

Leaf phenology effects on transpiration: leaf age-related stomatal conductance of *Dipterocarpus costatus* during the dry season in a Cambodian seasonally tropical evergreen forest

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មូលនិយមសង្ខេប

វដ្តជីវិតស្លឹកកំណត់រចនាសម្ព័ន្ធស្លឹក(តាមអាយុនៃស្លឹក)របស់ដើមឈើ ដែលអាចជាកត្តាគ្រប់គ្រងសកម្មភាពសរីរៈស្លឹក។ យើងបានវាយតម្លៃពីឥទ្ធិពលនៃអាយុស្លឹក ទៅលើកម្រិតស្រូប និងរំកាយចំហាយទឹករបស់ស្លឹកមួយទងនៃដើមឈើទាល(នាងដែង) (*Dipterocarpus costatus*) នៅក្នុងព្រៃស្រោងត្រូពិចតាមរដូវនៃតំបន់ទំនាប។ យោងលើសន្ទស័ន៍កម្រិតស្រូប និងរំកាយចំហាយទឹករបស់ស្លឹកឈើយើងបានស៊ើបអង្កេតពីអត្រារំកាយចំហាយទឹកនៃរន្ធស្លឹកម៉ាត (g_s) របស់ស្លឹកឈើដែលនៅល្អអំឡុងរដូវប្រាំង ក្នុងខេត្តកំពង់ធំ ប្រទេសកម្ពុជា។ g_s ដែលផ្អែកលើអាយុរបស់ស្លឹក ត្រូវបានរកឃើញថាមានកម្រិតខ្ពស់លើស្លឹកឈើដែលមានអាយុពាក់កណ្តាលពេញវ័យ (១៧ថ្ងៃបន្ទាប់ពីស្លឹកលា) ដែលបន្ទាប់ពីនោះវាបានថយចុះជាបន្តិចម្តងៗ ទោះបីជាវាអាចរក្សាកម្រិតបានហែល៦០%នៃកម្រិតខ្ពស់បំផុតរបស់g_s រហូតដល់៥ថ្ងៃមុនពេលស្លឹកឈើជ្រុះ។ កត្តាបរិស្ថានដូចជាសីតុណ្ហភាព និងសំណើមមានទំនាក់ទំនងតិចតួចជាមួយនឹងកម្រិតg_s។ ការសិក្សារបស់យើងក៏បានបង្ហាញផងដែរនូវម៉ូតូលាស់ស្លឹកខ្ពស់ពីរដងនៃឈើទាល ឧទាហរណ៍ លាស់ស្លឹកច្រើនដំបូងនៅអំឡុងដើមរដូវប្រាំង និងដំណាក់បន្ទាប់គឺនៅចុងរដូវប្រាំង។ លទ្ធផលនៃការសិក្សារបស់យើងបានបង្ហាញថា លើសពីកត្តាបរិស្ថានវដ្តលាស់ស្លឹក (ជាកត្តាកំណត់រចនាសម្ព័ន្ធអាយុស្លឹកនៃផ្នែកមែកស្លឹក) អាចជាកត្តាជួយក្នុងការសម្រេចចិត្តលើអត្រារំកាយចំហាយទឹកកម្រិតនៃដើមឈើទាលក្នុងអំឡុងរដូវប្រាំង។

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Abstract

Leaf phenology regulates the leaf-age structure of a tree crown, which possibly governs leaf physiological activity. We evaluated the effects of leaf age on single leaf-scale transpiration in the tall dipterocarp *Dipterocarpus costatus* in a lowland seasonally tropical evergreen forest. As an index of leaf transpiration, we investigated the stomatal conductance (g_s) of intact leaves during the dry season in Kampong Thom Province, Cambodia. Leaf-age-dependent g_s was found to peak in semi-mature leaves (17 days after unfolding), after which it gradually declined, although it remained at around 60% of the peak g_s until four days before leaf fall. Ambient factors such as temperature and humidity were less strongly related to g_s . Our study also indicated a bimodal leaf flushing peak of *D. costatus* i.e., peak leaf flushing primarily occurred during the early dry season and secondary flushing during the late dry season. The results of our study indicate that, in addition to ambient factors, leaf-flushing phenology, as the governing driver of leaf age structure of the crown, could be a decisive factor in tree-level transpiration of *D. costatus* during the dry season.

Keywords

Dipterocarpus costatus, leaf phenology, lowland dry evergreen forest, porometer, transpiration, seasonal tropical forest.

Introduction

Tropical dry forests are widely distributed in pantropics where annual rainfall ranges from 600 to 1,800 mm and there is a distinct dry season of 3–8 months (Murphy & Lugo, 1986). The factors governing tropical dry forest ecosystems have attracted interest, given that seasonal variation in irradiance and water availability often do not coincide (Wright & van Schaik, 1994). Intensive research on Amazonian tropical dry forests has revealed that seasonal controls on the exchange of water and carbon rely on light availability followed by leaf-phenology (Saleska *et al.*, 2003; Xiao *et al.*, 2005; Huete *et al.*, 2006; Hutrya *et al.*, 2007). On the other hand, pantropic comparative studies have indicated lesser light control in Asian tropical forests, where there is variation in governing factors from primarily water-limited drier forests to wet evergreen forests showing slight positive trends with light availability (Huete *et al.*, 2008).

Several studies on Southeast Asian tropical forests have clarified forest water cycles (Tanaka *et al.*, 2008; Mizoguchi *et al.*, 2009), where seasonally tropical evergreen forests demonstrate various transpiration patterns during the dry season. Peak transpiration was observed to occur at the end of the dry season in the less water-limited hill evergreen forests of northern Thailand (Tanaka *et al.*, 2004), and in both the early and late dry season in the lowland evergreen forests of central Cambodia (Nobuhiro *et al.*, 2009). In contrast, a lower transpiration rate was observed during the dry season in the water-limited evergreen forests of Sakaerat, Thailand (Pinker *et al.*, 1980; Tanaka *et al.*, 2008).

Hydrological process models have been used to simulate the water-cycle in Asian tropical dry forests (Tanaka

et al., 2004; Kumagai *et al.*, 2009). However, in the seasonally tropical evergreen forests in Cambodia, a model with vapor pressure deficit as the decisive factor failed to predict evapotranspiration peaks during the dry season (Nobuhiro *et al.*, 2009). In fact, the potential evaporation rate, which is indicative of the climatic conditions that encourage evaporation from the water surface, cannot account for the peaks, in which highly variable mid-values ($\sim 5.5 \pm 1.0 \text{ mm d}^{-1}$) and constant high values ($\sim 6.2 \pm 0.2 \text{ mm d}^{-1}$) were reported for the early dry season and the late dry season, respectively (Chann *et al.*, 2011). It is still not known why the peak of transpiration occurs in both the early and late dry season in seasonally tropical evergreen forests in Cambodia.

Leaf phenology, including leaf flush, maturation, senescence and fall, may be a key factor influencing ecosystem processes (Forrest & Miller-Rushing, 2010; Wu *et al.*, 2017). However, little attention has been given to tropical evergreen forests because their leaf mass is relatively constant (Richardson *et al.*, 2013). Leaf stomatal conductance (g_s) is positively and almost linearly related to transpiration (Burrows & Milthorpe, 1976; Ishida *et al.*, 2006), although Meinzer *et al.* (1995) pointed out the influence of boundary layer on the relationship between g_s and transpiration. Considerable changes in g_s have been observed during leaf maturation (Field, 1987; Brodribb & Holbrook, 2005; Pallardy, 2010; Kenzo *et al.*, 2016). In turn, leaf phenology regulates the leaf age structure in individuals, which may govern leaf physiological activity. Iida *et al.* (2013), who investigated the same study site as Nobuhiro *et al.* (2009), suggested that tree-scale transpiration depended on the leaf age structure of the crown for several tree species composing the low to mid layers of the canopy in seasonal tropical evergreen forest in Cambodia. We hypothesized that the peaks of

evapotranspiration during the dry season derives from high leaf-physiological activities that are associated with the leaf age structure of crowns. Based on this hypothesis, we expected that leaf age-related physiological activities would be observed for dominant tall tree species comprising the upper canopy layers of the forest. Moreover, we predicted that leaf phenology increases the physiological activities of crown layers via the exchange of old leaves with new ones during the dry season.

The objectives of our research were to investigate the leaf-age-related leaf g_s of tree species in a seasonally tropical evergreen forest in Cambodia. We examined a tall evergreen dipterocarp, *Dipterocarpus costatus* C.F. Gaertn (Dipterocarpaceae, Pooma, 2002; Tani *et al.*, 2007), composing the top layer of the forest. The leaf photosynthetic features of *D. costatus* have been documented in the forest, but only from fully mature leaves (Kenzo *et al.*, 2012). We measured the intact leaf g_s of two *D. costatus* trees during the dry season, covering both leaf-exchange and leaf-unfolding phenomena. In addition, we investigated the leaf-exchange phenology of the study trees. Based on the results, we discuss leaf phenology effects on transpiration at the tree scale. Finally, we consider the potential changes in seasonal variation in tree-scale transpiration that may accompany intermittent and multiple leaf flushings per year.

Methods

Study site and species

The study was conducted in Kampong Thom Province, central Cambodia (12.76°N, 105.48°E), in a lowland seasonally dry evergreen forest covering a flat, gently rolling alluvial plain at an altitude of 80–100 m above sea level (a.s.l.). The forest is located on extensive Quaternary sedimentary rock (Wakita *et al.*, 2004) with a typically sandy soil that is classified as Haplic Acrisol (Alumic, Profondic) in the world reference base system (Toriyama *et al.*, 2007, 2008). The groundwater table seasonally fluctuates from approximately 2 m to 10 m in depth (Araki *et al.*, 2008; Ohnuki *et al.*, 2008a, 2008b). Fine roots (<2 mm) grow in the deep soils near –10 m, corresponding to the groundwater table at the end of the dry season (Ohnuki *et al.*, 2008b).

Annual precipitation and average monthly temperature are 1,540 mm and 27°C (Kenzo *et al.*, 2012). Average monthly temperature ranges from 24 to 29°C (Chann *et al.*, 2011). The seasonal tropical climate is governed by monsoons and can be divided into three seasons: an early dry season (from October or November to December)

with little rain (50 mm), high groundwater levels (from –50 to –100 cm) and decreasing air temperature (from 25.5 to 24.5°C); a late dry season (from January to March or April) with little rain (100 mm), declining groundwater levels (from –125 to –200 cm) and increasing air temperature (from 25 to 28 °C); and a rainy season (from April or May to September or October) providing >90% of the annual precipitation, increasing groundwater levels (from –180 to –50 cm) and moderate air temperature (approximately 26°C) (Kabeya *et al.*, 2008; Chann *et al.*, 2011). Monthly averages for meteorological data are available from the website of the Changes in Water Cycle in the Mekong River Basin research project in Cambodia (www.ffpri.affrc.go.jp/labs/cwcm/dataset/EF/EF_E.htm). Daily maximum temperature in the canopy (40 m above ground) reaches 35°C in the early dry season, while a daily minimum temperature of 20°C has been recorded (November 2009, Kenzo *et al.*, 2012). Wind speeds at heights of 38 or 60 m range from 2.5 to 3.5 m s⁻¹ during the dry season, relatively higher than the wet season (from 2.0 to 2.5 m s⁻¹: www.ffpri.affrc.go.jp/labs/cwcm/dataset/EF/EF_E.htm). Monthly 10-m scalar wind speeds were estimated at 2.2–2.4 m s⁻¹ in January and December and 1.6–1.9 m s⁻¹ in February–March and November in surface JRA-55 reanalysis data (http://jra.kishou.go.jp/JRA-55/index_en.html) with a spatial resolution of 1.25°×1.25°. These wind speeds are far higher than 0.25 m s⁻¹, resulting in decoupling conditions between stomatal and boundary layer conductance (Meinzer *et al.*, 1995). The seasonal difference in solar radiation is 20%, ranging from 20 kJ m⁻² day⁻¹ in April to 16 kJ m⁻² day⁻¹ in September. The two months with the lowest radiation occur in the late rainy season (Chann *et al.*, 2011).

Dipterocarpus costatus Gaertn. f. (*Chhoeuteal Bankouy* in Khmer) was selected as our study plant. It is a tall evergreen tree belonging to the Dipterocarpaceae family (Pooma, 2002). This species is widely scattered in lowlands, hills and upper dipterocarp forests in India (Andaman Islands), Bangladesh, Myanmar, Thailand, Malaysia (Peninsular Malaysia), Laos, Cambodia, and Vietnam (Ashton, 1979, 1998; Toyama *et al.*, 2013). However, *D. costatus* is listed as Vulnerable in the IUCN Red List of Threatened Species (Ly *et al.*, 2017) and is a target species for logging in the study area (Kim Phat *et al.*, 2002). Its height commonly reaches 30–35 m (Toyama *et al.*, 2013), although it can reach heights of 45 m and stem diameters of 130 cm (Authors, unpublished data), thereby dominating the upper canopy layer of dry evergreen forests (Tani *et al.*, 2007).

Stomatal conductance measurement

We measured intact leaf g_s as an indicator of transpiration using a portable leaf porometer (SC-1: Decagon, Pullman, WA, USA). Tanaka-Oda *et al.* (2012) verified that g_s measurements (SC-1) were significantly correlated with the values measured with a portable photosynthesis meter (LI-6400: Li-Cor, Lincoln, NE, USA), but found that g_s measurements (SC-1) were lower than the values measured with the LI-6400 portable photosynthesis meter under humid conditions (relative humidity of ambient air = 65%). Thus, we first validated the g_s measurements (SC-1) by comparison with values measured with a LI-6400 using 39 identical leaves from branches cut from 18 individuals of 14 tree species, including 11 leaves of *D. costatus* at the study site in November 2009. Complete details of the LI-6400 measurement methods can be found in Kenzo *et al.* (2006, 2012). The g_s measurements (SC-1) were positively correlated with the maximum absolute conductance values measured using the LI-6400 ($r^2 = 0.35$ and $r^2 = 0.26$ for *D. costatus*), and a paired *t*-test confirmed that there was no significant difference between the measurements made by the two instruments ($p = 0.3966$). Similar correlations have been reported in several broadleaf trees (Tanaka-Oda *et al.*, 2012).

We selected two reproductive *D. costatus* individuals with similar tree crown sizes for g_s measurements. Tree I had a diameter at breast height (DBH) of 48 cm and height of 23.8 m, while Tree II had a DBH of 43 cm and height of 23.8 m. Tree II was located 1.5 km south-southeast of Tree I. Both trees were growing beside a road and so even mid-layer branches were fully exposed to the sun for part of the day. The time of sun exposure was different between the two trees because Tree I and Tree II were located on the west and east side of the road, respectively. We selected five to six branches per individual at a height of 12–13 m, and all of the leaves on the selected branches were marked for identification using a 12-m-high platform. A total of 140 leaves were measured, and the approximate flushing period of each leaf was estimated. The g_s of all marked leaves was measured concurrently with air temperature and humidity as ambient factors using the SC-1. Relative photosynthetic active radiation was not measured. Measurements were conducted in March 2009 for Tree I and from December 2009 to early March 2010 for Trees I and II. All measurements took place at least 1.5 hrs after sunrise to avoid low light intensities in early morning and before 1300 hrs to avoid midday photosynthesis depression (Kenzo *et al.*, 2003). We conducted daytime measurements to determine the degree of midday g_s depression at the study site on 3–4 March 2009 for 42 leaves. Each leaf was repeat-

edly measured 9–14 times. Measurement time ranged from 0843 to 1620 hrs. For newly flushed leaves, measurements commenced when the leaves had unfolded sufficiently to cover the porometer measurement area (6.3 mm diameter). We defined the leaf age as day 0 on the day of the first measurement.

Leaf-unfolding observation

To investigate branch-level leaf phenology, the maturity of all leaves on selected branches was confirmed for each g_s measurement using leaf colour: young (yellowish green, hairy), semi-mature (pale green, sparse hairs), mature (dark green, glabrous) and senescent (dull green with yellow or brown spots). The dates of leaf emergence and fall were recorded for all leaves on the branches studied.

Leaf size (length and width) was recorded for 36 (2 December 2009), 94 (12 December 2009) and 99 (2 March 2010) intact leaves. Leaves that fell during the measurement period ($n = 29$) were collected, and their sizes were recorded. The leaf expansion pattern was estimated from the relationship between the degree of leaf expansion relative to the full leaf size (%) and leaf age.

Litter trap measurement

The leaf exchange phenology of *D. costatus* was estimated from fallen leaves collected in litter traps between September 2010 and April 2011. Three litter traps covering an area of ~0.5 m² were set within a lowland evergreen forest stand located 1 km north of Tree I; therefore, the fallen leaves were not collected from Tree I or Tree II. Litter was collected three times per month, and was then oven-dried, sorted (into leaves and leaf bud scales of *D. costatus* and others) and weighed. Leaf bud scales cover new leaf buds and fall when the buds burst.

Statistical analysis

Relationships between mean g_s values and measurement date, leaf age and ambient factors were assessed using a generalised linear model (GLM) framework, incorporating individual leaves as a random effect. Significant differences among leaf ages were evaluated using the post hoc Tukey–Kramer HSD test. To examine the degree of midday g_s depression, the relationship of g_s values with measurement time was assessed using a GLM incorporating individual leaves as a random effect. Regression tree analysis was also used to assess when midday g_s depression occurred for each leaf. The most accurate predictive models were those with the lowest Akaike information criterion, corrected for small sample sizes (Akaike, 1974; Sugiura, 1978). Statistical analysis was conducted using JMP statistical software (ver. 10.0; SAS Institute Inc., Cary, NC, USA).

Results

Daily changes in leaf stomatal conductance

Intact leaf g_s averaged $196 \pm 85 \text{ mmol m}^{-2} \text{ s}^{-1}$ over the measurement period (Fig. 1). Average g_s values differed significantly from December 2009 to early March 2010 ($p < 0.05$) between Tree I ($231 \pm 83 \text{ mmol m}^{-2} \text{ s}^{-1}$) and Tree II ($178 \pm 78 \text{ mmol m}^{-2} \text{ s}^{-1}$). In addition, high g_s values were observed in different periods for Trees I and II. For Tree I, g_s peaked on 22 December 2009 and was high from 16 to 23 December 2009, whereas for Tree II, g_s peaked on 29 December 2009 and was high from 28 December 2009 to 12 January 2010, with another relatively high period from 19 to 26 December 2009.

Trends in stomatal conductance with leaf development and senescence

A clear trend was observed in g_s related to leaf age (Fig. 2). In summary, g_s was low but stable in newly flushed leaves, and then steadily increased to a peak, followed by a gradual decline. We divided leaf age into six phases based on a statistical interpretation: phase (i), newly

flushed and expanding leaves with low-level g_s ; phases (ii) and (iii), full size semi-mature leaves with low–mid and mid-level g_s , respectively; phase (iv), semi-mature leaves with peaking g_s ; and phases (v) and (vi), mature leaves with mid and low-level g_s , respectively (Table 1). We identified three critical leaf ages: day 0, at leaf unfolding (mean \pm SD: $113 \pm 45 \text{ mmol m}^{-2} \text{ s}^{-1}$); day 10, at the inflection point of the increasing curve of g_s (169 ± 77); and day 17, at the peak level of g_s (268 ± 88). Then, leaf ages were categorised based on whether there was a difference in mean g_s among the selected ages of leaves within the GLM framework. The mean g_s values of phases (i) and (vi) were the same as those of 0-day leaves. Only phase (iv) leaves differed significantly from the 10-day leaves in mean g_s . The mean g_s values of phases (iii), (iv) and (v) did not differ from that of 17-day leaves. After 85 days, significant trends were not apparent due to the small number of measurements.

No relationship was observed between g_s and leaf age for leaves older than three months in our study. Of the 46 leaves measured on Tree I in March 2009, 20% remained until March 2010 (i.e., longevity >1 year). Another 40% remained on the branch for at least nine months. These

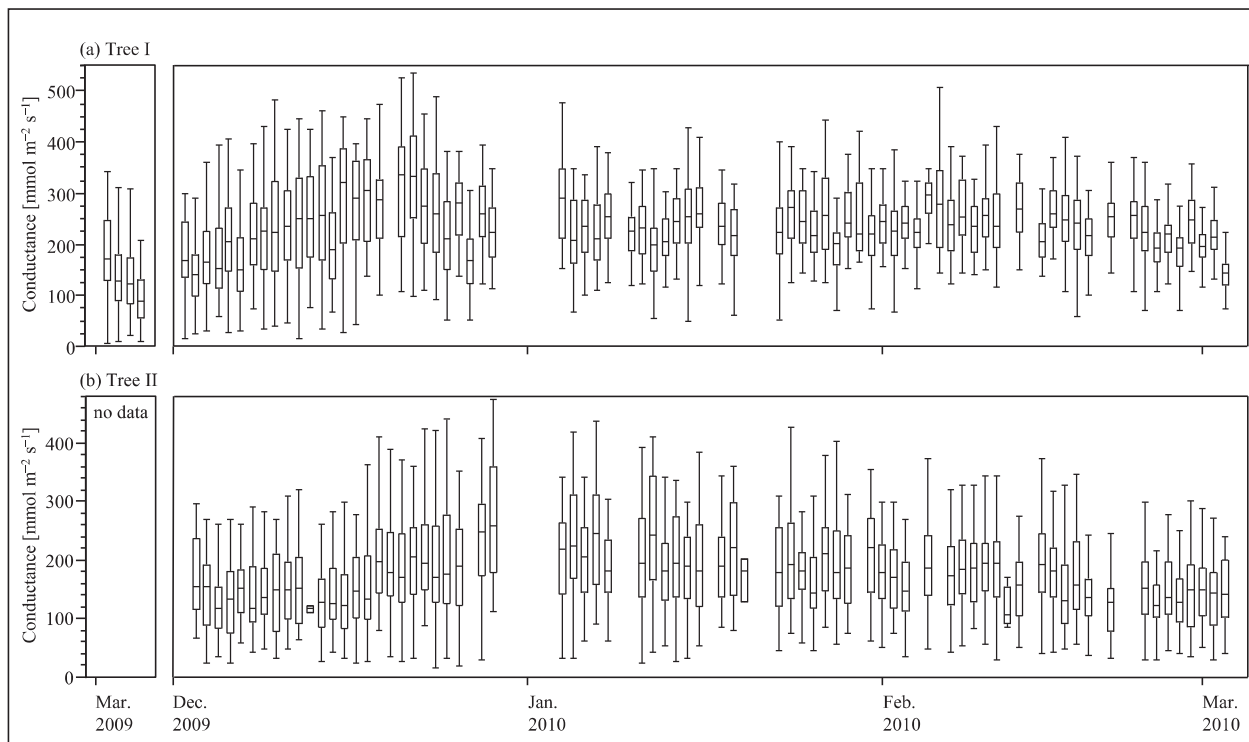


Fig. 1 Daily changes in stomatal conductance: a) Tree I, mature individual, b) Tree II, young individual. The data are presented as box-and-whisker plots (median, 25% and 75% quartiles, range). Average g_s values for measurements from December 2009 to early March 2010 differed significantly ($p < 0.05$) between Tree I and Tree II.

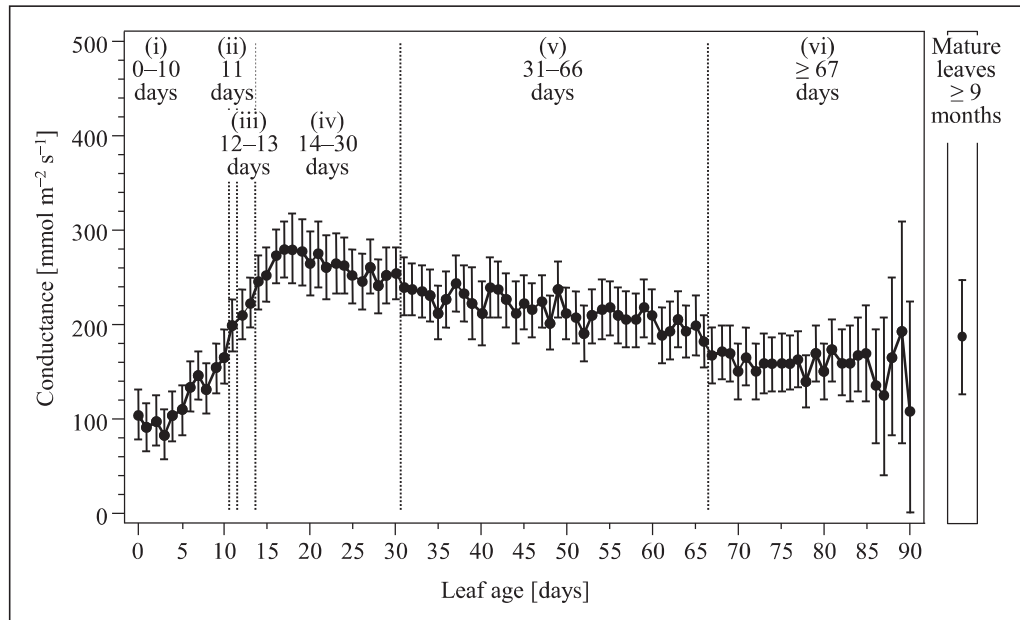


Fig. 2 Relationship between leaf age and stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$). Circles and bars indicate the mean and SD, respectively. Data for mature leaves (at least nine months after unfolding) are also shown. See Table 1 for details of the six phases recognised.

Table 1 Stomatal conductance related to leaf age of *Dipterocarpus costatus* in Kampong Thom Province, Cambodia.

Phase	Leaf age (days)	Conductance (mean \pm SD, $\text{mmol m}^{-2} \text{s}^{-1}$)	<i>n</i>	Description of conductance	Leaf maturation
(i)	0–10	125 \pm 62	316	Low-level	Young, expanding to full size
(ii)	11	199 \pm 98	27	Between low & mid-level	Semi-mature
(iii)	12–13	215 \pm 77	54	Mid-level	Semi-mature
(iv)	14–30	256 \pm 78	329	High-level	Semi-mature
(v)	31–66	214 \pm 76	764	Mid-level	Mature
(vi)	\geq 67	159 \pm 65	367	Low-level	Mature, senescent

long-lived, mature leaves had high g_s values ($186 \pm 66 \text{ mmol m}^{-2} \text{s}^{-1}$, $n = 843$) even at nine months after emergence (Fig. 2).

Changes in g_s in the days before leaf fall are shown in Fig. 3. The g_s of leaves one day before fall (mean \pm SD: $41 \pm 18 \text{ mmol m}^{-2} \text{s}^{-1}$, $n = 30$) was significantly lower than over four days before fall ($115 \pm 51 \text{ mmol m}^{-2} \text{s}^{-1}$, $n = 25$, $p < 0.05$). Visual features of leaf senescence were clearly identified 0–2 days before leaf fall, identified with some difficulty three days before fall (88%, $n = 8$), and were rarely identified four days before fall. Conductance gradually decreased in leaves from three days before fall

(average $< 100 \text{ mmol m}^{-2} \text{s}^{-1}$), whereas the g_s of leaves five days before fall did not differ significantly in any leaf group ($140 \pm 54 \text{ mmol m}^{-2} \text{s}^{-1}$, $n = 24$, $p < 0.05$). The g_s values averaged $164 \pm 68 \text{ mmol m}^{-2} \text{s}^{-1}$ for mature leaves 5–70 days before leaf fall ($n = 344$).

Ambient factors related to stomatal conductance

Air temperature and humidity during the measurement period averaged $29.2 \pm 1.8^\circ\text{C}$ and $66 \pm 6\%$, respectively. Neither meteorological factor alone was significantly related to g_s . The effect of measurement time (–0800–1300

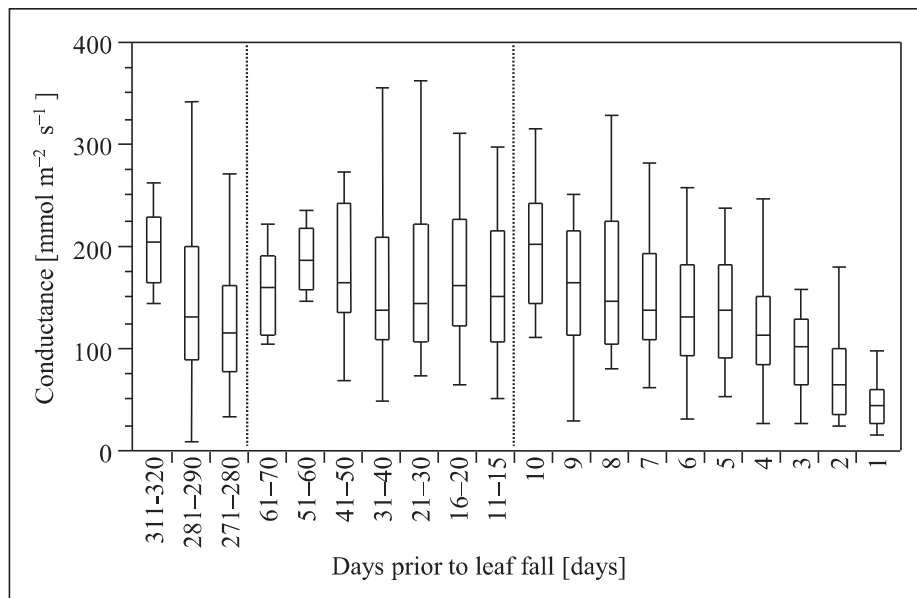


Fig. 3 Relationship between time before leaf fall and stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$). The data are presented as box-and-whisker plots (median, 25% and 75% quartiles, range).

hrs) was inconsistent, being positive in some cases but negative in others.

Of the three ambient factors in a GLM incorporating leaf age and the ambient factors at midday with individual leaves as a random effect, only humidity had a significantly negative effect ($F = 42.2$, $p < 0.0001$, $df = 1$). The coefficient of humidity (\pm standard error) in the selected GLM model was $-2.09 (\pm 0.32)$. Because humidity ranged from 55.2% to 79.0% in 95% of the measurements, the effect of humidity on g_s was estimated to be less than $50 \text{ mmol m}^{-2} \text{ s}^{-1}$. For midday g_s depression, a negative correlation was found between measurement time (hr) and g_s ($F = 12.1$, $p < 0.001$, $df = 1$). The coefficient of measurement time (\pm standard error) was $-3.27 (\pm 0.94)$, which indicates that the effect of measurement time on g_s was estimated as $-3.27 \text{ mmol m}^{-2} \text{ s}^{-1}$ per one-hour measurement time delay. Regression tree analysis indicated the first splitting criteria for 28 leaves (67% of total leaves measured), whereas no clear trend was observed for the remaining 14 leaves. Higher g_s values were observed in earlier measurement time zones for all the 28 leaves. The first splitting criteria of measurement time averaged (\pm standard error) 1329 hrs (± 47).

Intact leaf observation

Leaves of various ages were found on the crown of *D. costatus*, indicative of intermittent and multiple leaf flushings per year and long leaf longevity (Fig. 4). Branches could be distinguished as several sequential clusters with

distinctive gaps and clear differences between new end sections and senescent base sections. Each cluster was composed of a twig and a series of leaves that flushed over short periods.

The total number of leaves on the branches studied increased during the early dry season due to the temporal overlap between new and old leaves, and then decreased at a steady rate due to the shedding of old leaves (Fig. 5). This trend was in agreement with litter trap measurements. The amount of fallen leaves of *D. costatus* in litter traps peaked from late November to early December (Fig. 6a), and the amount of leaf bud scales also peaked during late November (Fig. 6b). A significant proportion of the leaves appeared to have long longevity (sometimes approximately two years). Tree I displayed leaf-flushing phenology slightly earlier than Tree II, with peaks occurring in November and December, respectively. In both study trees, leaf flushing was dominant in the early dry season. Leaf flushing in the late dry season and early wet season was more frequent on Tree I than Tree II (Fig. 5). During the measurement period, semi-mature leaves were dominant in December, and many leaves were unfolded between November and early December (i.e. the 2009 early dry season cluster). In early March, when the final measurements were taken, bursting buds were also observed on the branches, suggesting that the next cluster would appear in late March or early April.

When a new leaf opened (i.e. the date of the first measurement), the leaf was 84–86% of its full size. Leaves

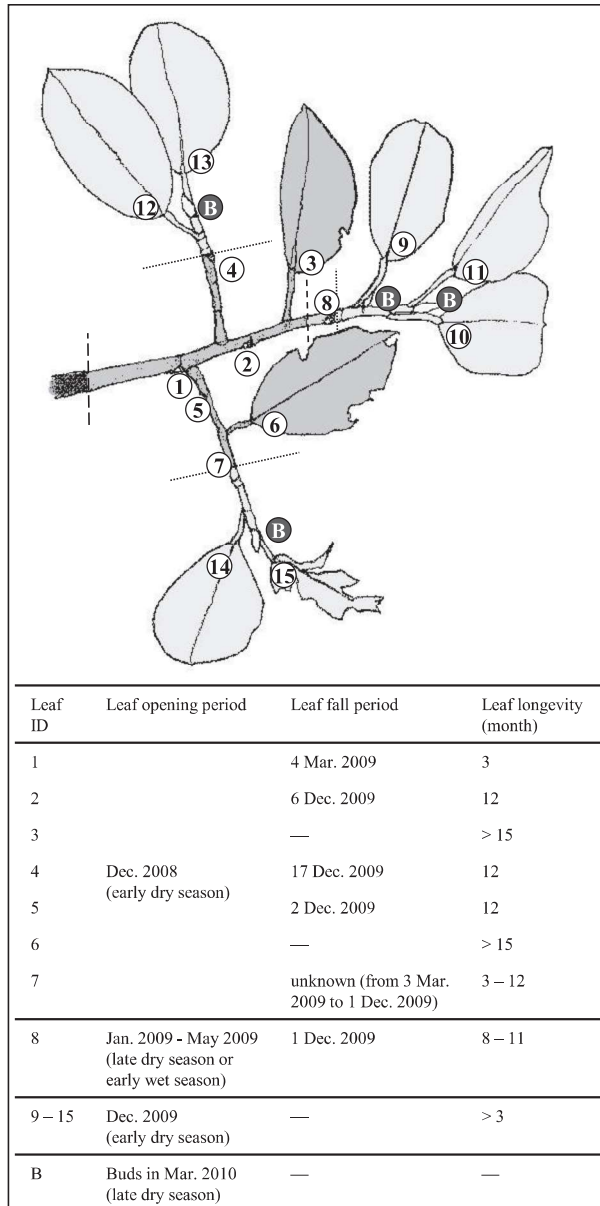


Fig. 4 Schematic diagram of a branch cluster of *D. costatus*. Branches could be divided into several clusters with distinctive gaps and differences between the new end sections and senescent base sections. Each cluster was composed of a twig and a series of leaves that flushed during a short period. Numbers in circles indicate leaves or leaf scars. The last observation of the branch was on 4 March 2010.

unfolded rapidly, grew to 88–92% of their full size five days after opening, and reached 97–100% of their full size 8–9 days after opening. The expansion of leaf size corresponded well with leaf maturation stage as indicated by the leaf colour observations. When the leaves unfolded to their full size (~8 days after opening), these were consid-

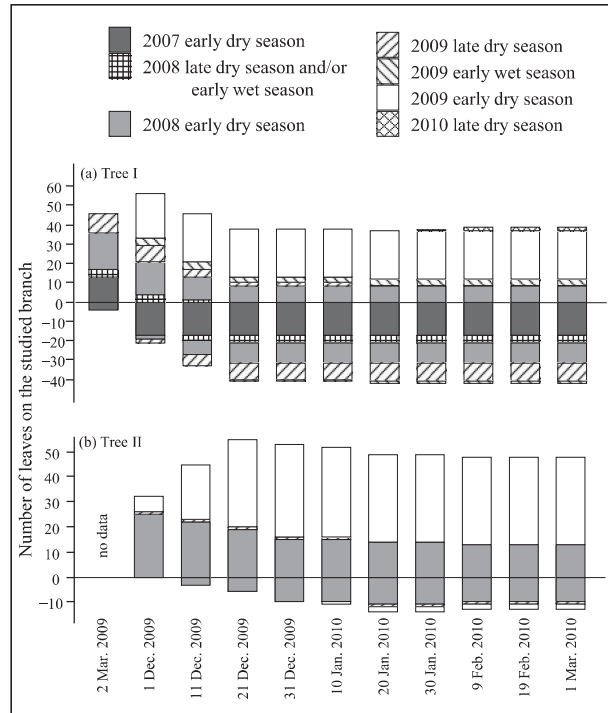


Fig. 5 Seasonal changes in leaf numbers for branches studied. (a) Tree I, (b) Tree II. The dates on the x axis indicate the observations of leaves on the branches. Positive and negative values on the y axis indicate the number of intact and shed leaves, respectively. The shadings of columns indicate the flushing period of each leaf estimated by branch clusters (see Fig. 4). Early dry season, November–December; late dry season, March–April; early wet season, May–June.

ered to have proceeded from young to semi-mature, which corresponded with the start of the rapid increase in conductance. The age at which leaves proceeded from the semi-mature to mature stage varied. The first leaf of a cluster was often small, rapidly reached the mature stage (e.g., 35 days), and often fell earlier (e.g., leaves of the 2009 early dry season cluster on Tree II, Fig. 5b). In contrast, leaves of second order or later were larger, proceeded slowly to the mature stage (> 60 day), and had greater longevity.

Discussion

Leaf-age-related stomatal conductance pattern

We found that leaf age influenced the g_s of *D. costatus* during the dry season more than air temperature, humidity, or measurement time during the morning, even though the data included cloudy conditions. Leaf-age-related g_s displayed an overall pattern of a steep

initial rise followed almost immediately by a gradual decline (Figs 2–3). This pattern is typically found in g_s at the maximum photosynthetic rate of leaves with a long lifespan (Čatský *et al.*, 1985), such as evergreen broad-leaved trees in warm-temperate forests (e.g., *Castanopsis sieboldii*: Miyazawa & Terashima, 2001), in a Mediterranean climate (Escudero & Mediavilla, 2003) and in Xishuangbanna, China, the northern limit of tropical rain forest in Southeast Asia (Cai *et al.*, 2005).

The leaf maximum photosynthetic rate in *D. costatus* may reach a maximum around peak g_s because many tropical tree species, including dipterocarp trees, generally show a strong correlation between maximum photosynthetic rate and g_s (Ishida *et al.*, 2006; Kenzo *et al.*, 2012, 2015, 2016; Inoue *et al.*, 2015). Patterns related to leaf age are also found in the photosynthesis rate of the leaves of evergreen plants (Šesták *et al.*, 1985) and deciduous broad-leaved trees in temperate forests (Koike, 1990; Pallardy, 2010). In seasonally dry tropical forests, a gradual decline in photosynthetic capacity related to leaf age has been found in upper canopy leaves in Panama, although a steep initial rise was not detected due to the long measurement span and the fact that measurements were only performed on fully expanded leaves (Kitajima *et al.*, 1997; Kitajima *et al.*, 2002).

The steep initial rise and peak we observed in g_s (17 days after unfolding: Fig. 2) is in striking contrast to deciduous dipterocarps in a dry deciduous forest located in Kratie Province of Cambodia (Kenzo *et al.*, 2016). Here, the g_s of immature leaves that flushed in the mid-dry season was one-sixth that of mature leaves in the rainy season (6–7 months after emergence) and one-third that of mature leaves in the early dry season (~9 months after emergence) in both *D. tuberculatus* (Khlong in Khmer) and *Shorea obtusa* (Phchek in Khmer). One possible reason for the difference in g_s of immature leaves between *D. costatus* and these deciduous dipterocarps is the difference in leaf flushing phenology and edaphic conditions related to soil water deficits. In most tree species in the dry deciduous forest in Kratie Province, except a glabrous *Terminalia alata*, leaves flush in the mid- to late dry season (Iida *et al.*, 2016; Ito *et al.*, 2017). Low g_s in immature leaves of deciduous dipterocarps has been suggested as an adaptation to the severe dry conditions in the mid to late dry season (Kenzo *et al.*, 2016), given the limited soil water available due to the shallow soil (Toriyama *et al.*, 2010). In contrast, the deep root systems of lowland seasonally dry evergreen forests in Cambodia have access to groundwater (Araki & Ito, 2009; Toriyama *et al.*, 2011), as do those in a Brazilian seasonally dry evergreen forests (Xiao *et al.*, 2005). The groundwater supply may mitigate the extent of drought caused by low seasonal

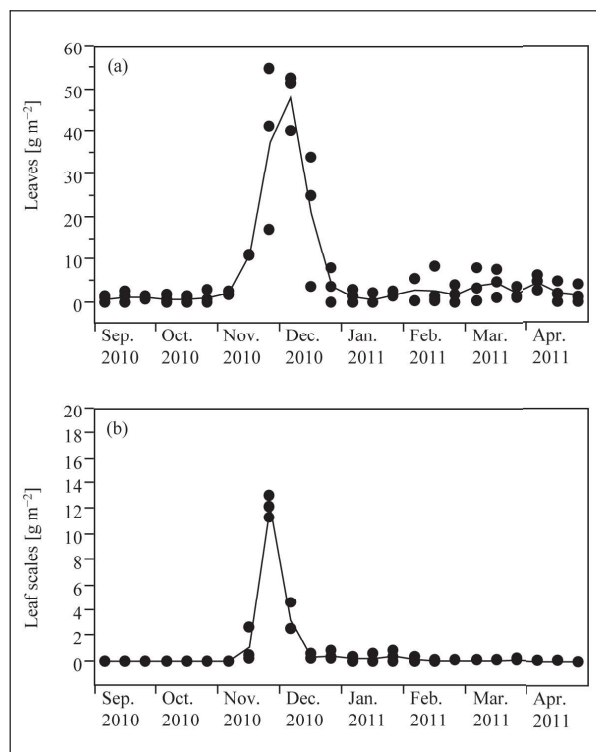


Fig. 6 Leaf and leaf bud scale shedding phenology of *D. costatus* in a Cambodian lowland evergreen forest. (a) Fallen leaves, (b) leaf bud scales. The lines indicate the average of three litter traps.

precipitation. Significantly lower g_s in a deciduous dipterocarp during the mid dry season is indicative of a strong suppression of transpiration (Kenzo *et al.*, 2016). After peaking, g_s gradually declined over two months, and then remained at around 60% of the maximum until a few days before leaf fall (Fig. 3). The g_s maintained by *D. costatus* may be indicative of the extent of leaf transpiration even during the dry season in the studied forest. To explicitly test the effects of drought stress on g_s and transpiration, future studies should measure leaf water potential and soil moisture conditions in addition to the factors we investigated.

Temporal variation in stomatal conductance associated with leaf phenology

The relatively high g_s we observed in different periods for Trees I and II (Fig. 1) was associated with semi-mature leaves flushed in late November (Tree I) or early December (Tree II), as the high g_s occurred in leaves 14–30 days after unfolding (phase iv: Fig. 2, Table 1). The difference between Trees I and II in the changing pattern in g_s during dry season can be explained by differences

in leaf-flushing phenology (Fig. 5). In addition, we observed bursting buds (Fig. 4) and flushing leaves (Tree I: Fig. 5) at the end of February, which were indicative of two peaks of leaf flushing in *D. costatus*. The g_s of newly flushed leaves during the late dry season might have increased around late March to early April if there were less water stress. Deep root systems of lowland seasonally dry evergreen forests in Cambodia have access to significant groundwater (Araki & Ito 2009; Toriyama *et al.*, 2011). Such groundwater supply may mitigate the extent of water stress during the late dry season.

When scaling between single leaf g_s measurements and tree-level transpiration, the total leaf area within a tree canopy could be a decisive factor because g_s is a measure of the relationship of stomatal opening to diffusion per unit area. The tree-level leaf area of *D. costatus* decreased minimally due to leaf exchange because the total number of leaves per branch remained unchanged (Fig. 5) and leaves expanded rapidly to full size before the peak in g_s . Therefore, the relatively constant leaf area of the crown likely has minimal influence on seasonal variation in transpiration. Given the leaf age related g_s , constant leaf area in the tree canopy, and no restriction from water stress, the dynamic changes in the proportion of young and old leaves within a tree canopy could be the decisive factor influencing tree-level transpiration in the dry season, as suggested by Iida *et al.* (2013). In other words, tree-level transpiration, normalised by ambient air factors, decreases synchronously with leaf exchange, then increases as the g_s of flushing leaves peaks, and then gradually decreases. We expect that the tree-level g_s of *D. costatus* becomes high at 2–4 weeks after the leaf flushing peak based on the high g_s in leaves 14–30 days after unfolding. However, because the number of trees analysed in our study was low ($n = 2$), the generality of our findings should be verified using a larger number of samples in future.

Ambient factors related to tree-scale transpiration

Tree-level transpiration often depends on the physical characteristics of the atmospheric environment, including solar radiation, vapour pressure deficit, air temperature and wind speed (Granier & Bréda, 1996; Granier *et al.*, 2000; Pallardy, 2010). Aside for air temperature and humidity which we measured using simple methods, the most important limitation of our study lies in the fact that we could not evaluate the relative importance of these various ambient factors on g_s , compared with the patterns of g_s related to leaf age. Further research is required to determine the strength of environmental controls on g_s , including its daily variation.

Conclusions

Our study indicates that leaf-flushing phenology, as the governing driver of leaf age structure of the tree crown, could be a decisive factor in tree transpiration of *D. costatus* during the dry season. Phenology-driven physiological activity has been reported at a stand scale in a Cambodian deciduous dipterocarp forest (Iida *et al.*, 2016) and in seasonally dry eastern Amazon rainforests (Huete *et al.*, 2006; Hutrya *et al.*, 2007), where leaf flushing during the dry season is associated with an increase in transpiration. Moreover, aggregate canopy phenology, not the seasonality of climate drivers, is the primary cause of photosynthetic seasonality (Wu *et al.*, 2016, 2017). Phenology varies within communities, and the phenology of individuals has a key role in determining how ecosystems are structured and function (Cleland *et al.*, 2007). Additional research on stand-scale leaf phenology in the seasonally tropical evergreen forest is required to determine the dynamic changes in leaf age structure in the crown layers, which could improve our understanding of the eco-hydrological processes of Cambodian forest ecosystems.

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