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Year-to-Year Differences in Sap Flow and Crown-Level Stomatal Conductance of Two Species in a Lowland Evergreen Forest, Central Cambodia

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Abstract

Although information about the hydrologic and ecological features of lowland evergreen forests in central Cambodia has been collected since the beginning of the 21st century, measurements of the transpiration process remain very limited. This paper describes the differences detected in transpiration (q) and crown-level stomatal conductance (G_S) between *Calophyllum inophyllum* (which undergoes successive leaf exchange) and *Drypetes* sp. (which performs irregular leaf exchange) (hereafter referred to as *Calophyllum* and *Drypetes*, respectively), and the analysis of these differences in consideration of their contrasting leaf phenologies. We evaluated q using sap flow measurements and obtained daily G_S values. *Calophyllum* and *Drypetes* had *high* and *low* periods between which q and G_S differed significantly. Within *high*/*low* periods, smaller scatter in the plot of G_S versus vapour pressure deficit (D) was found in *Calophyllum* compared to *Drypetes*. For a given value of D, q in *high* periods was 1.3 and 1.9 times larger than in low periods for *Calophyllum* and *Drypetes*, respectively. The smaller scatter for *Calophyllum* was the result of relatively constant physiological activity that was maintained by successive leaf fall. For both species, high periods were recorded after remarkable leaf-fall events; thus, our current data implied that leaf phenology is one of the most important factors affecting transpiration.

Discipline: Forestry and forest products
Additional key words: leaf phenology, riparian zone, sap flux density, transpiration, vapour pressure deficit

Introduction

In Cambodia, forests occupy 57% of the total land area, a percentage higher than in Thailand (37%), Vietnam (44%), and Myanmar (48%)[13]. Cambodia still retains forests in its lowland plains, unlike Thailand and Vietnam, where remaining forests are mostly found in mountainous areas[43]. Located on the Indochina Peninsula, Cambodia has distinct wet and dry seasons characteristic of the Asian monsoon. Although the dry season includes a few months of very little rainfall, evergreen forest is distributed in the central lowland area. The FAO (2010b) reported that evergreen forest makes up 34% of the total forest area of Cambodia. However, few studies have examined the hydrologic and/or environmental processes in evergreen forests. Intensive observations were thus recently initiated to acquire in-depth knowledge about related hydrologic and ecological features[37].

This paper reports the results obtained during two projects: "Establishment of the Integrated Forest Ecosystem Observation Site and Network in the Lower Mekong (2008–2011)" funded by the Ministry of the Environment of Japan, and "Estimation and Simulation of Carbon Stock Change of Tropical Forests in Asia (2011–2014)" funded by the Ministry of Agriculture, Forestry and Fisheries of Japan. Part of this work was supported by Grants-in-Aid for Scientific Research (No. 21710021) (2009–2011) from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

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Araki *et al.* (2007a) reported that soil water content in an evergreen forest is higher than in a deciduous and mixed forest during the dry season. Moreover, the soil matrix potential near the surface in the evergreen forest exceeds –80 kPa during the dry season[3]. The layer of soil in the evergreen forest is about 10-m thick[31] and significantly larger than that in a deciduous forest[30]. The soils in the evergreen forest also have a higher percentage of fine pores compared with those in the deciduous forest[44]. These characteristics result in a larger capacity to retain water in the soil even during the dry season, and evergreen trees can maintain water uptake through root systems that reach 9-m depths[31].

The annual evapotranspiration of Cambodia's evergreen forests, estimated using the energy-balance Bowen ratio method and water balance, was about 1100–1200 mm, corresponding to 70–80% of annual rainfall[19,28]. Evapotranspiration is essential to understand the hydrologic cycle in evergreen forests. Tamai *et al.* (2008) applied the Jarvis-Stewart model[39] to Cambodia's evergreen forests and confirmed that this model well describes the environmental responses of surface conductance. Kenzo *et al.* (2012) revealed that leaf morphological traits have simple and significant relationships with tree height in Cambodia's dry evergreen forests. However, no previous study had examined the transpiration processes by using sap flow techniques, which examine one of the most important sources of evapotranspiration[45]. The environmental response of stomatal conductance (G_S), which is important in controlling transpiration, is also unknown. Natural evergreen forests in Cambodia have multilayered canopies and contain many tree species[38]. To estimate transpiration and understand the responses of G_S to environmental factors at the forest scale, we must obtain the characteristics of transpiration for many species comprising these complex forests. *Calophyllum inophyllum* and *Drypetes* sp. (hereafter referred to as *Calophyllum* and *Drypetes*, respectively) are dominant species in the riparian zones of evergreen forests in central Cambodia. *Calophyllum* undergoes successive leaf exchange while *Drypetes* performs irregular leaf exchange; thus, the difference in leaf phenology between the two species probably results in different seasonal courses of transpiration (q) and crown-level stomatal conductance (G_S). If a difference in G_S exists between *Calophyllum* and *Drypetes*, the response of G_S to vapour pressure deficit (D)[32] would also differ between the two species. We carried out sap flow measurements on *Calophyllum* and *Drypetes* growing in riparian zones over a period of 44 months. We detected differences in the seasonal changes in q and G_S between *Calophyllum* and *Drypetes*, as the objective of this study was to determine whether differences in leaf phenology caused the different seasonal courses in q and G_S between the two species. We also analysed the effects of different leaf phenologies on the response of G_S to D.

Materials and methods

1. Site description

We conducted measurements in an area located about 30 m south of a 60-m tower set up in the lowland evergreen forest, Kampong Thom Province, Cambodia (12°44'N, 105°28'E)[28,38]. Annual rainfall was 1565.4 mm with mean air temperature of 26.4°C from November 2003 to October 2004[28]. Cambodia has wet and dry seasons, with the wet season usually extending from mid-May to mid-October[26,29]. Although the actual onset and withdrawal of wet seasons differ somewhat from year to year, our following analysis would not be affected. For simplicity, we regarded the wet season as occurring from 1 May to 31 October. There is a stream to the south of the observation plot, where the soil is very wet[4]. The observed stand has a distinct, multilayered and closed canopy, with overstory (> 20 m), secondary story (10–20 m), and lower story (< 10 m) layers[38]. The emergent tree species (with a height > 40 m) is *Myristica iners*, and the main species in the overstory layer are *Calophyllum* and *Drypetes*.

2. Measurements of sap flux density

We selected one tree of *Calophyllum* and one tree of *Drypetes*, and then measured their sap flux densities (F_D). We inserted a pair of Granier-type thermal dissipation probes[15] into each test tree. We used commercially produced sensors (type M sap-flow sensor; UP Gmbh, Cottus, Germany) from May 2007 to May 2010 and homemade sensors[22] from June to December 2010. The designs of the commercial and handmade sensors were similar: sensor length of 2.0 cm, sensor span of 15 cm, and with both sensors including a 0.2 W heater. Iida *et al.* (2006) and Iida and Tanaka (2010) have previously described the calculation of F_D.

The diameters at breast height (DBHs) of *Calophyllum* and *Drypetes* were 23.9 and 25.8 cm, heights were 22.8 and 24.7 m, and crown projection areas (*CPA*) were 14.4 and 33.6 m², respectively. *Calophyllum* and *Drypetes* are diffuse porous species, with sapwood widths of 3.0 and 2.0 cm, and corresponding sapwood areas (*SA*) of 171 and 137 cm², respectively, based on wood core sampling with an increment borer. The transpiration of a tree (q) can be calculated by using the following equation:

$$q = SA \cdot \overline{F_D}, \tag{1}$$

where, $\overline{F_D}$ is the weighted mean value of F_D over SA. Because the sensor was 2.0 cm in length, it was inserted to a depth of 0 to 2.0 cm and could detect $\overline{F_D}$ for *Drypetes*, but not for *Calophyllum* because its sapwood width is 3.0 cm. We inserted another sensor to a depth of 2.0 to 4.0 cm for *Calophyllum*. This deeper sensor contacted the heartwood (*i.e.* at a depth of 3.0 to 4.0 cm) and we applied the correction proposed by Clearwater *et al.* (1999).

3. Measurement of environmental factors and observations of leaf phenology

The downward shortwave radiation (S, type CM3; Kipp & Zonen, Delft, The Netherlands) and rainfall (P, type RG-2M; Onset Computer, Bourne, MA, USA) were measured at the top of the tower. Air temperature (T_a) and vapour pressure deficit (D) were also measured on the tower with a ventilated psychrometer (type MH-020T; Eko Instruments Co. Ltd., Tokyo, Japan) at a height of 34 m. The depth of the groundwater table has been manually measured each day near the site with a buzzer-type measuring tape since 2004 (well 2; Araki *et al.*, 2008), but data for 2010 were lacking. The missing data were filled in based on estimates derived from the relationship between the voltage outputs of a dielectric probe (type ECH2-10; Decagon Devices, Pullman, WA, USA) inserted 10 cm below the soil surface and the measurements of groundwater table depth ($R^2 = 0.85$).

Litter was collected around *Calophyllum* and *Drypetes* three times per month, and then oven-dried and weighed. Leaf phenology was assessed from intact and detached branches several times per year.

4. Calculation of crown-level stomatal conductance and its response to vapour pressure deficit

Aerodynamic conductance can be calculated by using the zero-plane displacement height and roughness length of this site[40], and surface conductance can be estimated from the Jarvis–Stewart model, as confirmed by data measured at this site[41]. We calculated the decoupling factor[27] (Ω) from estimated aerodynamic and surface conductances, and obtained daily mean Ω in the range 0.1 to 0.3. This stand is well coupled with the atmosphere, so we can calculate crown-level stomatal conductance as:

$$G_S = \frac{\gamma \lambda E}{C_p \rho D}, \tag{2}$$

where, γ is the psychrometric constant, λ the latent heat of vaporisation, E the single tree transpiration as q/CPA[21], C_P the specific heat of air at constant pressure, and ρ the density of moist air. Note that G_S was calculated as a daily average using mean D during daylight (*i.e.* duration when $S > 0$ W/m^2), thermodynamic variables based on daylight mean air temperature (T_A), and E summed over 24 h, but divided by daytime only[23,33]. To minimise the effect of very small D caused by rainfall on G_S, we excluded rainy days from the following analyses. We evaluated the response of G_S to D by using the following equation[32]:

$$G_S = -m \cdot \ln D + G_{Sref}. \tag{3}$$

The values of m and G_{Sref} were obtained from fitting analysis between observed G_S and D. m quantifies the sensitivity of G_S to D, and G_{Sref} is a reference conductance at $D = 1$ kPa[32].

Results and discussion

1. Observations of detached sample shoots and seasonal changes in leaf fall

In this study, we defined the period from November of one year to April of the next year as the dry season for that year (Fig. 1). The magnitudes of leaf fall for *Calophyllum* and *Drypetes* were generally higher in dry seasons than in wet seasons (Fig. 1), but the following differences between both species were derived from seasonal changes in leaf fall and in situ observations of intact and detached branches.

The successively leaf-exchanging *Calophyllum* flushed new leaves throughout the year, induced by continuous partial leaf shedding (Fig. 1A). Continuous leaf-exchange was also suggested by vagueness of the boundary on a branch that separated different durations of shoot elongation. Most detached branches had leaves at various phenological stages (*e.g.* young, light-green leaves; mature, dark-green leaves; senescent, yellowish leaves). As a result, *Calophyllum* only showed slight seasonal changes in leaf age composition in the crown, but rarely year-to-year changes. However, the degree of leaf shedding by *Calophyllum* during the dry season in 2009 was higher than that in the dry season in 2008 (Fig. 1A).

In contrast, the irregularly leaf-exchanging *Drypetes* displayed irregular leaf-shedding behaviour (Fig. 1B). Relatively homogeneous leaf ages were found on detached branches, suggesting that simultaneous flushing occurred in elongating shoots. Moreover, boundaries on a branch were often abrupt, and shoot units elongated simultaneously, showing various degrees of senescence among detached sample shoots. This suggests that very irregular leaf exchange occurs in *Drypetes*, in which branches often cease elongation and flushing for several years, and thus retain old leaves. In short, *Drypetes* displayed wide year-to-year changes in crown-leaf age composition, and seasonal changes could not be predicted. Although *Drypetes* shed most leaves in the dry season, a large degree of leaf shedding was observed in the wet season in 2009 (Fig. 1B).

The two study species displayed contrasting vegetative phenologies. Because *Drypetes* is an irregularly leaf-exchanging species, the remarkable shedding observed in the wet season in 2009 was probably reasonable. For example, although *Drypetes floribunda* and *Drypetes parvifolia* flushed leaves in the wet season in Ghana, almost no trees flushed leaves in the wet season of the following year[24]. However, the successively leaf-exchanging *Calophyllum* primarily shed leaves in the dry season in 2009. These

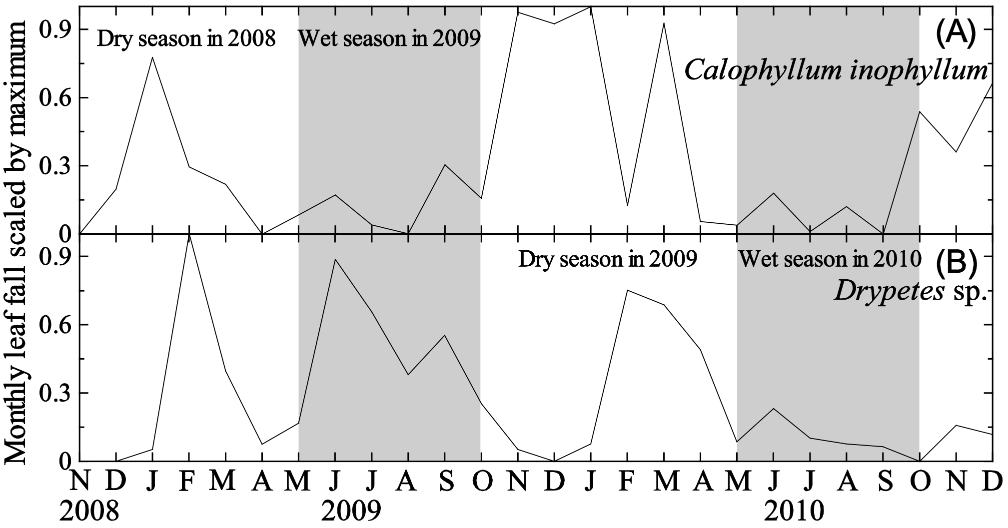

Fig. 1. Seasonal courses for oven-dry weights of monthly leaf fall scaled by the maximum for A) *Calophyllum inophyllum* and B) *Drypetes* sp.

Grey-coloured periods are wet seasons.

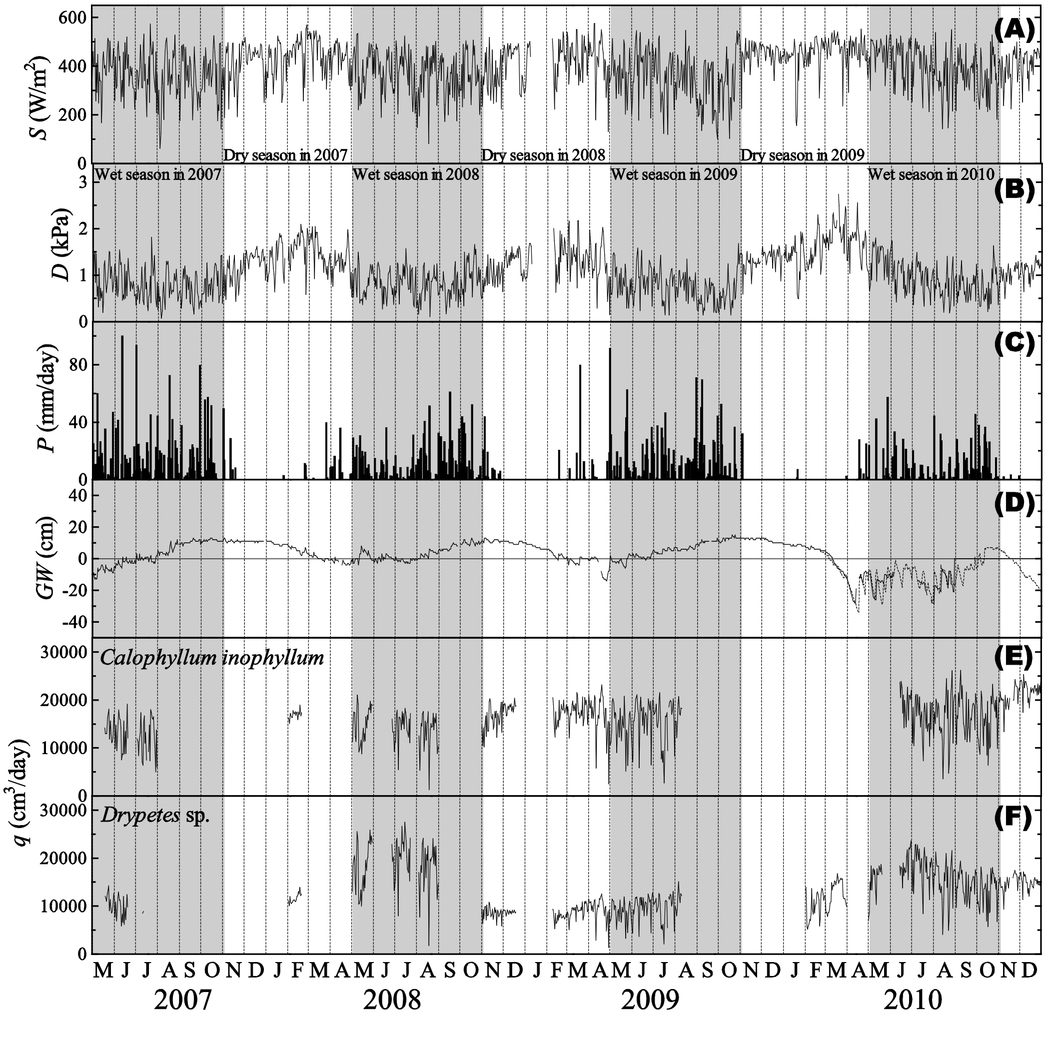

Fig. 2. Seasonal courses of environmental factors and amount of sap flow (*q*)

A) Daytime mean downward shortwave radiation (*S*), B) Daytime mean vapour pressure deficit (*D*), C) Daily rainfall amount (*P*), D) Height of groundwater table above ground level (*GW*), E) *q* of *Calophyllum inophyllum*, and F) *q* of *Drypetes*. sp. The dashed line in 2010 represents estimated *GW* (D). The grey-coloured periods are wet seasons.

remarkable leaf-exchange events in the two species imply significant differences between them in q and G_S.

2. Year-to-year differences in seasonal courses of environmental factors and *q*

The maximum S was almost constant among dry and wet seasons throughout the observation period; a higher S was common in the dry season due to the larger number of cloudless days compared with the wet season (Fig. 2A). D during the wet season was clearly smaller than in the dry season, and the highest D for the whole period was 2.5 kPa in March 2010 (Fig. 2B). Evaporative demand was higher in the dry than in the wet season. The more obvious seasonal courses of D compared with S were similar to observations in Thailand[42]. Large year-to-year differences in P were observed: P during the wet season was 1877.4 mm (2007), 1339 mm (2008), 1571 mm (2009), and 1069.2 mm (2010) (Fig. 2C). Moreover, P during the dry season in 2009 was only 116 mm, and significantly smaller than in the dry seasons in 2007 (284.8 mm) and 2008 (430.8 mm). Although large year-to-year differences in P were measured, the groundwater table was less than 40 cm below the soil surface (Fig. 2D), and the soil was wet throughout the experiment. From September to February (corresponding to the late wet season to mid-dry season), the groundwater table rose above the soil surface (Fig. 2D), and water was frequently found in concave areas on the forest floor.

The daily q for *Calophyllum* and *Drypetes* was higher on fine days when S and D were higher (Figs. 2E, F; 3). Day-to-day differences in q were larger in the wet season than in the dry season because daytime P reduced S and D, and resulted in small q. *Calophyllum* had relatively constant peak q for a few months regardless of season, from 2007 to 2009 (Fig. 2E). Although q of *Calophyllum* was higher in 2010 than in other years (Fig. 3A), similar constant peak q was obtained in 2010 (Fig. 2E). On the other hand, there were large and significant differences in q in *Drypetes* (Figs. 2F, 3B), particularly in the early wet season (May and June): small q in 2007 and 2009, but large q in 2008 and 2010. Higher q values were found after the remarkable leaf shedding observed in the dry season in 2009 for *Calophyllum* and in the wet season in 2009 for *Drypetes*.

3. Responses of G_S to *D* and observed '*high*'/'*low*' periods of *q* and G_S

The light saturation point for G_S of *Calophyllum* and *Drypetes* was at S around 200 W/m^2, and G_S decreased with increasing S (Fig. 4A, C). There was a high positive correlation between S and D ($R^2 = 0.78$), with D increasing on cloudless days. A decrease in G_S was caused by stomatal closure related to a larger D (Fig. 4B, D). For these two species, when $S > 200$ W/m^2, the effect of S on G_S was small and D mainly determined G_S.

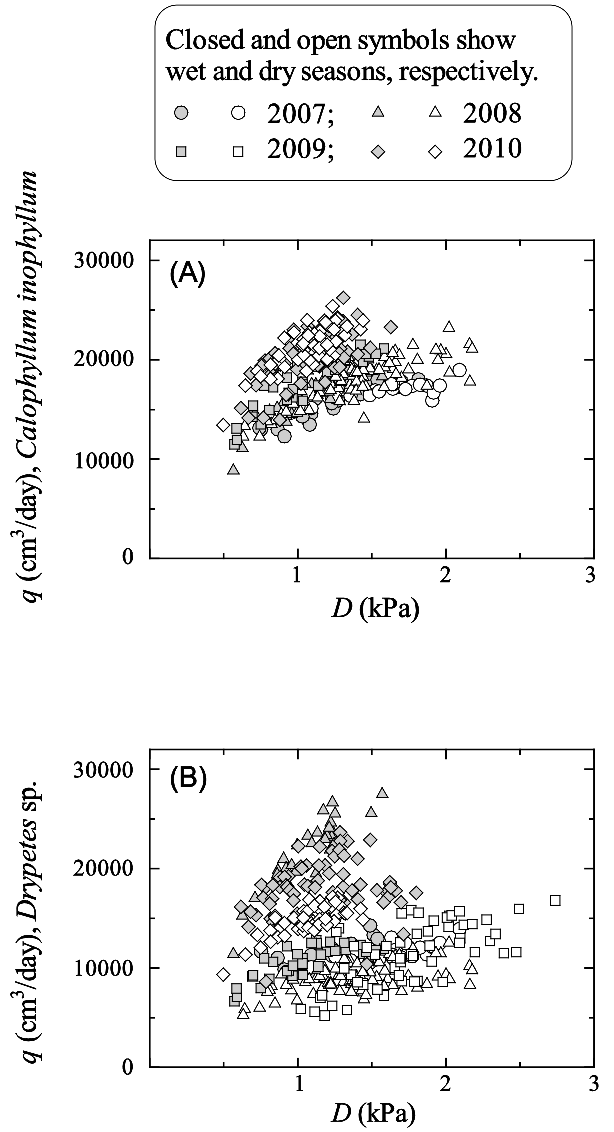

Fig. 3. Relationships between single tree transpiration (q) and daytime mean vapour pressure deficit (D) for A) *Calophyllum inophyllum* and B) *Drypetes* sp.

G_S decreased linearly with increasing ln$D$ (Fig. 4B, D). The larger q of both species resulted in a higher G_S for *Calophyllum* in the dry and wet seasons in 2010, and for *Drypetes* in the wet season in 2008 and the wet and dry seasons in 2010. We named these periods '*high*'. We obtained m and G_{Sref} for *Calophyllum* during *high* periods of the dry and wet seasons in 2010:

$$G_S = -2.9 \cdot \ln D + 4.7 \quad (R^2 = 0.66) \tag{4}$$

and during '*low*' periods:

$$G_S = -1.7 \cdot \ln D + 3.5 \quad (R^2 = 0.73) \tag{5}$$

For *Drypetes*, we obtained the next equation for *high* peri-

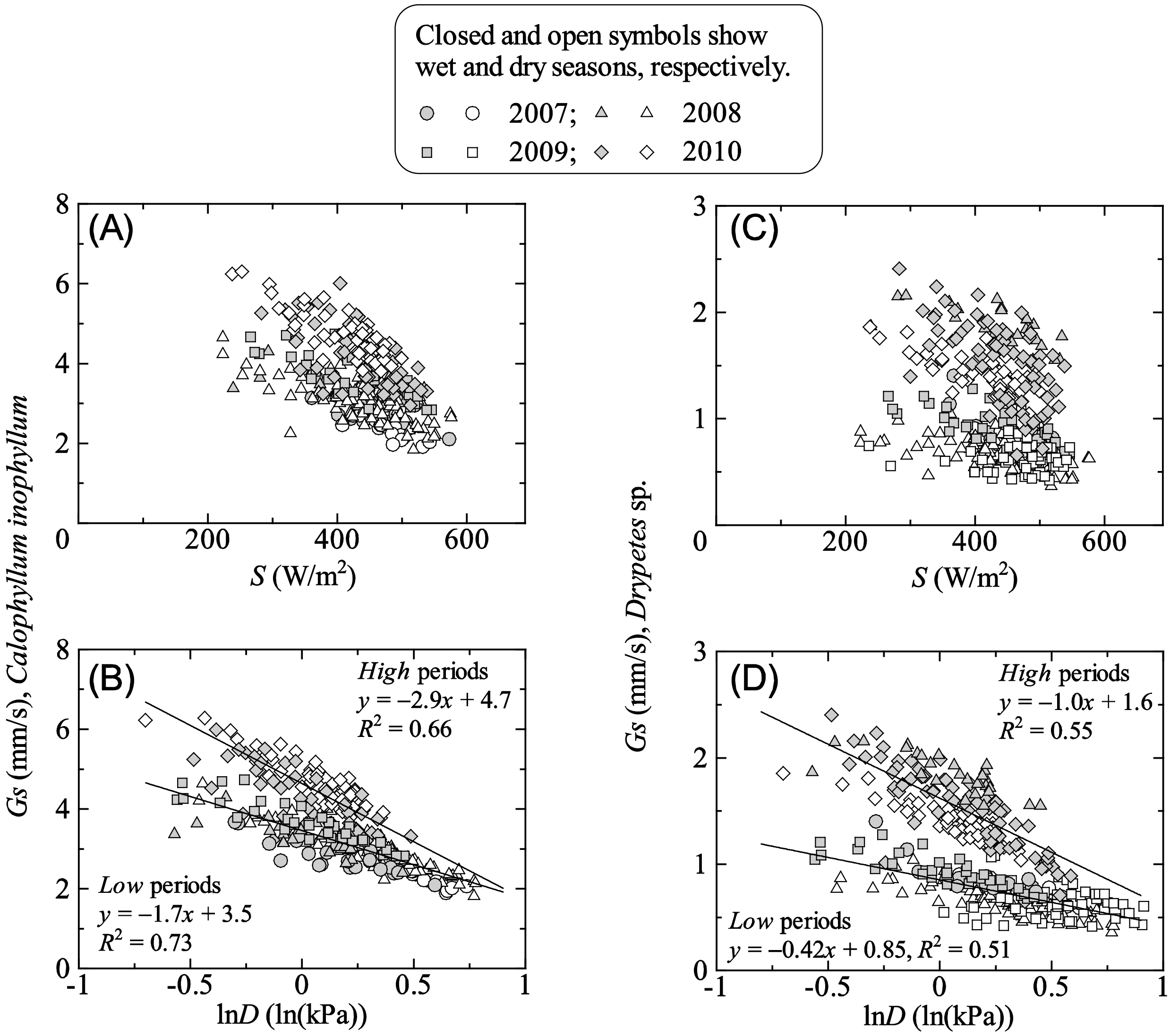

Fig. 4. Upper panels (A and C) show relationships between daytime mean downward shortwave radiation (*S*) and daily crown-level stomatal conductance (G_S), and lower panels (B and D) show relationships between daytime mean vapour pressure deficit (*D*) and G_S.

The left (A and B) and right (C and D) panels present data for *Calophyllum inophyllum* and *Drypetes* sp., respectively. *High* periods for *Calophyllum* were the wet and dry seasons in 2010, those for *Drypetes* were the wet season in 2008 and the wet and dry seasons in 2010, and the other periods were *low*.

ods in the wet season in 2008 and dry and wet seasons in 2010:

$$G_S = -1.0 \cdot \ln D + 1.6 \quad (R^2 = 0.55) \qquad (6)$$

and in *low* periods:

$$G_S = -0.42 \cdot \ln D + 0.85 \quad (R^2 = 0.51) \qquad (7)$$

The differences in *m* and G_{Sref} between *high* and *low* periods were significant for both species (ANCOVA, $P < 0.01$).

Because *Calophyllum* exchanged leaves throughout the year and had short-lived leaves, small seasonal changes in the leaf age composition in the crown probably resulted in relatively constant physiological activity[7]. As a result, we found that *Calophyllum* had similar G_S values with a given value of *D* within *high*/*low* periods (Fig. 4B). In contrast, *Drypetes* underwent irregular leaf exchange and thus had a crown composed of relatively similarly aged leaves. Its physiological activity probably changes over shorter periods, such as a few months, and larger scatter in the relationship between G_S and *D* was found within *high*/*low* periods (Fig. 4D). *High* periods observed after the occurrence of remarkable leaf fall in *Calophyllum* and *Drypetes* strongly suggest that the differences in *q* between *high* and *low* periods were the result of changes in G_S caused by large amounts of leaf exchange. Although we did not have data for leaf fall before November 2008, the observed *high* period in the wet season in 2008 strongly suggests that *Drypetes* exchanged a large portion of leaves in 2007.

The relationship between G_S scaled by G_{Sref} for each period (G_S/G_{Sref}) and ln$D$ was similar, irrespective of period and species (Fig. 5).

$$\frac{G_S}{G_{Sref}} = -0.52 \cdot \ln D + 1 \quad (R^2 = 0.60). \tag{8}$$

Here, $m/G_{Sref} = 0.52$, the absolute value of the slope in Equation 8, and is similar to $m/G_{Sref} \approx 0.6$, which has been reported for a range of tree species[1,10,11,16,32]. The ratio $m/G_{Sref} \approx 0.6$ results from the regulation of minimum leaf-water potential to prevent excess xylem cavitation[11,12,32]. *Drypetes* and *Calophyllum* controlled their minimum leaf potential irrespective of *high*/*low* periods to prevent any damage that would be induced by higher D in dry seasons due to the rapid decreases in G_S that occur with increasing D.

We assumed two simple cases: that a whole year is covered by a *high* period or a whole year is covered by a *low* period, and then determined the differences in q between both cases. The clear relationship between G_S/G_{Sref} and ln$D$ allows the simple estimation of G_S from only G_{Sref}, and thus q for a given value of D can be calculated from only G_{Sref}. If a *high* period continued for a whole year, q of *Calophyllum* and *Drypetes* would be 1.3 and 1.9 times larger, respectively, than that in a year that was completely encompassed by a *low* period.

4. Cues determining remarkable leaf fall and *high*/*low* periods

The huge leaf fall in *Calophyllum* during the dry season in 2009 (Fig. 1A), which probably drove the differences in G_S and q between *high* and *low* periods (Figs. 2E, 3A, 4B), could be related to smaller P in the dry season in 2009 compared to other years (Fig. 2C). At this site, the soil water condition was rich (Fig. 2D), but we recorded very high $D > 25$ kPa in the dry season in 2009 compared with other dry seasons, as caused by the small P (Fig. 2B). Our current data imply that the cue determining *high*/*low* periods for *Calophyllum* was probably an extremely small P, which resulted in a very high D in the dry season.

Drypetes had *high* periods after leaf shedding in the 2009 wet and dry seasons (Figs. 1B, 2F). Focusing on the wet seasons, the environmental conditions in 2008 and 2010 were similar to those in 2007 and 2009 (Fig. 2), but *high* periods were measured only during the 2008 and 2010 wet seasons. In addition, even in the 2010 wet season, when soil conditions were episodically dry (Fig. 2D), *Drypetes* had a *high* period, and q and G_S were similar to those in the 2008 wet season (Figs. 2F, 3B, 4D). At present, we cannot estimate the cue that determines remarkable leaf exchange events, resulting in *high* and *low* periods, for *Drypetes*.

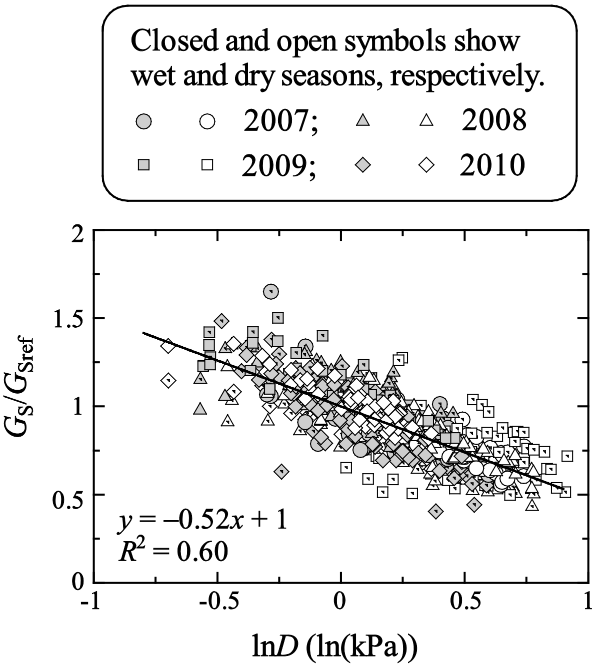

Fig. 5. Relationships between daily crown-level stomatal conductance (G_S) scaled by its reference value at D = 1 kPa (G_{Sref}) and daytime mean vapour pressure deficit (D)

Symbols without and with dots show *Calophyllum inophyllum* and *Drypetes* sp., respectively.

Some literature suggests that in tropical evergreen forests, the cues for leaf expansion and leaf fall are day length, air temperature, D, and S[9]. However, the observed remarkable leaf fall in *Drypetes* in the wet season was not completely explained by environmental factors (Figs. 1B, 2). The results suggest that endogenous whole-plant control, rather than environmental factors, is the cue for leaf phenology[5,6,34,35,36]. At our site, it is possible that endogenous control was more important as a cue than environmental factors. We measured q and obtained G_S for only one tree of *Calophyllum* and one tree of *Drypetes*. Tree-to-tree differences in the degree of flushing within *Drypetes floribunda* and *Drypetes parvifolia* were observed in a dry tropical forest in Ghana[24,25]. Although the *high*/*low* periods defined by changes in q and G_S were correlated with observed data for leaf fall, adding sample trees is highly recommended for future studies to confirm tree-to-tree differences in seasonal trends in q and Gs within the species, and to identify cues that determine remarkable leaf exchange for both species.

Conclusions

We measured q and G_S in two tree species, the successively leaf-exchanging *Calophyllum* and the irregularly leaf-exchanging *Drypetes*, based on sap flow measurements made in a lowland evergreen forest in central Cambodia.

Calophyllum and *Drypetes* had *high* and *low* periods between which q and G_S differed significantly. *High* periods occurred after remarkable leaf fall events in both species and probably resulted from high physiological activity in crowns composed of younger leaves.

Within *high*/*low* periods, smaller scatter in the plot of G_S versus D was found in *Calophyllum* compared with *Drypetes,* and this pattern corresponded with leaf phenology. *Calophyllum* sheds leaves successively, and its physiological activity could be relatively constant. Conversely, because *Drypetes* exchanges leaves irregularly, its leaf-age composition is relatively homogeneous, and the response of G_S to D changes gradually within *high/low* periods.

A clear relationship between G_S scaled by G_{Sref} and D was found irrespective of species and period. We obtained $m/G_{Sref} = 0.52$, which suggests that both species control the minimum value of leaf water potential to prevent excess xylem cavitation under high D in dry seasons. For a given value of D, q was determined using only G_{Sref} and was 1.3 and 1.9 times larger in high periods than in low periods for *Calophyllum* and *Drypetes*, respectively.

Our current data, which were collected from one tree of *Calophyllum* and one tree of *Drypetes*, imply that the cue for remarkable leaf fall events in *Calophyllum* was episodically smaller amounts of P, which resulted in extremely high D in the dry season. However, the cue for *Drypetes* cannot be estimated from our current data. Adding sample trees and maintaining measurements during long-term observations (*i.e.* > 5 years) are highly recommended to confirm tree-to-tree difference in q and Gs within species, and to determine the primary cue that causes remarkable leaf fall.

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References

1. Addington, R. N. et al. (2004) Stomatal sensitivity to vapor pressure deficit and its relationship to hydraulic conductance in *Pinus palustris*. *Tree Physiol.*, **24**, 561–569. DOI: 10.1093/treephys/24.5.561.
2. Araki, M. et al. (2007a) Changes of vertical soil moisture conditions of a dry evergreen forest in Kampong Thom, Cambodia. *In* Forest environments in the Mekong River basin, eds. Sawada, H. et al., Springer, Tokyo, 112–124. DOI: 10.1007/978-4-431-46503-4_10.
3. Araki, M. et al. (2007b) Soil moisture conditions in four types of forest in Kampong Thom, Cambodia. *In* Forest environments in the Mekong River basin, eds. Sawada, H. et al., Springer, Tokyo, 254–262. DOI: 10.1007/978-4-431-46503-4_23.
4. Araki, M. et al. (2008) Seasonal fluctuation of groundwater in an evergreen forest, central Cambodia: experiments and two-dimensional numerical analysis. *Paddy Water Environ.*, **6**, 37–46.
5. Borchert, R. (1994a) Induction of rehydration and bud break by irrigation or rain in deciduous trees of a tropical dry forest in Costa Rica. *Trees*, **8**, 198–204. DOI: 10.1007/BF00196847.
6. Borchert, R. (1994b) Water status and development of tropical trees during seasonal drought. *Trees,* **8,** 115–125. DOI: 10.1007/BF00196635.
7. Brodribb, T. J. & Holbrook, N. M. (2005) Leaf physiology does not predict leaf habit; examples from tropical dry forest. *Trees*, **19**, 290–295. DOI: 10.1007/s00468-004-0390-3.
8. Clearwater, M. J. et al. (1999) Potential errors in measurement of non-uniform sap flow using heat dissipation probes. *Tree Physiol.*, **19**, 681–687. DOI: 10.1093/treephys/19.10.681.
9. Eamus, D. & Prior, L. (2001) Ecophysiology of trees of seasonally dry tropics: Comparisons among phenologies. *Advan, Ecol. Res.*, **32**, 113–197. DOI: 10.1016/S0065-2504(01)32012-3.
10. Ewers, B. E. et al. (2001) Mean canopy stomatal conductance responses to water and nutrient availabilities in *Picea abies* and *Pinus taeda*. *Tree Physiol*, **21**, 841–850. DOI: 10.1093/treephys/21.12-13.841.
11. Ewers, B. E. et al. (2005) Effects of stand age and tree species on canopy transpiration and average stomatal conductance of boreal forests. *Plant Cell Environ.*, **28**, 660–678. DOI: 10.1111/j.1365-3040.2005.01312.x.
12. Ewers, B. E. et al. (2007) Interannual consistency in canopy stomatal conductance control of leaf water potential across seven tree species. *Tree Physiol.*, **27**, 11–24. DOI: 10.1093/treephys/27.1.11.
13. FAO (2010a) *Global Forest Resources Assessment 2010, Main report*. FAO Forestry Paper No. 16, FAO, Rome.
14. FAO (2010b) *Global Forest Resources Assessment 2010, Country report Cambodia*. FAO, Rome.
15. Granier, A. (1985) Une nouvelle méthod pour la mesure du flux de sève brute dans le tronc des arbres. *Ann. Sci. For.*, **42**, 193–200.
16. Gunderson, C. A. et al. (2002) Environmental and stomatal control of photosynthetic enhancement in the canopy of a sweetgum (*Liquidambar styraciflua* L.) plantation during 3 years of CO_2 enrichment. *Plant Cell Environ.*, **25**, 379–393.

DOI: 10.1046/j.0016-8025.2001.00816.x.

17. Iida, S. et al. (2006) Change of evapotranspiration components due to the succession from Japanese red pine to evergreen oak. *J. Hydrol.*, **326**, 166–180. DOI: 10.1016/j.jhydrol.2005.11.002.
18. Iida, S. & Tanaka, T. (2010) Effect of the span length of Granier-type thermal dissipation probes on sap flux density measurements. *Ann. For. Sci.*, **67**, 408. DOI: 10.1051/forest/2009128.
19. Kabeya, N. et al. (2008) Preliminary study of flow regimes and stream water residence times in multi-scale forested watersheds of central Cambodia. *Paddy Water Environ.*, **6**, 25–35. DOI: 10.1007/s10333-008-0104-3.
20. Kenzo, T. et al. (2012) Variations in leaf photosynthetic and morphological traits with tree height in various tree species in Cambodian tropical dry evergreen forest. *JARQ,* **46**, 167–180.
21. Köstner, B. M. M. et al. (1992) Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia,* **91**, 350–359. DOI: 10.1007/BF00317623.
22. Kumagai, T. et al. (2005) Effects of tree-to-tree and radial variations on sap flow estimates of transpiration in Japanese cedar. *Agric. For. Meteorol.*, **135**, 110–116. DOI: 10.1016/j.agrformet.2005.11.007.
23. Kumagai, T. et al. (2008) Transpiration and canopy conductance at two slope positions in a Japanese cedar forest watershed. *Agric. For. Meteorol.*, **148**, 1444–1455. DOI: 10.1016/j.agrformet.2008.04.010.
24. Lieberman, D. (1982) Seasonality and phenology in a dry tropical forest in Ghana. *J. Ecol.*, **70**, 791–806.
25. Lieberman, D. & Lieberman M. (1984) The causes and consequences of synchronous flushing in a dry tropical forest. *Biotropica*, **16**, 193–201.
26. Matsumoto, J. (1997) Seasonal transition of summer rainy season over Indochina and adjacent monsoon region. *Advan. Atmosph. Sci.*, **14**, 231–245. DOI 10.1007/s00376-997-0022-0.
27. McNaughton, K. G. & Jarvis, P. G. (1993) Predicting effects of vegetation changes on transpiration and evaporation. *In* Water Deficits and Plant Growth, vol. V, ed. Kozlowski, T. T., Academic Press, New York, 1–48.
28. Nobuhiro, T. et al. (2007) Year-round observation of evapotranspiration in an evergreen broadleaf forest in Cambodia. *In* Forest environments in the Mekong River basin, eds. Sawada, H. et al., Springer, Tokyo, 75–86. DOI: 10.1007/978-4-431-46503-4_7.
29. Nobuhiro, T. et al. (2010) Study of rainfall characteristics in lowland dry evergreen forest, Cambodia. *Kanto Journal of Forest Research*, **61**, 203–206 [in Japanese].
30. Ohnuki, Y. et al. (2008a) Distribution and characteristics of soil thickness and effects upon water storage in forested areas of Cambodia. *Hydrol. Process.*, **22**, 1272–1280. DOI: 10.1002/hyp.6937.
31. Ohnuki, Y. et al. (2008b) Seasonal change in thick regolith hardness and water content in a dry evergreen forest in Kampong Thom Province, Cambodia. *Geoderma,* **146**, 94–101. DOI: 10.1016/j.geoderma.2008.05.016.
32. Oren, R. et al. (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant Cell Environ.*, **22**, 1515–1526.
33. Phillips, N. & Oren, R. (1998) A comparison of daily representations of canopy conductance based on two conditional time-averaging methods and the dependence of daily conductance on environmental factors. *Ann. For. Sci.*, **55**, 217–235. DOI: 10.1051/forest:19980113.
34. Reich, P. B. (1995) Phenology of tropical forests: patterns, causes, and consequences. *Can. J. Bot.*, **73**, 164–174.
35. Reich, P. B. & Borchert, R. (1982) Phenology and ecophysiology of the tropical tree, *Tabebuia neochrysantha* (Bignoniaceae). *Ecology*, **63**, 294–299.
36. Reich, P. B. & Borchert, R. (1984) Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *J. Ecol.*, **72**, 61–74.
37. Sawada, H. et al. (eds.) (2007) *Forest environments in the Mekong River basin*. Springer, Tokyo, pp. 299.
38. Shimizu, A. et al. (2007) Runoff characteristics and observations on evapotranspiration in forest watersheds, central Cambodia. *In* Forest environments in the Mekong River basin, eds. Sawada, H. et al., Springer, Tokyo, 135–146. DOI: 10.1007/978-4-431-46503-4_12.
39. Stewart, J. B. (1988) Modelling surface conductance of pine forest. *Agric. For. Meteorol.*, **43**, 19–35. DOI: 10.1016/0168-1923(88)90003-2.
40. Tamai, K. et al. (2007) Measurements of wind speed, direction, and vertical profiles in an evergreen forest in central Cambodia. *In* Forest environments in the Mekong River basin, eds. Sawada, H. et al., Springer, Tokyo, 87–96. DOI: 10.1007/978-4-431-46503-4_8.
41. Tamai, K. et al. (2008) Effects of selective cutting of large trees on transpiration and surface temperature: A predictive study of evergreen broad-leaf forest in central Cambodia. *In* From headwaters to the ocean, eds.Taniguchi, M. et al., CRC Press, Boca Raton, FL, USA, 3–7.
42. Tanaka, N. et al. (2008) A review of evapotranspiration estimates from tropical forests in Thailand and adjacent regions. *Agric. For. Meteorol.*, **15**, 807–819. DOI: 10.1016/j.agrformet.2008.01.011.
43. Tani, A. et al. (2007) Principal forest types of three regions of Cambodia: Kampong Thom, Kratie, and Mondolkiri. *In* Forest environments in the Mekong River basin, eds. Sawada, H. et al., Springer, Tokyo, 201–213. DOI: 10.1007/978-4-431-46503-4_18.
44. Toriyama, J. et al. (2007) Soils under different forest types in the dry evergreen forest zone of Cambodia: Morphology, physicochemical properties, and classification. *In* Forest environments in the Mekong River basin, eds. Sawada, H. et al., Springer, Tokyo, 241–253. DOI: 10.1007/978-4-431-46503-4_22.
45. Wilson, K. B. et al. (2001) A comparison of methods for determining forest evapotranspiration and its components: sap-flow, soil water budget, eddy covariance and catchment water balance. *Agric. For. Meteorol.*, **106**, 153–168. DOI: :10.1016/S0168-1923(00)00199-4.