in different season results in large changes in  $E_{\text{canopy}}$ .

## 2. Materials and methods

### 2.1. Study site and meteorological observation

The study was conducted at the study site of Miyazawa et al. (2014) (Svay Bakav water cycle study site), Kampong Chhnang in central Cambodia (11°59'20" N, 104°44'27" E, 50 m a.s.l.) starting in March 2008. The site was located in a reforested area, which had been established on heavily degraded land in 1998. The Cambodian government designated the area as a '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 presently, timber cutting is forbidden.



**Fig. 1.** Meteorological data recorded at Svay Bakav for (a) rainfall and depth to groundwater table, (b) short-wave radiation, and (c) daytime atmospheric vapor pressure deficit (VPD) and air temperature ( $T_a$ ). Gray bars at the top of the figure indicate the rainy seasons, black bars indicate the dry seasons. Hatched areas indicate the periods for which data are lacking because of technical problems.

The region is subjected to the typical monsoon-Asian climate (Tanaka et al., 2008) with a distinct 4–5 month long dry season from the end of November to early-mid April and a rainy season from the end of April to November, during which nearly 90% of the annual precipitation falls (Fig. 1). The annual precipitation was 1777 mm in 2008 at this site and was typical of the region (annual precipitation in 2011–2014 was 1500–1790 mm). At a nearby weather station where rainfall data is available (90 km in the east of the study site,  $11^{\circ}57'N$ ,  $105^{\circ}34'E$ , 50 m a.s.l.), annual rainfall in the period of present study (2008–2010) was higher than the average in 2000–2012 (T.K. Lim, Cambodian Rubber Research Institute, personal communication).

The annual average air temperature was  $27.2^{\circ}C$  in 2008–2011. The daytime air temperature reaches the annual maximum in March and April (mean  $\pm$  standard deviation =  $33.7 \pm 0.7^{\circ}C$ ), and the annual minimum in December and January ( $29.1 \pm 0.9^{\circ}C$ ). The red-yellow podzol soil of this region (Save Cambodia's Wildlife, 2006) is 0–3 m deep, and study site has a sandy soil with minor fractions of silt and clay soil.

A weather station was established at the study site 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), air temperature-humidity sensors (HMP45D, Vaisala, Helsinki, Finland) and anemometer (Model 05305, R. M. Young, Traverse City, MI, USA). Volumetric soil water content was monitored using amplitude-domain reflectometry (ADR) sensors (ThetaProbe ML2x, Delta-T Devices, Cambridge, UK), which were installed at soil depths of 10, 20, 80 and 100 cm. A groundwater-level meter (HM-900-02-10, Sensez Co. Ltd., Tokyo, Japan) was installed in an observation well. Sensors were connected to a data logger (CR1000, Campbell Scientific, Logan, UT, USA), which scanned data every 10 s. Averages were recorded at a 10 min interval except for rainfall, which was recorded as pulse counts. Solar panels and batteries powered the weather station and sap flux measurement system (details provided below). Details related to the measurements of environmental conditions in this study

**Table 2**

Description of the study site and the studied species (means  $\pm$  standard deviation).

	Unit	Species	
Mean canopy height	m		10.8
Basal area of the stand	$m^2 ha^{-1}$	Total	8.62
		Acacia	1.71
		Eucalyptus	2.39
		Popel	2.22
		Tbeng	1.16
Leaf blade width	cm	Acacia	$2.8 \pm 0.6$
		Eucalyptus	$3.2 \pm 0.7$
		Popel	$8.8 \pm 2.3$
		Tbeng	$17.4 \pm 5.4$
Leaf area index	$m^2 m^{-2}$	Acacia	$3.57 \pm 0.20$
		Eucalyptus	$2.06 \pm 0.21$
		Popel	$3.06 \pm 0.64$
		Tbeng	$1.88 \pm 0.45$

are described elsewhere (Miyazawa et al., 2014). Technical problems prevented monitoring of rainfall from April to November 2010.

We determined the onset and end of the rainy season following Wang and LinHo (2002). Each year was divided into a total of 73 periods lasting 5 days each (73 pentads). The mean rainfall of the  $i$ th pentad was calculated as  $RR_i$  ( $mm day^{-1}$ ) and mean rainfall in January as  $R_{JAN}$  ( $mm day^{-1}$ ). The first pentad in which  $(RR_i - R_{JAN})$  exceeds  $5 mm day^{-1}$  was defined as the onset of the rainy season. Similarly, the pentad when  $(RR_i - R_{JAN})$  drops below  $5 mm day^{-1}$  between October and January was defined as the end of the rainy season. The pentads for the onset of the rainy season began on February 16 (2009), March 22 (2010) and March 12 (2011). The pentads marking the end of the rainy season were November 2 (2008) and November 7 (2009). In the calculation of the end of the rainy season in 2008, we used  $R_{JAN}$  in 2009 for the calculation of  $(RR_i - R_{JAN})$ . We could not determine the pentad marking the end of the rainy season in 2010, because of the failure of rainfall measurement equipment until November 2010. We assumed that the pentad marking the end of the rainy season in 2010 was the same as the average of 2008 and 2009 in Fig. 1 (November 5).

Among the composing ten woody species of the forest, we studied two native species, Tbeng (*Dipterocarpus obtusifolius* Teijsm. ex Miq.) and Popel (*Shorea roxburghii* G. Don.), and two artificially introduced non-endemic species, acacia (*Acacia auriculiformis* A. Cunn. ex Benth.) and eucalyptus (*Eucalyptus camaldulensis* Dehnh.). Details about the structure of the forest and the studied species are shown in Table 2. Native species tended to have very broad leaves and non-endemic species had broad leaves.

The observations of the villagers and Williams et al. (2008) indicate these species are evergreen broadleaved trees. Litter fall data revealed a peak in leaf fall from the end of dry season to the beginning of rainy season (February to April). However, leaf area index (LAI,  $m^2 m^{-2}$ ) remained constant in February, March, April and other months in the rainy season in 2008–2010 (Miyazawa et al., 2014). LAI was periodically measured for each sample tree for sap flow measurements from March 2009 at 3–4 month intervals using a fish-eye lens (FC-E8, Nikon Corp., Tokyo, Japan) attached to a digital camera (CoolPix 990, Nikon Corp.). One to three hemispherical photographs were taken at fixed points below the canopy of each tree and were used for the calculation of LAI with HemiView canopy analysis software version 2.1 (Delta-T Devices, Cambridge, UK). The obtained LAI of each species is shown in Table 2. Because the stand is a mixture of several species, the calculated LAI of each tree represents the LAI of the tree and the surrounding overstorey trees, except for Tbeng which formed a relatively monospecific stand.

## 2.2. Sap flow measurements

Stand mean xylem sap flux over the total stand sapwood area ( $J_s$ ,  $\text{g m}^{-2} \text{s}^{-1}$ ) was obtained by continuous monitoring of sap flux ( $F_d$ ,  $\text{g m}^{-2} \text{s}^{-1}$ ) using Granier-type sensors (Granier, 1987) installed at breast height, as described briefly below. Each sensor consists of a pair of 20 mm long probes (heater and reference probes) that were inserted into the stem. Both probes measure temperature. The heater probe emits heat of a known power (0.2 W), and the reference probe was set 15–20 cm below the heater probe. Each sensor was connected to a four-line cable with two lines connecting the heater in the heater probe to a power controller board and other two lines connected the thermocouples to the data logger to measure the temperature difference between the probes ( $\Delta T$ , °C). An aluminum cover and a heat insulator shielded each sensor to avoid the effects of solar radiation on the temperature data.

Sensors were installed in April 2008 on the selected trees of the four species (Table 3). Each tree was installed with two to three pairs of sensors to monitor the circumferential variation in sap flux. Because the sapwood area was small and less than 30 mm in depth from the bark, we assumed that each sensor covered the entire range along the radial profile of the sap flux gradient. The sensors were checked periodically for breakage. When ants or rats broke a sensor, which occurred every 6–12 months, it was replaced. Two data loggers (CR1000) with attached multiplexers (AM16/32, Campbell Scientific) scanned  $\Delta T$  at 10-s intervals and recorded an average  $\Delta T$  at a 30-min interval.

In August 2009, a water-soluble dye (safranin) solution was injected into the cut end of the stem of trees of each species near the study site ( $n=5$  per species) to visualize the sap wood area in transverse section for the non-destructive estimation of sapwood area. After injection, the trees were felled to regress sapwood area ( $A_s$ ,  $\text{cm}^2$ ) with diameter at breast height (dbh, cm). Measurements from the felled trees were used to establish allometric equations used to determine leaf mass–dbh relationships. Tree-level leaf mass was converted to total leaf area (LA,  $\text{m}^2$ ) by multiplication by the specific leaf area (leaf area/leaf dry mass, SLA,  $\text{m}^2 \text{kg}^{-1}$ ), which was obtained using individually sampled leaves.

For each tree,  $\Delta T$  was converted to  $F_d$ . The  $J_s$  of a given species  $j$  ( $J_{sj}$ ) was calculated using Eq. (1) following Kumagai et al. (2007);

$$J_{sj} = \frac{\sum_{i=1}^N A_{si,j} \cdot F_{di,j}}{\sum_{i=1}^N A_{si,j}} \quad (1)$$

where  $i$  denotes the number of the sample tree and  $N$  is the sample size for sap flow measurements for each species. Stand-scale transpiration rate of species  $j$  is expressed as  $E_j = J_{sj} (A_{s,\text{stand}j}/A_G)$  using the total sapwood area within the stand of the species ( $A_{s,\text{stand}j}$ ,  $\text{m}^2$ ) and the surface area of the stand ( $A_G$ ,  $\text{m}^2$ ).

## 2.3. Measurements of leaf ecophysiological traits

Leaf-level ecophysiological traits were measured periodically from September 2008 to January 2010. Using a portable photosynthesis measurement system (Li-6400, 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 for excised leaves of the trees selected for sap flow measurements. Fully expanded young leaves were selected for photosynthesis measurements from parts of the crown that were well-exposed to the sun and within reach of a pole pruner (5–15 m above the ground). Although excision is thought to influence leaf 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 after excision following the procedure of Miyazawa et al. (2011). For each species, three trees were selected and six leaves on excised branches were used for the measurements of the  $A$ – $C_i$  relationship.

We first measured  $A$  and stomatal conductance of  $\text{H}_2\text{O}$  ( $g_{\text{sw}}$ ,  $\text{mol m}^{-2} \text{s}^{-1}$ ) at light saturation for carbon assimilation ( $\text{PAR}=1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), ambient air temperature (26–31 °C), and  $\text{CO}_2$  concentration at  $380 \mu\text{mol mol}^{-1}$  in the cuvette. Air vapor pressure deficit (VPD, kPa) of the cuvette air was less than 1.5 kPa. Light was supplied with the attached light source (Li-6400-2B, Li-cor). We then determined the parameter described by Farquhar et al. (1980):  $V_{\text{cmax}}$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ).  $V_{\text{cmax}}$  of the leaves was obtained by measuring  $A$  at six levels of  $\text{CO}_2$  concentration

**Table 3**  
Description of the sample trees for sap flow measurements.

	Tree	dbh (cm)	Number of sensors	Leaf area ( $\text{m}^2 \text{tree}^{-1}$ )	Sapwood area ( $\text{cm}^2 \text{tree}^{-1}$ )
Eucalyptus	1	8.8	2	0.60	23.08
	2	8.7	2	0.58	22.46
	3	12.9	2	1.27	48.28
	4	16.5	2	2.49	70.40
	5	15.5	2	2.07	64.26
	6	18	2	3.28	79.62
	7	24.4	2	10.76	118.96
Popel	1	14.5	3	5.73	50.17
	2	14.8	3	6.04	52.60
	3	14	2	5.25	46.11
	4	11.4	2	3.34	25.01
	5	15.2	2	6.47	55.85
	6	14.2	3	5.44	47.74
	7	12	2	3.70	29.88
Tbeng	1	15.4	2	4.71	61.05
	2	10.9	2	1.93	33.04
	3	12	2	2.40	39.89
	4	12.3	2	2.55	41.75
	5	8.7	2	1.25	19.35
	6	10.2	2	1.68	28.68
	7	10.5	2	1.78	30.55



**Table 4**

The extinction coefficients of leaf ecophysiological traits along the canopy profile.

Species <sup>a</sup>	Extinction coefficient			
	$V_{\text{cmax}25}$		$R_d$	
	Dry season	Rainy season	Dry season	Rainy season
Acacia	0.19	0.18	0.10	0.14
Popel	0.14	0.12	0.22	0.18

<sup>a</sup> Extinction coefficient for eucalyptus and Tbeg are assume to be the same as those of acacia and Popel, respectively.

less than  $400 \mu\text{mol mol}^{-1}$  and by regressing  $A$  with  $C_i$  using Eq. (2):

$$A = \frac{V_{\text{cmax}}(C_i - \Gamma^*)}{C_i + K_c(1 + (O/K_o))} - R_{\text{d,day}} \quad (2)$$

where  $K_c$  and  $K_o$  are the Rubisco Michaelis–Menten constants for  $\text{CO}_2$  and  $\text{O}_2$ , respectively, and  $\Gamma^*$  is the  $\text{CO}_2$  compensation point without diurnal respiration with the temperature dependencies (Table 1) (Harley et al., 1992; von Caemmerer et al., 1994).  $R_{\text{d,day}}$  is the day respiration rate at light saturation ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), and  $O$  is the  $\text{O}_2$  partial pressure in the chloroplast ( $210 \text{ mmol mol}^{-1}$ ). Photosynthetic capacity was calculated as  $V_{\text{cmax}}$  at a common leaf temperature  $25^\circ\text{C}$  ( $V_{\text{cmax}25}$ ) using the equation of Harley et al. (1992) and the parameters for temperature dependencies of de Pury and Farquhar (1997). Another parameter for photosynthetic capacity, maximum rate of electron transport at  $25^\circ\text{C}$  ( $J_{\text{max}25}$ ) was calculated as  $1.97 V_{\text{cmax}25}$ , which is the slope of the  $J_{\text{max}}-V_{\text{cmax}}$  relationship forced through the origin among 109 plant (Wullschlegel, 1993). After measurements of the  $A-C_i$  relationship, leaves were kept in the dark for more than 20 min to measure the dark respiration rate ( $R_d$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) under ambient air temperature ( $28-30^\circ\text{C}$ ).

Acacia and Popel trees form deep crowns. Leaves at the bottom of their crowns were excised and used for the determination of  $V_{\text{cmax}25}$  and  $R_d$ . Obtained  $V_{\text{cmax}25}$  and  $R_d$  were used to construct the canopy profile as  $f(\xi) = f(0) \exp(-k_n \xi)$ , where  $f(\xi)$  is either  $V_{\text{cmax}25}$  or  $R_d$  at cumulative LAI from the top of the canopy =  $\xi$ , and  $k_n$  is the extinction coefficient. The values of  $k_n$  were obtained by calculating the LAI and  $V_{\text{cmax}25}$  or  $R_d$  of leaves at the top and bottom of the canopy as  $1/f(\text{LAI}) \ln[f(0)/f(\text{LAI})]$ . The values of  $k_n$  for  $V_{\text{cmax}25}$  and  $R_d$  during both the dry and rainy seasons were obtained for acacia and Popel (Table 4). Because eucalyptus has a small canopy depth, we assumed that their  $k_n$  values were the same as those of acacia, and for Tbeg the same as those of Popel because of the similarity in the crown shape in appearance in their dense stand.

During the measurement period in the rainy (21–23 September 2009) and dry (15–17 January 2010) seasons, intensive measurements of leaf ecophysiological traits were conducted using well-exposed intact leaves (ca. 1.5 m height from the ground) of trees of each species facing canopy gaps. Diurnal courses of leaf gas exchange rates were monitored at 1–3 min intervals to determine the parameters in the model of stomatal control for each leaf (six leaves per species). The environmental conditions in the cuvette were maintained the same as the ambient ones using ambient light through the transparent cuvette top and the temperature controller of the Li-6400.

To express the stomatal control of the leaves, the parameter  $m$  of Ball et al. (1987) was obtained for stomatal conductance for  $\text{CO}_2$  ( $g_{\text{sc}} = 1.56 g_{\text{sw}}$ ,  $\text{mol m}^{-2} \text{s}^{-1}$ ) using Eq. (3):

$$g_{\text{sc}} = m \cdot A \cdot h_s / C_s + b \quad (3)$$

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  $g_{\text{sc}}$  at  $A = 0 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The value for  $m$  is known to be related to the ratio of  $C_i$  to the ambient  $\text{CO}_2$  concentration ( $C_i/C_a$  ratio) (Ball, 1988).

**Table 5**

Description of meteorology in the study site during the simulation periods in dry and rainy seasons.

		Dry season 30 August–18 September 2009	Rainy season 5 January–24 January 2010
Air temperature	$^\circ\text{C}$	$30.00 \pm 1.92$	$29.96 \pm 1.66$
Solar radiation	$\text{MJ day}^{-1}$	$15.17 \pm 4.35$	$13.54 \pm 3.22$
VPD	kPa	$1.96 \pm 0.54$	$0.87 \pm 0.29$
Groundwater table depth	m	$1.28 \pm 0.09$	$0.07 \pm 0.03$
Rainfall <sup>a</sup>	$\text{mm month}^{-1}$	0	200.2

<sup>a</sup> Rainfall for one month before the period.

Plant water status was assessed by measuring predawn and midday water potential ( $\Psi_{\text{leaf}}$ , MPa) with a Scholander-type pressure chamber (PMS Instruments Ltd., Corvallis, OR, USA) with  $\text{N}_2$  balancing gas. For each species,  $\Psi_{\text{leaf}}$  was measured for three sample trees for sap flux measurements and six leaves per tree were sampled from the sun-exposed side of crown surface (5–15 m in height).  $\Psi_{\text{leaf}}$  was obtained during the measurement period in the rainy (21–23 September 2009) and dry (15–17 January 2010) seasons.

#### 2.4. Model simulation of canopy-scale transpiration

Leaf-level gas exchange rates ( $A$  and transpiration rate) of leaves in different vertical positions within the canopy were simulated using an ecophysiological–meteorological model.  $E_{\text{canopy}}$  was computed by integrating the vertical profile of the leaf-level transpiration rate. The model used in this study is basically the same as that in Leuning et al. (1995), which integrates  $\text{CO}_2$ , water vapor, and energy exchange at five layers of different depths measured from the top of the canopy. The model takes into consideration: (1) a radiative transfer of energy through the canopy for direct beam and diffusive irradiance separately, with the profile of the area ratio of leaves exposed to the direct beam, (2) coupled submodels for the carbon assimilation and stomatal conductance (Collatz et al., 1991), (3) leaf surface energy balance equations based on the isothermal net radiation and leaf boundary-layer conductance for  $\text{CO}_2$ , water vapor and heat, and (4) effects of leaf temperature on  $V_{\text{cmax}}$  and the dark respiration rate for each layer. Both direct and diffuse solar radiation was further divided into visible and near-infrared radiation because leaves absorb them differently. Visible radiation makes up about half the total solar radiation received by the canopy while near-infrared radiation makes up most of the remainder (Campbell and Norman, 1998), enabling estimates of solar radiation penetration into the canopy.

The transpiration rate from each layer was computed using the Penman–Monteith equation, reproducing leaf temperature via energy balance equations (Campbell and Norman, 1998). Leaf temperature controls physiological reactions related to leaf gas exchange and in turn affects feedback to leaf transpiration. By repeating this procedure, this model simulated the microenvironments (wind speed profile inside the canopy and air temperature, VPD and  $\text{CO}_2$  concentration of the leaf boundary layer) and the gas exchange rates of  $\text{CO}_2$  and water vapor at each layer, i.e.,  $A$ ,  $g_{\text{sw}}$  and leaf-level transpiration rate.

We simulated the  $E_{\text{canopy}}$  computed by integrating all layers' transpiration rates on 10 days before and after the intensive measurements of leaf gas exchange. Simulations were carried out using the leaf ecophysiological parameters obtained in this manner combined with meteorological data in both the dry and rainy seasons (Table 5). The modeled period in the dry season corresponds to the period when  $\text{SF}_n$  of Popel started to decrease with the progression of lowering of the water table and that in the rainy season

**Table 6**

Description of the model simulation of canopy scale transpiration rate of the four species based on the measured leaf gas exchange traits ( $V_{cmax25}$  and  $m$ ). Model simulation was carried out under the environmental conditions in dry or rainy season. DRY and RAINY denote usage of the leaf gas exchange parameters obtained in dry and rainy seasons, respectively.

Cases	Season for model simulation and meteorological input				
	Dry season		Rainy season		
	$V_{cmax25}$	$m$	$V_{cmax25}$	$m$	
Case 1	DRY	DRY	RAINY	RAINY	
Case 2	Case 2-1	DRY	RAINY	–	
	Case 2-2	RAINY	DRY	–	
	Case 2-3	RAINY	RAINY	–	
Case 3	Case 3-1	–	–	DRY	RAINY
	Case 3-2	–	–	RAINY	DRY
	Case 3-3	–	–	DRY	DRY

corresponds to the period under flooding when eucalyptus showed a 50% reduction in  $SF_n$  from its annual peak (Miyazawa et al., 2014).

Mean canopy stomatal conductance was calculated as the sum of  $g_{sw}$  of the canopy layers weighed by the total leaf area of the layer (leaf area density, LAD,  $m^{-1}$ ) ( $G_{sw} = \sum_{i=1}^5 (g_{swi} \cdot LAD_i / LAI) \Delta z_i$ ,  $mol\ m^{-2}\ s^{-1}$ ) (Lai et al., 2000), where subscript  $i$  indicates the  $i$ th canopy layer from the top of the canopy and  $\Delta z_i$  (m) is the length of the  $i$ th canopy layer.

### 2.5. Description of model simulations

The three model simulations, named cases 1, 2 and 3, were conducted with different inputs for leaf ecophysiological parameters summarized in Table 6. In Case 1,  $E_{canopy}$  was calculated for both the dry and rainy seasons using the weather data and leaf ecophysiological parameters obtained in the respective seasons to validate the model outputs: for each species, modeled and measured leaf-scale transpiration rates ( $E_{Lmod}$  and  $E_{Lsap}$ , respectively,  $mm\ day^{-1}$ ), which were estimated by dividing  $E_{canopy}$  by LAI, were compared.  $E_{Lsap}$  was obtained for each tree as  $J_s \cdot A_s / LA$  where  $A_s$  and LA of an individual tree was calculated using the allometric equation for each species (Miyazawa et al., 2014).

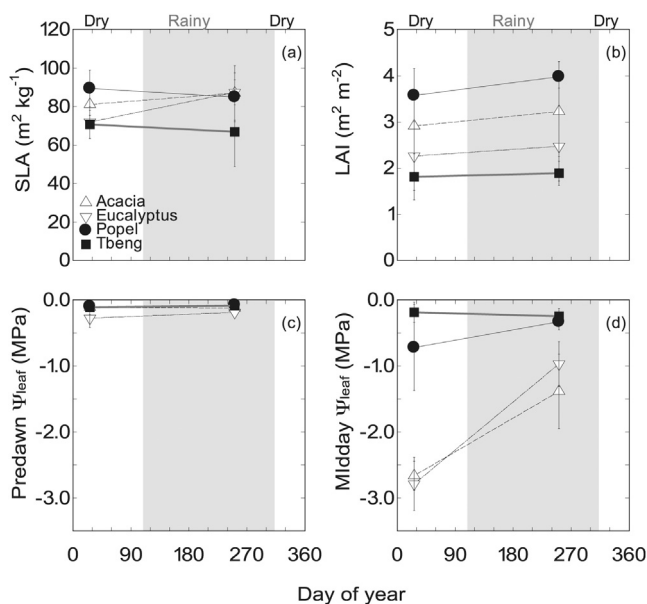
In Case 2,  $E_{Lmod}$  in the dry season was calculated using either leaf ecophysiological parameters ( $V_{cmax25}$  and/or  $m$ ) obtained in the rainy seasons to investigate the impacts of their seasonal changes on  $E_{Lmod}$  (Case 2-1–2-3, Table 6). The difference in  $E_{Lmod}$  between Case 1 and Case 2-1–2-3 represents the reduction in transpiration by changing the leaf ecophysiological traits in response to the onset and progress of dry season. Similarly, for Case 3  $E_{Lmod}$  in the rainy season was calculated for each species with the leaf ecophysiological parameters obtained in the dry season (Case 3-1–3-3, Table 6).

## 3. Results

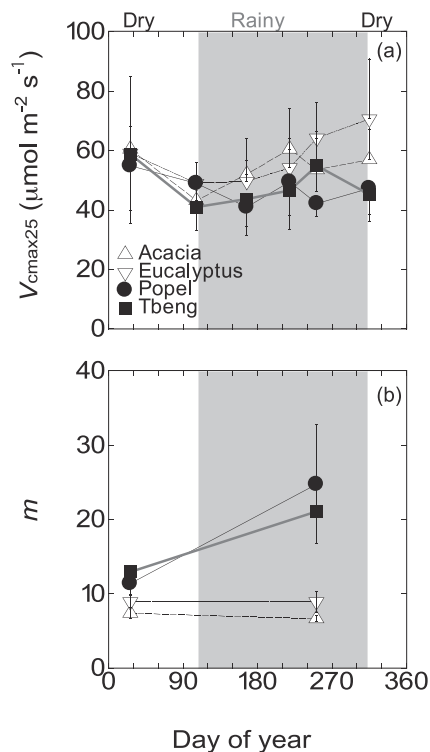
### 3.1. Leaf ecophysiological traits and seasonal trends

SLA and LAI remained constant in the dry and rainy seasons (Fig. 2a and b).  $\Psi_{leaf}$  in predawn, which is a good approximation for the water potential of the soil surrounding the roots, remained constant at high levels even during the dry season (Fig. 2c). Meanwhile, midday  $\Psi_{leaf}$  decreased in the dry season in non-endemic species, while those for native species (Popel and Tbeng) remained relatively constant in both the dry and rainy seasons (Fig. 2d).

In most species,  $V_{cmax25}$  was constant in the flooding period (day of year, DOY = ca. 230–330) when  $SF_n$  was reduced in eucalyptus (Miyazawa et al., 2014), or during the drought period (DOY = ca. 20–160) when  $SF_n$  declined in Popel (Fig. 3a). Only in Tbeng, a



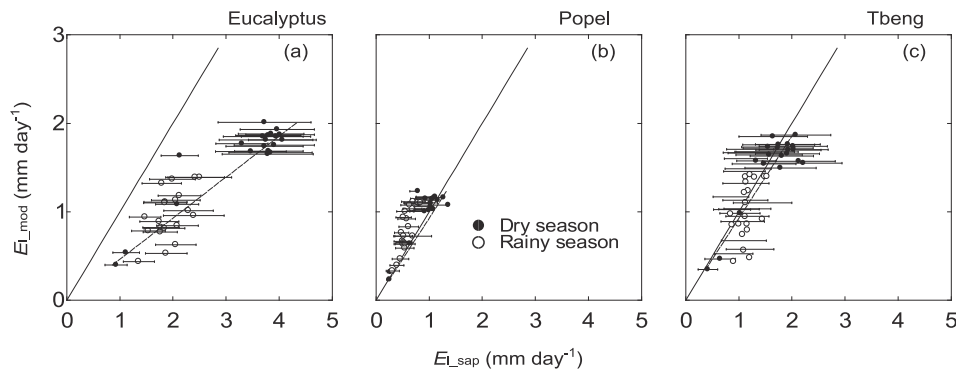
**Fig. 2.** Specific leaf area (SLA) (a), leaf area index (LAI) (b) and leaf water potential ( $\Psi_{leaf}$ ) measured at predawn (c) and at midday (d) (means  $\pm$  standard deviation) for the four measured species at the study site. Shaded period indicates the rainy season.



**Fig. 3.** The maximum rate of the RuBP carboxylation rate at 25 °C ( $V_{cmax25}$ ) and Ball-Berry's  $m$  in Eq. (3) for the four studied species (means  $\pm$  standard deviation). Shaded period in each panel indicates the rainy season.

significant difference in  $V_{cmax25}$  was observed between the flooding period and drought period ( $p = 0.023$ ,  $t$ -test).  $V_{cmax25}$  remained constant before and after the main litterfall event for all species (March–May).

While native species had higher  $m$  values in the rainy season than in the dry season, non-endemic species showed little changes in  $m$  (Fig. 3b). In both dry and rainy seasons, native species



**Fig. 4.** The relationship between the modeled ( $E_{Lmod}$  in Case 1) and measured ( $E_{Lsap}$ ) leaf-scale transpiration rates (means  $\pm$  standard deviation) based on sap flow measurements for each species in the dry (●) and rainy (○) seasons. The broken line in each panel represents the regression line for the pooled data of dry and rainy seasons with the  $E_{Lmod}$  intercept forced to zero; the solid line represents a 1:1 line.

had significantly higher  $m$  than non-endemic species, and  $m$  did not significantly differ within non-endemic species and within native species. The value  $b$  in Eq. (3) was 0.005–0.03 mol m<sup>-2</sup> s<sup>-1</sup> in each species and did not significantly differ between seasons and between species (data not shown).

### 3.2. Modeled canopy transpiration rate and sap flux

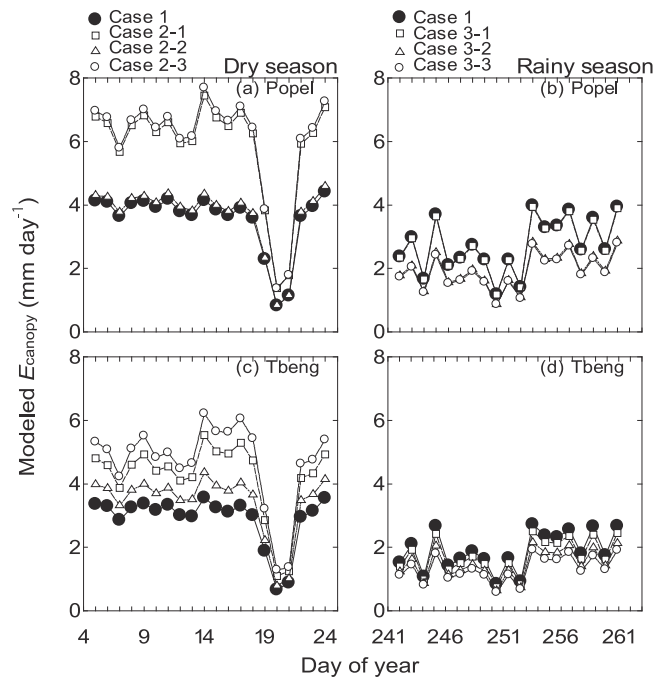
Significant positive correlations were observed between  $E_{Lsap}$  and  $E_{Lmod}$  in Case 1 in each species when all data in both the dry and rainy seasons were pooled. The slope of the regression line was near unity for Popel (Fig. 4b) and Tbeng (Fig. 4c). Although the slope of the regression line in eucalyptus was 0.5, the seasonal and day-to-day trends in  $E_{Lsap}$  were well captured by  $E_{Lmod}$ . In Popel, however,  $E_{Lsap}$  was 50% of that in  $E_{Lmod}$  on three days near the end of the measurement period during the dry season. Similarly, on days with high  $E_{Lmod}$  in the rainy season,  $E_{Lsap}$  of Popel and eucalyptus were lower than the levels estimated from the regression lines and  $E_{Lmod}$ .

Because  $V_{cmax25}$  and  $m$  remained stable between seasons in acacia and eucalyptus, simulations of  $E_{canopy}$  in Case 2 and 3 were conducted only for Popel and Tbeng.  $E_{canopy}$  in Case 2 differed from  $E_{canopy}$  in Case 1 in the dry season (Fig. 5a and c).  $E_{canopy}$  in Case 2-1 and 2-3 was remarkably higher than  $E_{canopy}$  in Case 1 in each species.  $E_{canopy}$  in Case 2-2 was similar to  $E_{canopy}$  in Case 1 in Popel. Additionally, in Tbeng,  $E_{canopy}$  in Case 2-2 and 2-3 was higher than  $E_{canopy}$  in Case 1 and in Case 2-1, respectively.

Similarly,  $E_{canopy}$  in Case 3-1 and Case 3-3 was lower than  $E_{canopy}$  in Case 1 in Popel and Tbeng (Fig. 5b and d), but to smaller degree compared with the degree observed in Case 2. In Tbeng,  $E_{canopy}$  in Case 3 was not remarkably different from  $E_{canopy}$  in Case 1 in each species.

In midday (10:00–15:00),  $G_{sw}$  in each species decreased with atmospheric VPD in both the dry and rainy seasons (Fig. 6). In the rainy season,  $G_{sw}$  in Case 1 was twice as high as that in the dry season both in Popel and Tbeng. A relatively small difference was observed between  $G_{sw}$  in Case 1 in the rainy season and  $G_{sw}$  in Case 3-3, which were calculated using the same leaf ecophysiological parameters (Table 6).

In the rainy season,  $G_{sw}$  differed among cases in patterns similar to those for  $E_{canopy}$  (Fig. 5) but the differences in  $G_{sw}$  between cases were clearer than those in  $E_{canopy}$  (Fig. 6). In Tbeng, while differences in  $E_{canopy}$  among cases were less clear,  $G_{sw}$  largely differed among cases, suggesting that the different  $G_{sw}$  observed here among cases was not reflected in  $E_{canopy}$ . Similarly, in the dry season, the differences between cases were larger in  $G_{sw}$  than in  $E_{canopy}$ .

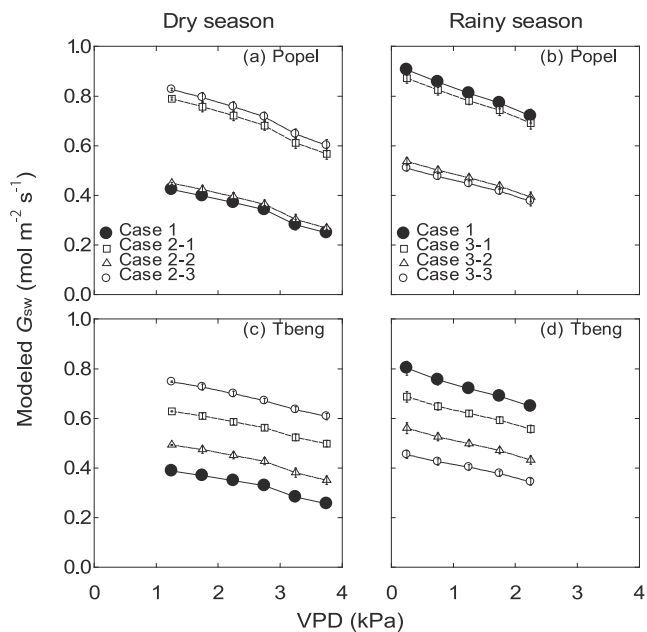


**Fig. 5.** Modeled  $E_{canopy}$  of each species with different inputs of photosynthetic traits (see Table 6) for the dry (a and c) and rainy (b and d) seasons.

## 4. Discussion

### 4.1. Instantaneous leaf gas exchange traits

Obtained  $V_{cmax25}$  (Fig. 3) and  $A$  at light saturation were higher than estimated ones in late successional tree species in central Cambodia (Kenzo et al., 2012) and those in other areas of the Indochina Peninsula affected by the monsoon (Han et al., 2010; Ishida et al., 2006; Norisada and Kojima, 2005) and nearby tropical rainy forests (Eschenbach et al., 1998; Kenzo et al., 2006; Kumagai et al., 2006). Species that are often planted in fast growing plantations, such as *Hevea brasiliensis*, (Kositsup et al., 2009; Kumagai et al., 2013), other *Eucalyptus* spp. (Huang et al., 2008; Novriyanti et al., 2012; Whitehead and Beadle, 2004) and *Acacia* spp. (Gimeno et al., 2010; Han et al., 2010; Pryor et al., 2006) have  $V_{cmax25}$  similar to the species in this study. The high  $V_{cmax25}$  reflects the successional status of the species measured in this study: eucalyptus and acacia were planted here as fast growing species (Forestry Administration of Cambodia, personal communication) and Tbeng and Popel successfully survive in this study site under frequent disturbance



**Fig. 6.** The relationship between the atmospheric vapor pressure deficit (VPD) and modeled canopy-scale stomatal conductance ( $G_{sw}$ ) for Popel and Tbeng in the dry (a and c) and rainy (b and d) seasons. Symbols represent the modeled values with different inputs of leaf ecophysiological traits.

by human activities and wild fires, through resprouting from the stumps. Among native species in natural forests in this region, only species adapted to frequent disturbance usually survive under severe growth competition during the repetitive disturbance (Top et al., 2004). Other native species with lower  $V_{cmax25}$  might have failed to survive here and would be found only in the natural forests (Top et al., 2009).

We did not find clear seasonal changes in  $V_{cmax25}$  in response to the fluctuating groundwater table or the atmospheric environments; this finding was different from species in other study sites that show lower net photosynthetic rates during the dry season (Franco, 1998; Ishida et al., 2006; Prior et al., 2004). The constant  $V_{cmax25}$  and no changes in LAI suggested the plants have access to the stable groundwater sources even in the middle of the dry season (Franco et al., 2005; Prior et al., 2004; Tanaka et al., 2003). Maintenance of  $V_{cmax25}$  and LAI throughout dry season would contribute to rapid initiation of carbon assimilation in response to the episodic rainfall in mid dry season and the annually varying first rainfall event at the beginning of the rainy season (Chapotin et al., 2006). For trees that reduce  $V_{cmax25}$  and/or LAI in the dry season, rapidly initiating carbon assimilation in response to the rainfall after dry periods is difficult because leaf production and the subsequent increase in leaf photosynthetic capacity take time. The importance of the maintenance of high  $V_{cmax25}$  and LAI at the beginning of the rainy season was suggested by the leaf phenology in central Indochina Peninsula where many deciduous tree species expand leaves in the midst of dry season and during drought (Williams et al., 2008) despite the high cavitation risk caused by the low  $\Psi_{leaf}$ . Because the duration of the rainless period changes inter-annually, while we had data of leaf ecophysiological traits for only 2 years, further studies should investigate whether extreme drought events can reduce  $V_{cmax25}$  and LAI and how frequently such drought events occur to fully understand the transpiration characteristics of forests in this region.

Reductions in  $m$  or  $C_i/C_a$  during the dry season have been reported in evergreen trees in other studies in the Amazon (Choat et al., 2006; Craven et al., 2011), in monsoon regions (Liu et al., 2010; Prior et al., 2004), in savanna habitat (Eamus et al., 1999;

Franco et al., 2005; Mielke et al., 2000), and in the Mediterranean region (Goulden, 1996). While most species in these studies also reduced  $A$  at light saturation, species in this study reduced  $m$  alone. In the rainy season,  $m$  of the studied species was higher than those in previous studies, especially in native species (Baldocchi, 1997; Kumagai et al., 2006; Lai et al., 2000; Lloyd et al., 1995), suggesting that leaves were oriented for the high  $g_{sw}$ ,  $G_s$  and  $E_{canopy}$  (Figs. 3, 5 and 6) supported by the unlimited water availability from the shallow groundwater (Miyazawa et al., 2014). The high  $m$ , and the low intrinsic water use efficiency ( $A/g_{sw}$ , Eq. (3)), in the studied species is thought to reflect the ready availability of water in the original habitat of the species. Aside from Tbeng and Popel, which are native to the study site, the studied eucalyptus and acacia species are known to be species of water-abundant habitats (O'Grady et al., 2009; Orchard et al., 2010). Orchard et al. (2010) similarly showed that species from habitats with differing level of water availability had different  $C_i/C_a$  [ $=1 - 1/(1.56m \cdot h_s)$ ] (Ball, 1988). This occurred even if seedlings were grown in the common garden, indicating that the high  $m$  of the studied species was caused by both the acclimation of the species to the high level of water availability at the present study site during the rainy season and their adaptation to the native habitat. Further, for Popel and Tbeng, reduced  $m$  (and increased intrinsic water use efficiency) in dry season is thought to be the response to the rapidly decreasing water availability in this region.

#### 4.2. Model simulation and the comparison with the measured transpiration rates

Despite the systematic underestimation for eucalyptus,  $E_{l,mod}$  successfully reproduced the measured data of the temporal variation (day-to-day and seasonal trends) in  $E_{l,sap}$  (Fig. 4), suggesting that the controlling factors for the transpiration in this study site were taken into consideration in the model, i.e., responses of leaf ecophysiological traits to the environments, as factors. The good fit of  $E_{l,mod}$  and  $E_{l,sap}$  in Popel and Tbeng showed the quantitative reliability of the model calculation and the underlying processes, although we acknowledge that one of the important model inputs, LAI, included the influence of other trees near the sample trees. As found in  $E_{l,sap}$ ,  $E_{l,mod}$  in Popel was lower than other species (Fig. 4b) because of the lower ratio of  $E_{canopy}$  to LAI observed there. Previous studies also successfully reproduced canopy-level gas exchange rates in temperate deciduous species by inputting the temporal changes in photosynthetic traits (Baldocchi, 1997; Lai et al., 2000; Law et al., 2000; Wilson et al., 2001) and demonstrated the influence of seasonally changing leaf ecophysiological traits on canopy-level gas exchange. Additionally, some studies found discrepancies between results based on leaf-level porometric methods and sap flux measurements because these studies did not take into consideration the high decoupling occurring between the atmosphere and the leaf surface (Meinzer et al., 1993; Wullschlegel et al., 1998) and/or vertically heterogeneous environments and  $g_{sw}$  within a canopy (Kostner et al., 1992).

Higher  $E_{l,sap}$  than  $E_{l,mod}$  in eucalyptus was possibly caused by the emergent nature of eucalyptus trees in this study site. Some eucalyptus trees had foliage above nearby trees (personal observation) and are thought to be exposed to full solar radiation. While  $E_{l,sap}$  reflects the strong solar radiation in parts of the emergent crown,  $E_{l,mod}$  assumed that the entire canopy was surrounded by adjacent tree canopies. Therefore,  $E_{l,mod}$  was thought to underestimate received solar radiation and  $E_{l,mod}$ .

The comparison of  $E_{l,mod}$  and  $E_{l,sap}$  also revealed the existence of unknown factors that controlled the species-specific seasonal changes in sap flux. In the rainy season, eucalyptus and Popel showed lower  $E_{l,sap}$  than the regressed level using  $E_{l,mod}$ , suggesting that trees could not increase  $E_{l,sap}$  beyond a certain threshold



level as a result of factors not considered in this model (Fig. 4). At higher time resolutions (10-min intervals), modeled  $E_{\text{canopy}}$  of eucalyptus increased with increasing VPD and reached a peak VPD at 12:00–14:00, but  $J_s$  stopped increasing before the peak in VPD on sunny days (Miyazawa and Kumagai, unpublished data). In this study site,  $SF_n$  of eucalyptus showed a monotonic decrease with rising groundwater table during the rainy season 2009 (Miyazawa et al., 2014), suggesting hypoxic flooding effects influence root water uptake (Aroca et al., 2012; Traver et al., 2010, but see McJannet, 2008; Oren et al., 1999) and restrict  $E_{\text{L,sap}}$  in sunny midday. At the leaf level, however, we found Popel had a high  $m$  and no reduction in  $V_{\text{cmax25}}$  during a flooding period (Fig. 2a and b). Thus, the mechanism underlying the overestimation of  $E_{\text{L,mod}}$  remains unknown.

Similarly, on three days at the end of the measurements period in the dry season,  $E_{\text{L,mod}}$  overestimated  $E_{\text{L,sap}}$  in Popel (Fig. 3b), possibly representing the restriction in water uptake as a result of the lowered groundwater table. After the period for the computation of  $E_{\text{canopy}}$  as ‘dry season’ in this study (Table 5),  $SF_n$  decreased with a lowering of the groundwater table to the annual minimum level (Miyazawa et al., 2014). Overestimation of  $E_{\text{L,sap}}$  by  $E_{\text{L,mod}}$  suggested that decreased  $SF_n$  in the dry season was not caused by processes considered in this model, such as a seasonal decrease in LAI,  $V_{\text{cmax25}}$  or  $m$ ; this overestimation was caused by factors that had not been considered in this study, such as hydraulic limitation in the soil–plant–atmosphere water transport processes as suggested by Williams et al. (1996). Interestingly, Popel with reduced  $SF_n$  was capable of maintaining midday  $\Psi_{\text{leaf}}$  at high levels while eucalyptus with lowered midday  $\Psi_{\text{leaf}}$  did not show either a reduction in  $SF_n$  or an overestimation by  $E_{\text{L,mod}}$ . Possibly, while Popel reduced  $g_{\text{sw}}$  under drought stress to avoid an excessive reduction in  $\Psi_{\text{leaf}}$  (species minimizing cavitation, Manzoni et al., 2013) eucalyptus reduced midday  $\Psi_{\text{leaf}}$  to as low levels as trees of the same species in drought conditions (Liu et al., 2004; Thorburn et al., 1993) allowing it to maintain high  $E_{\text{canopy}}$  and  $g_{\text{sw}}$  (species maximizing  $g_{\text{sw}}$ ).

Results did not suggest that the ongoing plantation of non-endemic species increases forest transpiration in a way that would cause a threat to local water resources during the investigated periods in the rainy and dry seasons. Among the important factors controlling forest transpiration (Law et al., 2001), non-endemic species had similar  $V_{\text{cmax25}}$  and even lower  $m$  than native species (Fig. 3), with mixed results for another factor, LAI. This study revealed that fact that this region has experienced high transpiration rates by native species, especially Popel, with the tree’s ecophysiological traits oriented for the same high transpiration rates as were seen in the commercial plantation species that allow rapid growth, even during the dry season.

#### 4.3. Impacts of changes in stomatal control on transpiration

In native species,  $E_{\text{canopy}}$  was under the strong influence of the atmospheric evaporative demand and the species-specific seasonal changes in leaf ecophysiological traits, especially  $m$ , which changed in accordance with the soil water environment (Figs. 1 and 2). Although  $E_{\text{canopy}}$  was higher in the dry season than rainy season because of the high atmospheric evaporative demand, Popel and Tbeng effectively avoid an excessive increase in  $E_{\text{canopy}}$  by reducing  $m$ , and  $V_{\text{cmax25}}$  in Tbeng, during the dry season. Similarity in midday  $\Psi_{\text{leaf}}$  between the dry season and the rainy season suggests that reduced  $m$  balanced the foliage water demand for transpiration and hydraulic limitation, which is the function of hydraulic architecture and the soil water environments (Katul et al., 2003; Meinzer et al., 1999). Reduced  $m$  under drought conditions explained the reduced leaf- and canopy-level transpiration in previous studies (Baldochi, 1997; Baldochi and Meyers, 1998; Sala and Tenhunen, 1996).

Williams et al. (1996) emphasized the control of transpiration by hydraulic limitation in the soil–plant–atmosphere water pathway and their later works found that the calculated transpiration rate at midday overestimated the measured ones if the model did not take hydraulic limitation into consideration (Williams et al., 1998, 2001). Our models do not include the effects of hydraulic limitation, but  $E_{\text{L,mod}}$  well captured  $E_{\text{L,sap}}$  in the dry season except for three-days in Popel, suggesting the small effects of hydraulic limitation on transpiration in this study site even during the middle of the dry season. Thus,  $E_{\text{L,mod}}$  and  $G_{\text{sw}}$  were under control of species-specific seasonal changes in  $m$ , and therefore, frequent measurements of the leaf ecophysiological traits are important for understanding the transpiration characteristics of forests in this region. Additionally, forest transpiration would be well modeled with less-intensive measurements of  $V_{\text{cmax25}}$  because of its aseasonality.

Plants are known to respond to reduce soil water availability not only by changing  $m$ , but also by changes in  $V_{\text{cmax25}}$  (Reichstein et al., 2003) and reduced LAI (Zeppel et al., 2008). Thus the ecological setting, as discussed in Section 4.1, should be the reason why native species in this study site reduce transpiration by reducing  $m$  alone but not by reducing  $V_{\text{cmax25}}$  and LAI for rapid initiation of carbon assimilation in response to the episodic rainfall during the dry season (Fig. 1a) or to the first rainfall of the rainy season (Chapotin et al., 2006). Furthermore, the relatively shallow groundwater table in the study area would have allowed the species to access groundwater and to maintain both  $V_{\text{cmax25}}$  and LAI without drought-induced cavitation (Tyree and Sperry, 1988).

Seasonal changes in leaf ecophysiological traits resulted in larger changes in  $G_{\text{sw}}$  than in  $E_{\text{canopy}}$  (Figs. 5 and 6), especially in Tbeng where  $E_{\text{canopy}}$  in Case 1 and Case 3-1–3-3 did not differ remarkably during the rainy season (Fig. 5), as a result of the highly decoupling condition between the leaf surface and the atmosphere (Jarvis and McNaughton, 1986). Under such conditions, leaves had to drastically reduce  $m$  and  $G_{\text{sw}}$  in the dry season because a slight reduction in  $m$  cannot effectively reduce  $E_{\text{canopy}}$  (Meinzer et al., 1993). Strong decoupling was observed in native species with broad leaf blades in the rainy season when leaves had high  $m$  (Fig. 3) and  $G_{\text{sw}}$  (Fig. 6). In other words, the high decoupling allowed the leaves to achieve very high  $m$ , and possibly high  $A$ , in the rainy season; this occurs without increasing  $E_{\text{canopy}}$  to the levels beyond the water uptake capacity of the roots and stem.

## 5. Conclusion

The introduction of non-native species into forests dominated by native species was less likely to drastically increase the stand-level transpiration rate, but would alter the seasonality of the transpiration rate in response to seasonal flooding and drought. Species with different responses in transpiration rates to changing groundwater table differed in  $m$  and its seasonality. Large differences in  $E_{\text{L,mod}}$  among cases with different model inputs demonstrated the strong control of species-specific leaf ecophysiological traits over the whole tree transpiration rate and its seasonality (Miyazawa et al., 2014).

The introduction of non-native species should alter the susceptibility of the forest to drought-induced mortality. Popel reduces the transpiration rate and  $G_{\text{sw}}$  at relatively high leaf water potential and therefore would be susceptible to carbon starvation in a prolonged dry season (McDowell et al., 2008). Additionally, eucalyptus that maintained a transpiration rate and  $G_{\text{sw}}$  at leaf water potential near the critical levels for cavitation may be susceptible to hydraulic failure during severe drought.

Our multilayer model successfully reproduced the stand-level transpiration rate and should be a useful tool in quantifying it. Because the species studied here did not seasonally change  $V_{\text{cmax25}}$

or LAI even in mid-late dry season, frequent measurements of  $m$  should be important for the successful quantification of transpiration and its comparison among species. Model simulation, however, could not reproduce species-specific changes in the transpiration rate (reduction in transpiration rates under flooding in eucalyptus and under drought in Popel), suggesting the effects of other processes on their transpiration. Additional research will be required to identify the mechanisms underlying the different transpiration characteristics among species and to evaluate the impacts of changing species composition on transpiration and its response to changing intensities of flooding or drought caused by climatic changes.

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