

Bimodal leaf fall in a lowland dry evergreen forest in Cambodia

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វដ្តជីវិតស្លឹកគឺជាសមាសភាគដ៏សារៈសំខាន់មួយនៃស្ថានប្រព័ន្ធប្រៃឈើ ដោយវាជាអ្នកកំណត់នូវបរិមាណ និងសកម្មភាពសីរៈនៃស្លឹក(សរីរាង្គធ្វើស្មើសំយោគ)។ យើងបានធ្វើការវាយតម្លៃលើវដ្តជីវិត និងលាស់ថ្មីនៃស្លឹកតាមប្រៃស្រោងតំបន់ទំនាបស្ងួតខេត្តកំពង់ធំនៃប្រទេសកម្ពុជា។ ការសិក្សាលើស្លឹកឈើដែលជ្រុះបានបង្ហាញថា រុក្ខជាតិជម្រុះស្លឹកច្រើនបំផុតនៅអំឡុងដើមរដូវប្រាំងចំពោះពពួកអំបូរឈើទាល(*Dipterocarpus costatus* និង *Anisoptera costata*) ប៉ុន្តែនៅក្នុងអំឡុងចុងរដូវប្រាំងវិញសម្រាប់ប្រភេទដើមឈើដែលជ្រុះតាមគម្របព្រៃកម្ពស់មធ្យម និងទាប។ តាមការសង្កេតលើវដ្តជីវិតនៃពន្លក និងគម្របព្រៃបានបង្ហាញថា ការជម្រុះស្លឹកបានកើតឡើងនាដើមរដូវប្រាំងសម្រាប់អំបូរឈើទាលដែលជាគម្របព្រៃខ្ពស់ៗ។ ម៉ាស់ស្លឹក(កំណត់តាមអុបទិកជាសន្ទស្សន៍ផ្ទៃស្លឹក) បានថយចុះតិចតួច ពីរដងគឺ ម្តងនៅដើមរដូវប្រាំង និងម្តងទៀតនៅចុងរដូវប្រាំង។ លទ្ធផលនេះបានបង្ហាញថា ការជម្រុះស្លឹកនៃប្រភេទឈើដែលជ្រុះតាមគម្របព្រៃកម្ពស់មធ្យម និងទាបកើតមានឡើងក្នុងដំណាក់កាលចុងក្រោយនៃចុងរដូវប្រាំង។ យើងស្នើឲ្យមានការពន្យល់បែបសម្មតិកម្មពីសារៈប្រយោជន៍អេកូឡូស៊ីនៃលំនាំវដ្តជីវិតដែលខុសប្លែកនេះ។ ព្រឹត្តិការណ៍ជម្រុះស្លឹកមិនធម្មតានេះក៏ប្រទះឃើញផងដែរ នៅពេលដែលរដូវប្រាំងមានរយៈពេលវែង។ ការវិចលនាព្រៃរួមមាន ការដកហូតព្រៃអំបូរឈើទាលខ្ពស់ៗ កំពុងបន្តកើតមានឡើងនៅក្នុងប្រៃស្រោងតំបន់ទំនាបស្ងួត។ ទាំងនេះ ប្រហែលជាអាចធ្វើឲ្យមានការផ្លាស់ប្តូរយ៉ាងសំខាន់ លើស្ថានប្រព័ន្ធប្រៃស្រោងតំបន់ទំនាបស្ងួត តាមរយៈការផ្លាស់ប្តូរវដ្ត និងម៉ាស់ស្លឹករុក្ខជាតិ។

Abstract

Leaf phenology is an important component of forest ecosystems as it determines the quantity and physiological activity of leaves, the organs that carry out photosynthesis. We assessed the phenology of leaf shedding and flushing in a lowland dry evergreen forest in Kampong Thom Province, Cambodia. Leaf litter surveys indicated that the peak of leaf shedding occurred during the early dry season for tall dipterocarps (*Dipterocarpus costatus* and *Anisoptera costata*), but during the late dry season for mid- to low-canopy tree species. Bud scale drop phenology and canopy observations suggested that flushing occurred early in the dry season in upper-canopy dipterocarps. Stand-scale leaf mass, measured

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optically as leaf area index, showed two periods of slight, but significant reduction: one in the early dry season and the other in the late dry season. This indicates that flushing in low- and mid-canopy species occurred in the last phase of the dry season at the latest. We propose hypothetical explanations for the ecological advantages of these discrete phenological patterns. An anomalous leaf shedding event was also found in association with a lengthy monsoon break. Forest degradation, including the removal of tall dipterocarp trees, is ongoing in lowland dry evergreen forests. This may lead to substantial changes in lowland dry evergreen forest ecosystems by altering stand-scale leaf phenology and leaf mass.

Keywords *Anisoptera costata*, *Dipterocarpus costatus*, ENSO, forest degradation, leaf area index, leaf phenology, lowland dry evergreen forest

Introduction

Evergreen forests occupied 15.8 % of the land area in Cambodia as of 2016 (Fig. 1; Ministry of Environment, 2018). Evergreen forests in Cambodia are classified into four subtypes, based on lowland or sub-montane location and moist or dry climate, using the classification system of the *Terrestrial Vegetation and Land-use Patterns* map published by the Ministry of Environment (MoE) in 2007 (cited in Brun, 2013). This subdivision is based on elevation, with 650 m used as the boundary between lowland and sub-montane vegetation types, as well as other bioclimatic criteria that differentiate the humid coastal ranges (moist, annual precipitation ca. >2000 mm), lower-humidity inland forests (dry) and hinterlands (Brun, 2013) (Fig. 2). Lowland dry evergreen forest, one of the four evergreen forest subtypes, is referred to as dry evergreen forest in the classification system of the Cambodian Forestry Administration (FA, 2011). Lowland dry evergreen forests in Cambodia typically develop on sandy alluvial plains, where soils are deep. Despite the seasonal tropical climate in which little rain falls for half the year (Kabeya *et al.*, 2007), plants in lowland dry evergreen forests have access to abundant groundwater (Araki *et al.*, 2008; Ohnuki *et al.*, 2008b; Toriyama *et al.*, 2011) via their deep root systems (Tanaka *et al.*, 2004; Ohnuki *et al.*, 2008a). This facilitates year-round foliage retention, resulting in evergreen forests. Such habitats occur to the north of the Tonlé Sap flood basin and west of the Mekong River (Fig. 3; Rundel, 1999). These areas are referred to as “Semi-Evergreen Forest on Alluvial Plains” in Rundel’s (1999) classification and details of the forest classification systems used in Cambodia have been described by Brun (2013).

Lowland dry evergreen forests comprise multi-story forests of trees that maintain their leaves throughout the year, as is typical for evergreen forests (FA, 2011). Despite relatively constant leaf mass (Richardson *et al.*, 2013), the physiological activity of the canopy in evergreen forests may not be constant. This is because physiological activity in leaves typically changes during leaf maturation

(Pallardy, 2010), as demonstrated by a tall dipterocarp in a lowland dry evergreen forest (Ito *et al.*, 2018). In other words, the leaf age structure of the canopy can govern physiological activities in the canopy (Field, 1987; Brodribb & Holbrook, 2005).

Leaf phenology refers to the recurring temporal aspects of natural phenomena associated with leaves, such as leaf flush, maturation, senescence and defoliation. As a result, it may be important for understanding the seasonality of eco-hydrological processes in tropical dry forests (Hutyra *et al.*, 2007; Wu *et al.*, 2016, 2017). Leaf phenology may vary according to community composition because dynamic changes in leaf age structure within the canopy can arise from the combined phenology of individual tree species at the stand scale. Understanding stand-scale leaf phenology may provide insight into ecosystem structure and function in forest systems (Cleland *et al.*, 2007). As a consequence, clarifying stand-scale leaf phenology in the lowland dry evergreen forests of Cambodia may enhance understanding of forest ecosystems nationally and inform conservation planning for these.

Thus far, leaf phenology in Cambodian forests has mainly been studied in the context of remote sensing and land/forest classification. Clear differences in phenology have been observed between evergreen and deciduous forests during the dry season, whereby deciduous forests showed marked and spatially-uniform losses and subsequent gains in new leaf area, whereas evergreen forests exhibited less pronounced changes (e.g., Ito *et al.*, 2008). Almost all remote sensing studies of the phenology of evergreen forests have assumed either negligible intra-annual variability (e.g., Langner *et al.*, 2014) or unimodal seasonal changes, i.e., that leaf flushing occurs once a year (Venkatappa *et al.*, 2019; Scheiter *et al.*, 2020). An exception is the study of Ito *et al.* (2008), who used satellite imagery to demonstrate that the leaf phenology of Cambodian evergreen forests is spatially and temporally heterogeneous. Although Ito *et al.* (2008) found that approximately 30% of evergreen forests shed a detectable

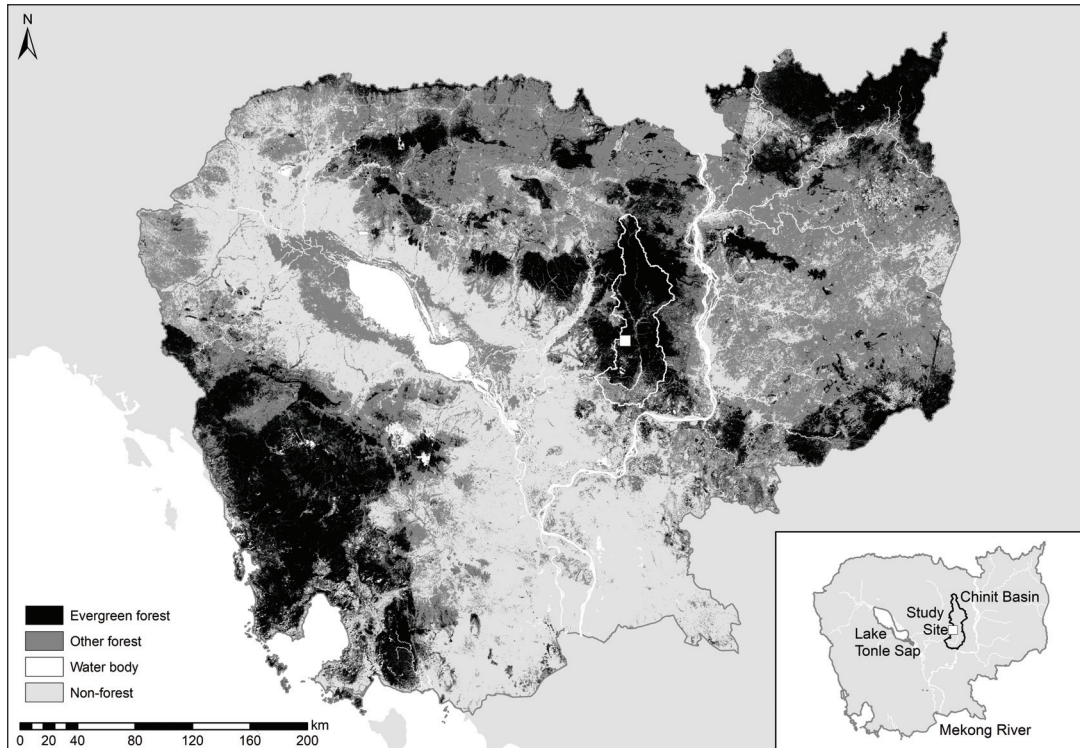


Fig. 1 Distribution of evergreen forests in Cambodia. Classification based on FA (2011). The open square represents the study site and the white line indicates the basin of the Chinit River.

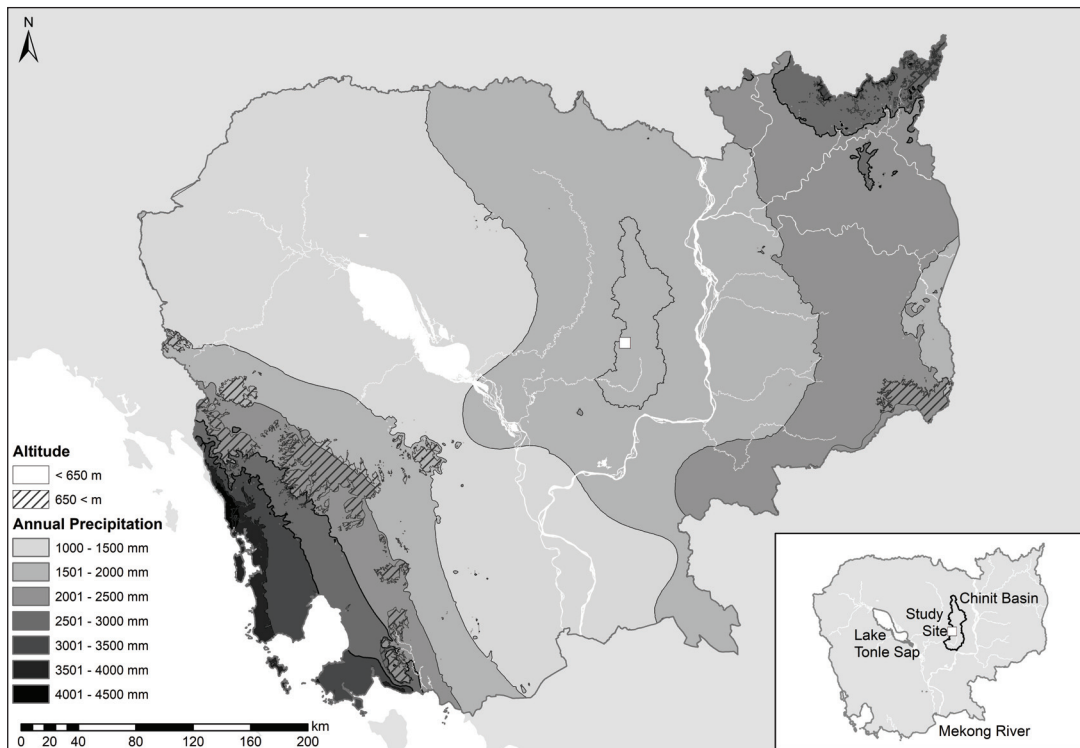


Fig. 2 Annual precipitation and elevation classes in Cambodia. Precipitation data obtained from the WorldClim global climate and weather database (<https://www.worldclim.org/data/index.html>). The open square represents the study site and the black line indicates the basin of the Chinit River.

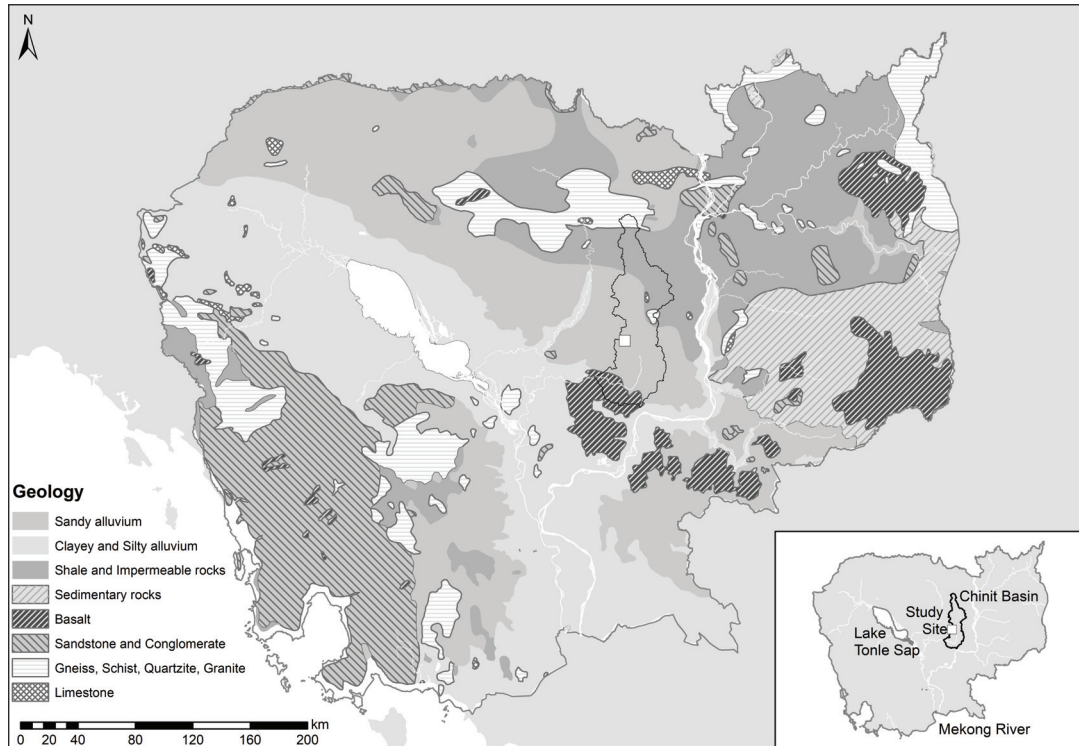


Fig. 3 Geology of Cambodia. Data provided by the Forestry Administration (Cambodia). The open square represents the study site and the black line indicates the basin of the Chinit River.

volume of leaves twice during a single dry season (i.e., early and late in the dry season), they did not explicitly link this heterogeneity to the characteristics of the sites or species present in each forest. Species-specific leaf phenological characteristics have been widely reported for species in the Dipterocarpaceae (reviewed by Ghazoul, 2016). This family includes many of the major component species of Cambodian forests (FA & Cambodia Tree Seed Project, 2003), although available reports do not include dipterocarp species that occur in lowland dry evergreen forests. To the best of our knowledge, no reports based on empirical field data exist on the stand-scale leaf phenology of lowland dry evergreen forests in Cambodia.

The objective of our study was to investigate leaf phenology in a lowland dry evergreen forest in central Cambodia. We measured leaf and bud-scale fall using litter traps, directly observed leaf flush and optically measured seasonal changes in leaf mass. We also consider hypothetical explanations for the ecological functions of the phenological patterns observed. Finally, we consider how extreme climate events and forest degradation may influence leaf phenology and related ecosystem processes.

Methods

Study site

The study site was located in Kampong Thom Province (12°76'N, 105°48'E; Figs 1–3), within the Stung Chinit River catchment where the Stung Chinit River flows through the central plains of Cambodia into Tonlé Sap Lake. While elevations within the Chinit catchment range from 19 to 653 m, 90% of the drainage area is below 140 m (Kabeya *et al.*, 2021). The study site was situated in a flat, gently rolling alluvial plain 80–100 m above sea level (a.s.l.), on sandy alluvium with shale distributed in the upstream area (Fig. 3). The forest at the study site was classified as lowland dry evergreen forest in the *Terrestrial Vegetation and Land-use Patterns* map published by MoE in 2007 (cited in Brun, 2013). The study forest had a basal area of 42.3 m² ha⁻¹ and a tree density of 1,817 trees ha⁻¹ (diameter at breast height [DBH] > 5 cm), based on a census conducted within a 30 × 80 m permanent sample plot in 2011. Two tall dipterocarp species, *Dipterocarpus costatus* C.F. Gaertn and *Anisoptera costata* Korth., dominated the upper canopy layer of the forest (Pooma, 2002; Tani *et al.*, 2007) and details of the plant species composition of the study area are provided in Annex 1.

Seasonal and interannual variations in precipitation

Cambodia has a subtropical climate driven by two monsoon seasons: the cool, dry northeastern monsoon from November to March, and the humid southwestern monsoon from May to October (Kabeya *et al.*, 2021). The seasonal tropical climate of our study area can generally be divided into three seasons: an early dry season with little rain (ca. 50 mm) and decreasing air temperature (from 25.5 to 24.5 °C), a late dry season with little rain (ca. 100 mm, pre-monsoon rain, Kabeya *et al.*, 2007) and increasing air temperature (from 25 to 28 °C), and a rainy season providing >90 % of the annual precipitation, with moderate air temperature (approximately 26°C) (Kabeya *et al.*, 2008; Chann *et al.*, 2011). We defined the timing of these three seasons as follows: early dry season (late October–late December), late dry season (early January–mid May), and rainy season (late May–mid October).

The monsoon exhibits substantial interannual variability which is closely related to El Niño/Southern Oscillation (ENSO) (Räsänen & Kumm, 2013). In Southeast Asia and Oceania, the El Niño phase tends to result in high temperatures and water shortages, whereas substantial rainfall tends to occur during the La Niña phase. According to Kabeya *et al.* (2021) for 2007–2016 and our data for 2000–2006 and 2017–2019 (classified using the same methods), an El Niño phase occurred in the central lowlands of Cambodia during 2005, 2010 and 2015–2016, whereas a La Niña phase occurred during 2000–2001, 2006, 2008–2009 and 2011–2012 and a neutral phase during 2002–2004, 2007, 2013–2014 and 2017–2019 (El Niño and La Niña phases were distinguished based on Southern Oscillation Index values of -10 and +10, respectively). Based on observations in 2007–2016, the annual rainfall of neutral, La Niña, and El Niño years near the study site was approximately 1,600 mm, >1,800 mm and 1,100–1,200 mm, respectively (Kabeya *et al.*, 2021).

Kabeya *et al.* (2021) reported the mean onset and withdrawal dates of the rainy season in 2007–2016 as 26 May (± 18 days) and 25 October (± 13 days), respectively. These were based on Matsumoto (1997) in defining “the onset (withdrawal) of the summer rainy season is that of the first (last) pentad (5-days) when the mean pentad precipitation exceeds annual mean pentad precipitation [$P_m = (\text{Annual precipitation}) / 73$] in at least three consecutive pentads, following (before being) lower than it in more than three consecutive pentads. The middle date of this defined pentad is considered the onset or withdrawal date”. Onset and withdrawal dates for 2004–2006 were obtained by Kabeya *et al.* (unpublished data). The summer rainy season is sometimes divided into two rainy seasons based on breaks similar to short dry seasons, known as monsoon breaks (Matsumoto, 1997). Monsoon

breaks were defined as periods when pentad precipitation was lower than P_m for more than three consecutive pentads (Kabeya *et al.*, 2021). A relationship between monsoon breaks and ENSO phase has been suggested (Kabeya *et al.*, 2021). From 2007 to 2016, monsoon breaks were observed in 2008, 2009, 2012 and 2016 at the study site (e.g., four out of 10 years, with three of the four year being in the La Niña phase) (Kabeya *et al.*, 2021). Breaks typically began around the end of July or early August and had a mean duration of 36 days (Kabeya *et al.*, 2021).

Seasonal variations in groundwater level and solar radiation

Soils at the study site are generally sandy and classified as Haplic Acrisols (Alumic, Profondic) in the *World Reference Base for Soil Resources* (Toriyama *et al.*, 2007, 2008). The depth of the groundwater table varies substantially due to the gently undulating nature of the overlying topography. The depth of the groundwater table and corresponding rooting depth are ca. -10 m at the end of the dry season (Araki *et al.*, 2008; Ohnuki *et al.*, 2008a, 2008b) and the soils dry rapidly in December (Araki *et al.*, 2008). Interannual variations in monthly mean groundwater levels are available for 2004–2007 (Fig. 4a, revised from Chann *et al.*, 2011).

Meteorological data have been collected at the site using a 60 m tall observation tower since 2004, although data gaps have resulted from mechanical breakdowns caused by lightning and other factors (Nobuhiro *et al.*, 2009; Chann *et al.*, 2011). Seasonal variations in solar radiation are relatively minor, despite the presence of distinct rainy and dry seasons. This is because rainfall is concentrated in the evening (Nobuhiro *et al.*, 2010). Seasonal differences in solar radiation in the study area were typically < 10%, with the exception of the last two months of the rainy season, when the difference was 20% (Fig. 4b, revised from Chann *et al.*, 2011).

Leaf phenology

We investigated stand-scale leaf phenology using the following three methods.

1. *Litter traps*—Litter collection was used to assess leaf shedding phenology from September 2004 to January 2015. This period was divided into three phases in data analyses. During Phase I (September 2004–February 2007), a 1 m² frame was employed for litter collection in the study forest. During Phase II (February 2007–February 2009), a second 1 m² frame was added for litter collection. During Phase III (March 2009–January 2015), four litter net traps with a total area of 2 m² were employed within a 50 x 100 m forest stand.

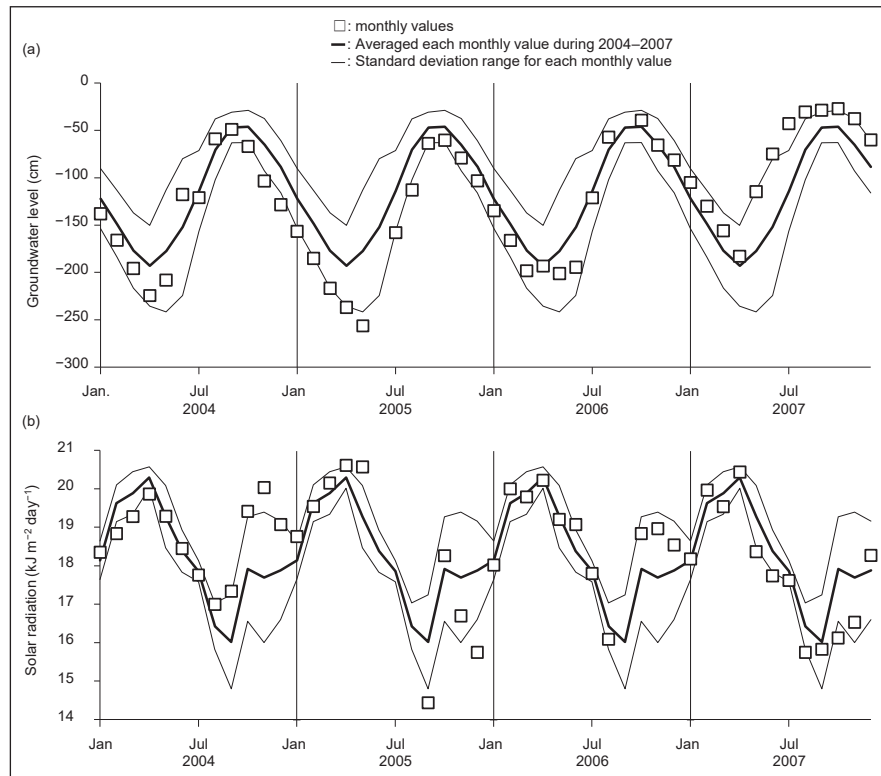


Fig. 4 Variations in monthly mean groundwater level (a) and monthly mean daily solar radiation (b) at the study site in 2004–2007. Data were unavailable for June 2005 and September 2006 for groundwater level and for June–August 2005 and September 2006 for solar radiation.

Litter was generally collected three times per month. However, longer collection intervals occurred on three occasions during the early stages of Phase I (namely a 47-day collection interval from 24 September 2004–10 November 2004, a 20-day collection interval from 30 December 2004–19 January 2005 and a 40-day collection interval from 19 January 2005–28 February 2005) (Fig. 5).

All litter collected was divided according to species and the oven-dried weights for each species were recorded. We report the weights for tall dipterocarps (*D. costatus* ['Chhoeuteal Bankouy' in Khmer] and *A. costata* ['Phdiek']), mid-layer dipterocarps (*Vatica odorata* (Griff.) Symington ['Chromas'] and *Hopea recopei* Pierre ex Laness. ['Chromas Trang']), and other mid- to understory tree species. Litter collected from trees in the middle to understory layers included an abundance of material from *Diospyros* spp. and *Syzygium* spp. These layers also included some mid-sized to tall tree species such as *Lophopetalum duperreanum* Pierre and *Sindora siamensis* Teysm. ex Miq. and further information on these species is given in Annex 1. Some shrub (e.g., *Psydrax pergracilis* (Bourd.) Ridsdale) and vine (e.g., several species of *Uvaria* (Annonaceae), *Willughbeia edulis* Roxb. (Apoc-

ynaceae), and *Peltophorum dasyrhachis* (Miq.) Kurz (Fabaceae)) species were also represented in the litter. We also counted the number of tree species producing fallen leaves during each collection interval. The amount of fallen leaves was corrected for trap area (g m^{-2}), but not for collection interval, except for the longer collection intervals previously mentioned.

Because *Dipterocarpus* species produce a distinctive bud scale indicative of leaf flushing, the amount of bud scales collected by litter traps was used to estimate the leaf flushing phenology of *D. costatus*. These data, collected from October 2006 to February 2007 (during Phase I), were used for reference only due to errors made by local collectors whereby uncollected scales were carried over to later collection intervals.

2. *Direct crown observations*—Crown observations were conducted using binoculars to confirm the leaf flush phenology of *D. costatus* and *A. costata*. Observations were made from 29 September 2004 to 19 September 2005 and from 30 October 2006 to 30 June 2012. Observations were made three times per month, generally on the 10th, 20th and 30th, but sometimes varied by 1–2 days. Three

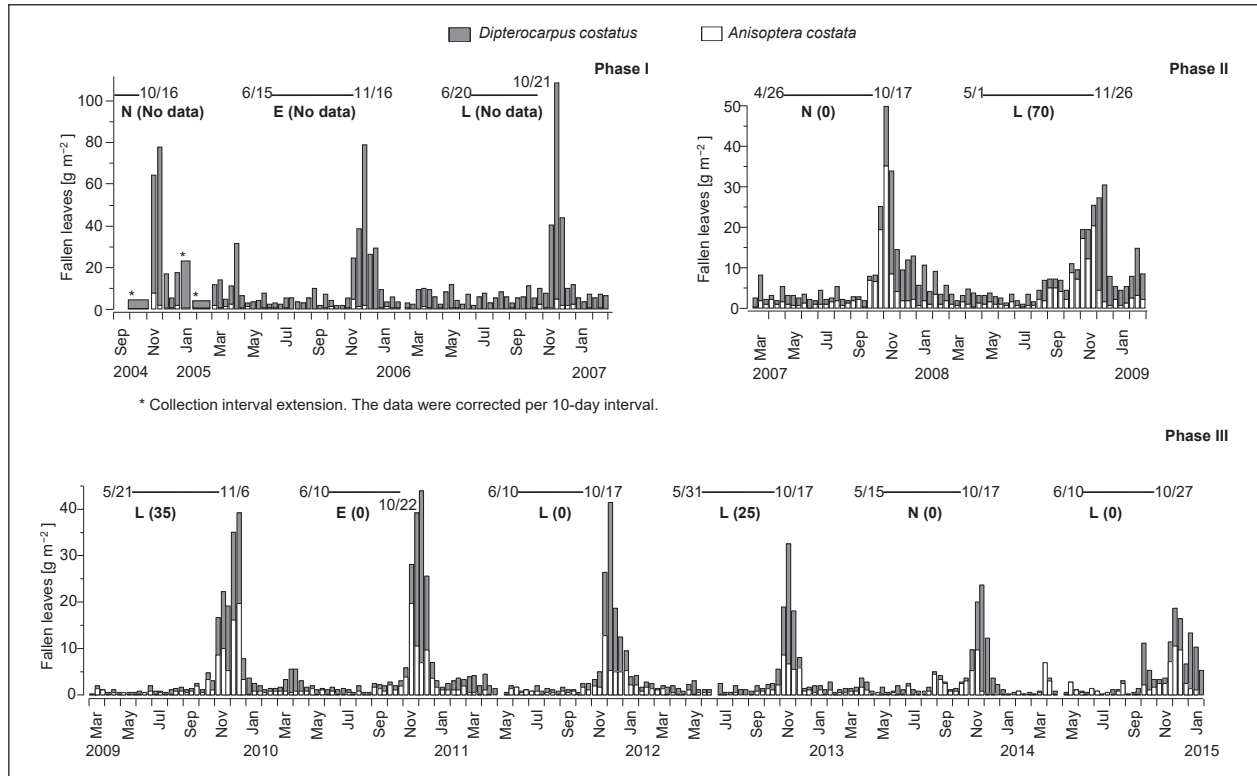


Fig. 5 Leaf shedding phenology of tall dipterocarps in a Cambodian lowland evergreen forest. Horizontal lines indicate the duration of the rainy season, with onset and withdrawal dates. Bold capital letters and numbers in parentheses refer to the El Niño/La Niña phase, and the length (in days) of the monsoon break (0 if it did not occur): E, El Niño; L, La Niña; N, neutral. No data are shown for the 2004–2006 monsoon break. Dates were derived from Kabeya *et al.* (2021) and Kabeya *et al.* (unpublished data). Asterisks (*) in Phase I indicate notes regarding collection interval extension (see text for details). The data for the three phases were corrected for 10-day intervals.

individuals of each tree species were observed and the presence or absence of leaves in the canopy was recorded. We also recorded whether pale green leaves were present in the canopy, which were assumed to be freshly developed. The recording threshold was set at 10% or more of total leaves in the canopy being newly flushed.

3. *Optical measurement of leaf area index*—Seasonal changes in leaf area at the stand scale were estimated using non-destructive optical methods (plant canopy analyser, LAI-2000, Li-Cor, Nebraska, USA) to determine the leaf area index (LAI, $m^2 m^{-2}$). The LAI was estimated at ten points, which produced different measurements. When using the plant canopy analyser, the sensor’s azimuthal field of view was limited to 90°. These measurements were typically made once a month from March 2003 to May 2012, although measurement interval varied. In addition, we also estimated LAI on the basis of hemispherical photographs (Tani *et al.*, 2011). These were taken on the same day and at the same locations as the

plant canopy analyser measurements, except in 2008 (due to equipment loss).

Leaf mass per area

The leaf mass per area (LMA) of *D. costatus* was measured from fallen leaves collected in litter traps for intervals with at least ten leaves from August 2005 to July 2006. Five constant-area (30 mm²) discs were punched out from a collected leaf, oven-dried and individually weighed. Shrinkage of drying fallen leaves relative to fresh leaves was neglected. In total, 585 leaves collected on 14 days were measured.

Statistical analysis

Seasonal changes in leaf litter weights in four categories (*D. costatus*, *A. costata*, mid-layered dipterocarps, and other mid- to understory species) were assessed using a generalized linear model (GLM) framework. The GLM incorporated collection date as a categorical explana-

tory variable (10 day periods, 36 periods per year). The amounts of litter per category were influenced by trap location and individual trees. Importantly, numerical data could not be directly compared across collection phases. For this reason, we incorporated collection phase (i.e., PHASE I, II, or III) into the GLM as a categorical random effect. We excluded data up to February 2005 (Phase I) from the analysis due to the extended collection intervals. The hypothesis that each parameter had a value of zero was evaluated using *t*-tests. The GLM estimated the least square means (LSMs) of litter weights in four categories for each collection date. LSMs represent the predicted values across the various collection dates when other model factors were held constant at the average coefficient over all levels for each factor. The amount of litter that fell during each of three periods, i.e., the early dry season (late October–late December), the late dry season (early January–mid May), and the rainy season (late May–mid October), was estimated by summing the predicted LSMs from each collection date. The percentage of leaf fall occurring in each period was calculated based on the total annual leaf fall.

LAI data collected between March 2003 and June 2004 (totalling 16 measurement periods) using the plant canopy analyser were assessed to determine seasonal changes. We used a GLM framework incorporating measurement date as a categorical explanatory variable and measurement point ($n = 10$) as a random effect. Significant differences among measurement dates were evaluated using post-hoc Tukey-Kramer HSD tests.

We observed occasional fluctuations in the plant canopy analyser data collected after July 2004. These may have been caused by the deterioration of the sensors during the measurement period, but this cannot be confirmed. The data for the entire period, as measured using the two methods (plant canopy analyser and hemispherical photographs), were subjected to the following statistical analyses to detect seasonal trends in LAI while mitigating the effects of instrument malfunctions, differences between instruments, uneven measurement dates and inter-annual variations in canopy conditions due to tree growth and mortality. Seasonal changes in LAI were assessed using a GLM framework incorporating measurement date as a categorical explanatory variable (10-day periods, 36 periods per year), and measurement point, measurement method (plant canopy analyser or hemispherical photographs), measurement year, and the interaction of the latter two variables as random effects. Since LAI was not measured on the same day every month, each measurement date was classified into 10-day periods (i.e., 36 periods per year), then converted into categorical data and incorporated into the GLM. No

data were available for mid-April. The hypothesis that each parameter had a value of zero was evaluated using *t*-tests. The GLM estimated LSMs for each measurement date. Annual mean (\pm SD) and range were estimated by averaging and ranging the LSM for each measurement date.

Seasonal variations in LMA were assessed using a GLM framework incorporating collection date as an explanatory variable and individual leaf as a random effect. Significant differences among dates were evaluated using post-hoc Tukey-Kramer HSD tests. The GLM estimated LSMs for each sampling date. All statistical analysis was conducted using JMP statistical software (ver. 10.0, SAS Institute Inc., North Carolina, USA).

Results

Phenology of leaf and bud scale shed

Leaf and bud scale shedding phenology are shown in Figs 5–7. The tall dipterocarps *D. costatus* and *A. costata* shed leaves during the early dry season (Fig. 5). The shedding peak of *A. costata* was 0–20 days earlier than that of *D. costatus*. For *D. costatus*, sporadic leaf shedding was observed in the early rainy season (Fig. 5). The peak of leaf shedding for tall dipterocarp species in the early dry season was generally sharp, excluding blunt peaks observed in 2008–2009 (Fig. 5, Phase II), or from 2014 to 2015 (Fig. 5, Phase III). The dates of onset and termination and the duration of the rainy season or El Niño/La Niña phase, and the occurrence and lengths of monsoon breaks (derived from Kabeya *et al.*, 2021; Kabeya *et al.*, unpublished data) are also shown in Fig. 5.

Mid- and lower layer components of the forest, including other dipterocarps (*Vatica odorata* and *Hopea recopei*) mainly shed leaves in the late dry season (Fig. 6). The number of species shedding leaves was relatively large in the late dry season, with peaks in January–February for most species (Fig. 6). The peak of leaf shedding for low- and mid-canopy species was relatively blunt, except for a sharp peak in February 2009 (Fig. 6, Phase II).

The fall of *D. costatus* bud scales typically peaked between mid-November and mid-December (Fig. 7). The peak of bud scale fall (i.e., the peak of leaf flushing) coincided with peak leaf fall in *D. costatus* (Fig. 5). Bud scale fall from *D. costatus* was also observed during the late dry season and early in the rainy season (Fig. 7).

Leaf fall patterns were further generalized through GLM analysis (Fig. 8). Significantly elevated levels of leaf shedding continued over 40 days and 60 days in the early

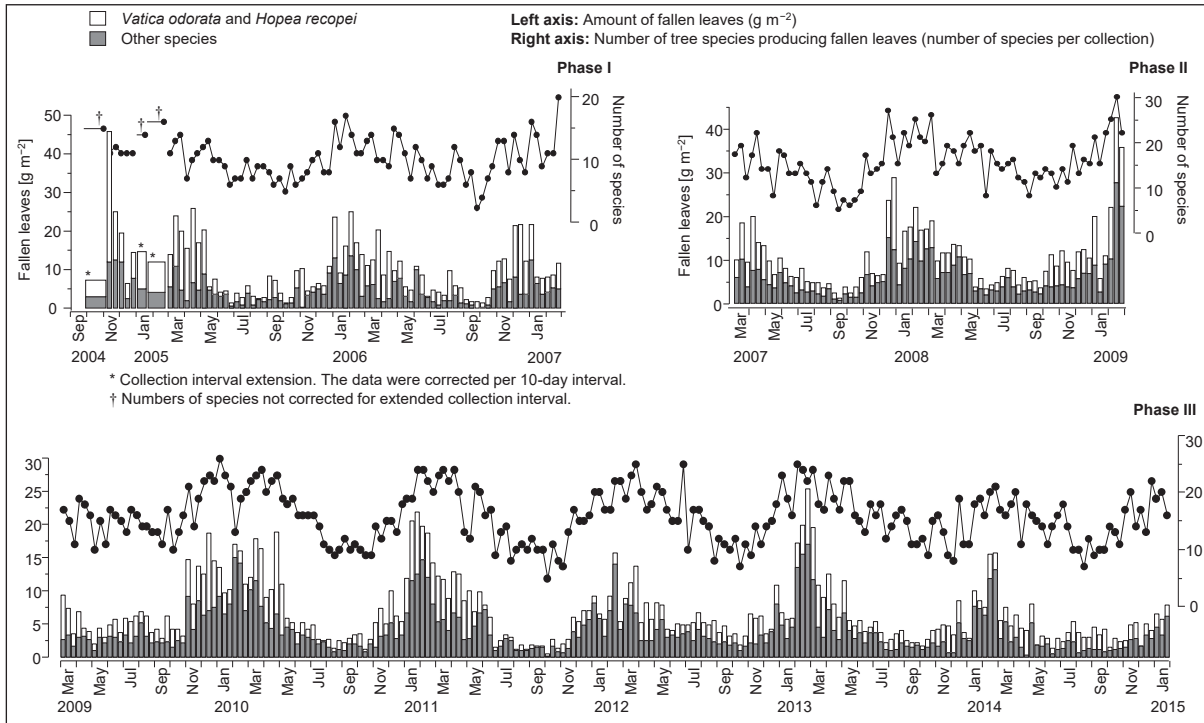


Fig. 6 Leaf shedding phenology of species in the middle and understory layers. Columns indicate the volume of fallen leaves (left axis), whereas lines indicate the number of other litter-producing tree species (i.e., all species aside from *D. costatus*, *A. costata*, *V. odorata* and *H. recoupei*; right axis). Asterisks (*) in Phase I indicate extended collection intervals (see text for details). The data for the three phases were corrected for 10-day intervals. Numbers of species were not corrected for trap area or collection interval. † in phase I indicates the total number of species collected during extended intervals.

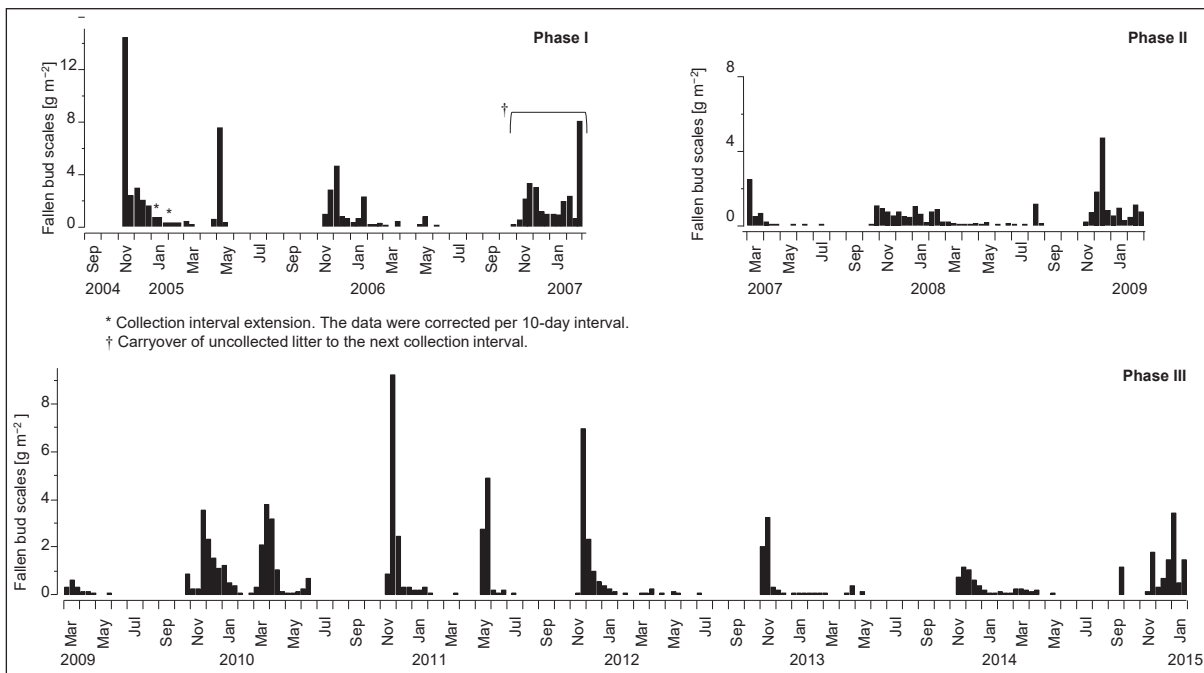


Fig. 7 Bud scale shedding phenology of *D. costatus*. Asterisks (*) in Phase I indicate extended collection intervals (see text for details). The data for the three phases were corrected for 10-day intervals. † in Phase I indicates carryover of uncollected litter to the next collection interval.

dry season for *D. costatus* and *A. costata*, respectively (Fig. 8a–b). Peaks in leaf shedding were less clear and lasted longer during late dry season in mid- to low-canopy species (Fig. 8c–d).

According to our GLM, 50.8% and 58.2% of total annual leaf fall occurred during the early dry season for *D. costatus* and *A. costata*, respectively. During the late dry season, 27.9% and 19.9% of total annual leaf fall occurred for *D. costatus* and *A. costata*, respectively. Meanwhile, 21.4% and 18.3% of the annual leaf fall for mid-layer dipterocarps and other mid- and understory species occurred in the early dry season, respectively. During the late dry season, 54.4% and 58.9% of annual leaf fall occurred for the mid-layer dipterocarps and other mid- and understory species, respectively. Some mid- to low-canopy species displayed leaf shedding throughout the dry and rainy seasons. For example, leaf litter from *Peltophorum dasyrhaichis* (Miq.) Kurz (Fabaceae) and *Syzygium syzygioides* (Miq.) Merr. & L.M. Perry (Myrtaceae) were found on 87% and 82% (respectively) of all collection dates in Phase III ($n = 213$). However, the peak of leaf shedding occurred during the late dry season (February) rather than the early dry season.

Direct crown observations

Direct observations confirmed that leafless branches were rarely observed on *D. costatus* and *A. costata* throughout the year. Leaf flushing occurred mainly during November and December in these two tall dipterocarps. The peak of leaf flushing was slightly earlier in *A. costata* (mid-late November) than *D. costatus* (late November–early December) (Table 1).

Leaf area index

Leaf area index measurements collected with the plant canopy analyser during the first study year (March 2003 to June 2004) are shown in Table 2. Maximum and minimum values were observed in mid-July (4.66 m^{-1}) and late April (3.85 m^{-1}), respectively. The annual difference (0.81 m^{-1}) corresponded to 17% of the largest observed LAI value. We consistently observed relatively large values during the rainy season, which did not differ significantly from the maximum observed values. Values decreased in mid-November (4.15 m^{-1}) as the rainy season shifted towards the onset of the dry season, and then gradually increased in late December and mid-January. LAI decreased rapidly between mid-January (4.26 m^{-1}) and late April (3.85 m^{-1}), but began to increase again (3.88 m^{-1}) in mid-May, before the rainy season started. The increase in mid-May was observed in both 2003 and 2004.

The GLM based on the full dataset estimated that annual mean (\pm SD) LAI was $3.93 \pm 0.23 \text{ m}^{-1}$ and ranged from 3.53 to 4.39 m^{-1} (Fig. 9). The annual difference (0.86 m^{-1}) was equivalent to 20% of the largest observed LAI value. The largest and second largest LAI occurred in early August (4.39 m^{-1}) and late June (4.35 m^{-1}),

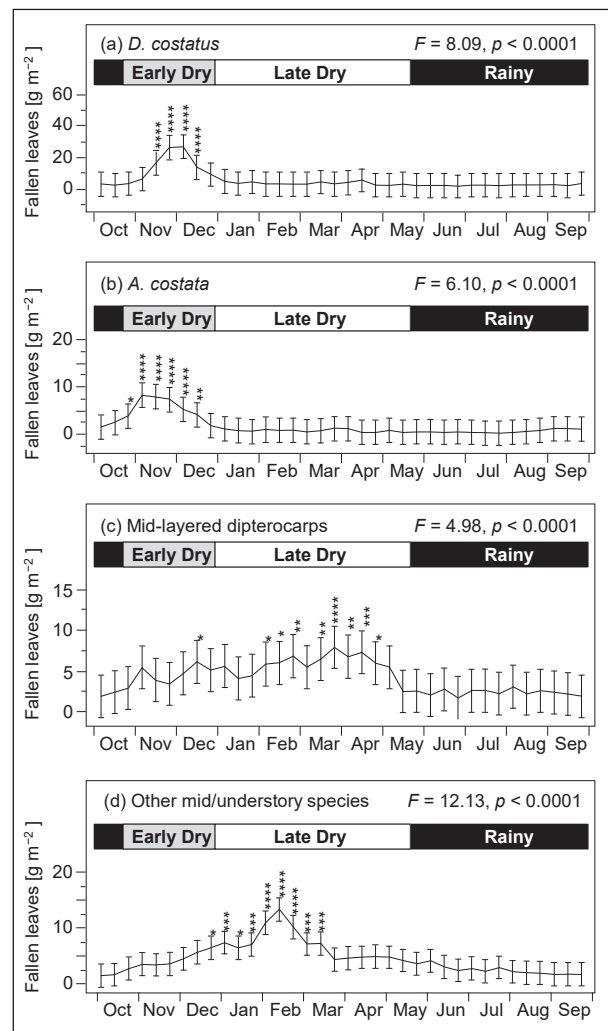


Fig. 8 GLM analysis of leaf shedding phenology in a lowland dry evergreen forest in Cambodia. Fallen leaf litter weights were estimated for each collection date (ten-day periods in each month, 36 dates per year) for four categories: (a) the tall dipterocarp *D. costatus*, (b) the tall dipterocarp *A. costata*, (c) the mid-layer dipterocarps *V. odorata* and *H. recopei*, and (d) other mid- and understory species. The line charts with error bars show the least squares means and the upper and lower 95% confidence intervals. Collection dates which showed significant positive values are indicated with asterisks: **** < 0.0001; *** < 0.001; ** < 0.01; and * < 0.05. Statistical *F*- and *p*-values are given in the upper right corner of each panel.

respectively. The lowest and second lowest LAI occurred in early March (3.53 m m⁻¹) and late November (3.55 m m⁻¹), respectively. Collection dates for which *t*-tests indicated significant positive or negative parameter values typically occurred during the rainy and dry seasons, respectively. In contrast, we identified two periods in the year when LAI gradually increased while continuously exhibiting neutral parameter values: mid-December to early January and late April to mid-May.

The GLM results also indicated no significant differences between the two data collection methods during 2003–2007, but significantly higher and lower LAI values were found for the plant canopy analyser relative to the hemispherical photographs in 2008 and 2009–2012, respectively (data not shown). As potential effects of mechanical aging of the plant canopy analyser and missing data in hemispherical photographs could not be accounted for, we do not discuss inter-annual variation in LAI.

Leaf mass per area

The mean LMA of *D. costatus* was 138.0 g m⁻². LMA showed slight but significant differences relative to leaf falling date ($F_{13,567.4} = 4.74, p < 0.0001$, Table 3). Post-hoc

Tukey-Kramer HSD tests indicated that leaves that fell early in the dry season (10 November and 19 November, Table 3) had relatively high LMA values.

Discussion

Leaf phenology is discrete in lowland dry evergreen forests

Our study revealed discrete leaf shedding phenology in two tall dipterocarp tree species, which peaked in the early dry season, and low- to mid-forest layer species, which peaked in the late dry season (Figs 5–6, 8). We also assessed the leaf flushing phenology of two tall dipterocarp tree species based on the phenology of bud scale fall (Fig. 7) and canopy observations (Table 1). These flushed immediately after leaf shedding. That LAI decreased early in the dry season and increased soon after (Table 2, Fig. 9) is consistent with this observation.

The leaf flushing phenology of species in the low to middle tree layers was not directly assessed, but may be indirectly estimated based on seasonal changes in LAI. LAI gradually decreased in the later portions of the dry season (Table 2, Fig. 9), when species in the low to

Table 1 Leaf flushing phenology based on direct observations. Numbers of observed trees with newly flushed leaves in the crown are shown. ‘–’ indicates a value of zero. Three individual trees of each species were observed. Direct observations were made three times per month from February to September, but no leaf flushing was observed.

Species	Year	Late Rainy Season			Early Dry Season			Mid Dry Season						
		October			November			December			January			
		10	20	30	10	20	30	10	20	30	10	20	30	
<i>A. costata</i>	2004–05	–	–	–	–	2	3	1	–	–	–	–	–	–
	2006–07	–	–	–	1	3	3	3	3	–	–	–	–	–
	2007–08	–	1	2	3	1	–	–	–	–	–	–	–	–
	2008–09	–	–	–	1	2	3	2	–	–	–	–	–	–
	2009–10	–	–	–	3	3	3	2	2	1	–	–	–	–
	2010–11	–	–	–	–	2	3	2	2	–	–	–	–	–
	2011–12	–	–	–	1	2	3	2	2	2	–	–	–	–
<i>D. costatus</i>	2004–05	–	–	–	–	2	3	2	1	–	–	–	–	–
	2006–07	–	–	–	3	3	3	3	2	–	–	–	–	–
	2007–08	–	–	–	3	3	3	3	–	–	–	–	–	–
	2008–09	–	–	–	–	–	1	2	3	3	2	–	–	–
	2009–10	–	–	–	1	2	3	3	3	3	2	–	–	–
	2010–11	–	–	–	1	1	3	3	2	1	–	–	–	–
	2011–12	–	–	–	–	3	3	3	3	3	–	–	–	–

Table 2 Leaf area index (LAI, m² m⁻²) values obtained in the lowland dry evergreen forest, Cambodia. Values lacking a common superscript letter are significantly different at $p < 0.05$ based on Tukey's honest significant difference.

Year	Date	Season	Mean ($n=10$)	SD	
2003	Mar. 14	Late-Dry	3.96 ^{fgh}	0.72	
	Apr. 10	Late-Dry	3.97 ^{efgh}	0.82	
	May 18	Late-Dry	4.27 ^{bcde}	0.78	
	Jun. 17	Rainy	4.46 ^{abc}	1.00	
	Jul. 18	Rainy	4.66 ^a	0.90	
	Aug. 17	Rainy	4.54 ^{ab}	0.94	
	Sep. 14	Rainy	4.38 ^{abcd}	0.90	
	Oct. 16	Rainy	4.40 ^{abc}	0.91	
	Nov. 16	Early-Dry	4.15 ^{cdefg}	0.77	
	Dec. 21	Early-Dry	4.18 ^{cdefg}	0.78	
	2004	Jan. 20	Late-Dry	4.26 ^{bcdef}	0.78
		Feb. 27	Late-Dry	4.07 ^{defgh}	0.84
Mar. 27		Late-Dry	4.03 ^{efgh}	0.78	
Apr. 25		Late-Dry	3.85 ^h	0.72	
May 18		Late-Dry	3.88 ^{gh}	0.70	
Jun. 20		Rainy	4.02 ^{efgh}	0.73	

middle layers had shed their leaves (Fig. 6), but began to increase shortly before the end of the late dry season and continued to increase gradually throughout the first half of the rainy season (Table 2, Fig. 9). This suggests that species in the low to middle layers flush, at the latest, during the last month of the dry season. However, it is unclear how long the flushing lasted, because the gradual increase in LAI during the first half of the rainy season may be attributable not only flushing but also leaf expansion.

Bimodal leaf shedding behaviour during the dry season has been observed optically in ca. 30% of the evergreen forests in Cambodia via analyses of satellite imagery (Ito *et al.*, 2008). It is possible that the stand-scale leaf dynamics we observed are common in Cambodian evergreen forests.

Ecological advantages of leaf flushing in the early dry season

Leaf flushing in the early dry season was displayed by a few upper-canopy species in our study i.e., *D. costatus* and *A. costata* (Table 1, Fig. 5). Our LMA measurements for *D. costatus* may provide insights into the advantages

Table 3 Seasonal changes in leaf mass per area (LMA, g m⁻²) of fallen leaves of *D. costatus*. Values lacking a common superscript letter are significantly different at $p < 0.05$ based on Tukey's honest significant difference.

Year	Date	Season	LSM	<i>n</i>	
2005	Aug. 30	Rainy	146.4 ^{abcd}	12	
	Sep. 10	Rainy	129.8 ^e	26	
	Sep. 29	Rainy	143.6 ^{abcde}	18	
	Nov. 10	Early-Dry	151.1 ^{ab}	10	
	Nov. 19	Early-Dry	146.2 ^a	48	
	Dec. 10	Early-Dry	137.4 ^{bcde}	207	
	Dec. 20	Early-Dry	137.8 ^{abcde}	62	
	Dec. 30	Early-Dry	137.0 ^{bcde}	78	
	2006	Jan. 10	Late-Dry	135.8 ^{abcde}	24
		Jan. 30	Late-Dry	134.1 ^{abcde}	17
		Apr. 20	Late-Dry	137.5 ^{abcde}	16
		May 9	Late-Dry	130.9 ^{de}	20
May 19		Late-Dry	132.8 ^{cde}	31	
Jun. 20		Rainy	146.9 ^{abc}	16	
Mean ± SD			138.0 ± 17.8		

of this behaviour (Table 3). The leaf characteristics of dipterocarp trees depend on tree height and thick and hard leaves are found in the upper part of the tree canopy (Kenzo *et al.*, 2006, 2012), as in other forests (e.g., Cavaleri *et al.*, 2010). High LMA values imply that fallen leaves originated in the upper canopy layers. Relatively high LMAs were observed in leaves that fell in early to mid-November, just after the onset of the dry season (Table 3). This suggests that the upper portion of the canopy sheds its leaves early in the dry season. Moreover, given the assumption of ca. 1-year leaf longevity (Ito *et al.*, 2018), the elevated LMA of fallen leaves during the early dry season implies that the upper part of the tree canopy flushes leaves during the early dry season. Leaf expansion requires a large supply of water (Dale, 1988). The two tall dipterocarp tree species considered here commonly reach 30–35 m in height (Toyama *et al.*, 2013). We have also found that they can reach maximum heights of 45 m and stem diameters of 130 cm (Ito *et al.*, unpublished data). Thus, it may be advantageous to exchange upper-canopy leaves in the early dry season, when the ground-water level is still high (Fig. 4a; Araki *et al.*, 2008).

Moreover, leaf flushing in the early dry season may be advantageous given seasonal variation in solar radia-

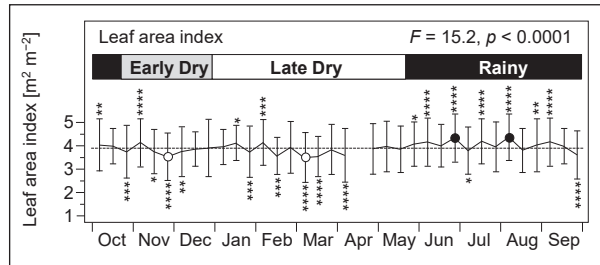


Fig. 9 Seasonal changes in leaf area index (LAI) in Cambodian lowland dry evergreen forests. The LSMs of LAI and 95% prediction intervals for each collection date are shown as connected straight lines and vertical lines, respectively. Collection dates which showed significant positive or negative parameter values are indicated with asterisks above and below the vertical lines, respectively: **** < 0.0001; *** < 0.001; ** < 0.01; and * < 0.05. Closed circles indicate the largest and second largest LAI. Open circles indicate the lowest and second lowest LAI. The horizontal dashed line indicates the mean value (3.93). No data were available for mid-April.

tion. The annual difference in solar radiation was generally small (<10%) but decreased by 20 % in the last two months of the rainy season (Fig. 4b). Therefore, the early dry season represents a period of increased solar radiation and relatively abundant soil moisture, wherein newly flushed leaves with high physiological activity may be advantageous to an individual tree.

Ecological advantages of leaf retention early in the dry season

For low and mid-canopy species, we observed leaf retention and gradual leaf shedding early and late in the dry season respectively (Fig. 6), and estimated leaf flushing from the last phase of the dry season (around mid-May in Table 2 and late April in Fig. 9). Flushing has been widely reported as occurring late in the dry season in tropical dry forests (Borchert, 1994; Elliott *et al.*, 2006). The reasons why new leaves develop prior to rainfall have been discussed, and the phenomenon appears to be particularly common among species that are drought-tolerant (Reich & Borchert, 1984) or deeply rooted (Wright & van Schaik, 1994). The discrete leaf phenological patterns we observed raise an additional question: why does the phenology of low- and mid-canopy species differ from that of co-existing upper-canopy species? While we cannot fully answer this question, we discuss the ecological advantages of leaf retention in the early dry season below.

It should be noted that light resources for low- and mid-canopy species are influenced not only by climatic

conditions, but also by the leaf mass of upper-canopy species. Our data indicate that the volume of leaves in the canopy is temporarily reduced early in the dry season by leaf shedding among upper-canopy species, whereas low- and mid-canopy species retain their leaves. It can be inferred that light availability for low- and mid-canopy species is optimal in the early dry season. Retaining leaves and continuing photosynthesis may be an adaptive behaviour for low- and mid-canopy species in the early dry season, when light conditions are most favourable. Light and water may be less severely limiting in lowland dry evergreen forests compared to other forests in tropical Asia (Huete *et al.*, 2008) and the Neotropics (Saleska *et al.*, 2003; Xiao *et al.*, 2005; Huete *et al.*, 2006; Hutrya *et al.*, 2007), but the availability of these resources varies according to canopy position. Plants may exhibit a variety of adaptive phenological behaviours, and the main driver of leaf phenology in tropical East Asia remains unclear (Corlett, 2014). Further clarification of the proximate and ultimate factors driving leaf phenology will advance our understanding of how extreme weather events may influence lowland dry evergreen forests.

Anomalous leaf shedding phenology and its association with lengthy monsoon breaks

An anomalous, gradual leaf shed by tall dipterocarps occurred in the middle of the rainy season in August–September 2008 (Fig. 5, Phase II). The La Niña phase was identified during the 2008 rainy season, whereby a monsoon break began in early August 2008 and lasted 70 days (Fig. 5; Kabeya *et al.*, 2021). This break was twice the mean length of monsoon breaks observed in the study area (36 days: Kabeya *et al.*, 2021). Monsoon breaks are regarded as short dry seasons (Kabeya *et al.*, 2021) and it is possible that the unusual shedding event that we observed was associated with this lengthy monsoon break. While this situation occurred only once during our study period, it may be indicative of a response to extreme weather conditions that could occur more frequently in the future.

Following the blunt peak in leaf shedding for tall dipterocarps in the early dry season in 2008 (Fig. 5, Phase II), we observed a relatively sharp peak in leaf shedding of low- and mid-canopy species in February 2009 (Fig. 6, Phase II). This may also be tied to the lengthy monsoon break. Plausible causes for the latter include the direct effect of water shortage during this period. Unfortunately, we do not have direct data on the quantity and timing of leaf flushing for low- and mid-canopy species during the 2008–2009 dry season. However, if the early and rapid leaf shedding was caused by water shortages, we can assume that the subsequent leaf flushing

would have occurred later than usual, and that stand-scale leaf mass remained low until the onset of the rainy season provided sufficient moisture. Conversely, the early, gradual leaf shedding exhibited by upper-canopy dipterocarps may have created an unusually long period of favourable light conditions for low- and mid-canopy species. Other studies have noted the need for further investigation of the effects of anomalies in rainfall on forest water cycles (Tanaka *et al.*, 2008). Comprehensive assessments of the impacts of long monsoon breaks on phenology and site environmental conditions is necessary to surmise how extreme weather events will affect lowland dry evergreen forest ecosystems.

Potential changes in leaf phenology resulting from forest degradation

Anthropogenic forest degradation cannot be ignored when assessing the future of lowland dry evergreen forest ecosystems in Cambodia. Deforestation in Cambodia has slowed, but not stopped (MoE, 2018). Due to rapid development in the region, evapotranspiration-related impacts of climate change on river flow in the Mekong River basin have become a concern (Thompson *et al.*, 2013). Evergreen forests have been degraded by selective logging (FA, 2011). Dipterocarps, which are the dominant species in typical lowland dry evergreen forests (Rundel, 1999), are among the primary targets for illegal and unreported logging (Kim Phat *et al.*, 2002). Forest degradation and phenological changes could have significant impacts on the regional water cycle due to feedbacks between vegetation and the climate system (Saleska *et al.*, 2003; Richardson *et al.*, 2013).

Degradation in lowland dry evergreen forests may affect local meteorological conditions in the following three respects. First, the removal of tall dipterocarp trees would inevitably reduce stand biomass, as dipterocarp trees account for more than 50% of the total volume of dense (>300 m³ ha⁻¹) forests (Kim Phat *et al.*, 2000; Kao & Iida, 2006). This is likely to influence total evapotranspiration at the stand level. Second, removing large trees may reduce transpiration late in the dry season because the remaining small trees are likely unable to access deep soil moisture (Tamai *et al.*, 2008).

Third, forest degradation may alter stand-scale leaf phenology. Our results imply that the removal of tall dipterocarps would reduce newly flushing leaves in the early dry season. Tree-scale transpiration depends on the leaf age structure of the crown and leaf age-dependent physiological activity (Iida *et al.*, 2013; Ito *et al.*, 2018). Altering the proportions of young and old leaves within the canopy may affect transpiration. Our results also indicate that the selective logging of tall dipterocarps

alters the bimodal seasonal pattern in total leaf area. Leaf area is a key parameter for assessing transpiration in forests (Stewart, 1988; Iida *et al.*, 2016). Although seasonal changes in total leaf area at our study site were less pronounced than those observed in a deciduous dipterocarp forest (17–20% versus ca. 70%, Table 2, Fig. 9; Iida *et al.*, 2020), this variation and further alterations, may affect transpiration at the stand scale. Furthermore, the effects of forest degradation may be compounded by climate change, as discussed in the previous section. As a consequence, further studies should incorporate factors related to leaf phenology into a multi-layer evapotranspiration model (e.g., Tanaka *et al.*, 2002, 2003) to assess potential future forest ecosystems.

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Annex 1 List of tree species in the study area with a DBH >5 cm

Family	Species	Tree density (trees ha ⁻¹)	Basal Area (m ² ha ⁻¹)	Maximum DBH (cm)
Anacardiaceae	<i>Mangifera duppereana</i> Pierre	33.3	0.44	22.2
Annonaceae	<i>Melodorum fruticosum</i> Lour.	4.2	0.01	5.5
Apocynaceae	<i>Willughbeia edulis</i> Roxb.	8.3	0.03	7.4
	Apocynaceae spp. (vine)	12.5	0.04	6.9
Calophyllaceae	<i>Calophyllum</i> sp.	4.2	0.03	9.8
Capparaceae	<i>Capparaceae</i> sp.	16.7	0.16	14.4
Celastraceae	<i>Lophopetalum duperreanum</i> Pierre	58.3	0.46	14.8
Clusiaceae	<i>Garcinia benthamii</i> Pierre	4.2	0.11	18.1
	<i>Garcinia lanessanii</i> Pierre	4.2	0.02	8.4
	<i>Garcinia merguensis</i> Wight	4.2	0.01	5.4
Connaraceae	<i>Ellipanthus tomentosus</i> Kurz	4.2	0.01	5.7
Dipterocarpaceae	<i>Anisoptera costata</i> Korth.	45.8	8.73	92.7
	<i>Dipterocarpus costatus</i> C.F.Gaertn.	25.0	10.86	129.8
	<i>Hopea recopei</i> Pierre ex Laness.	337.5	3.96	24.1
	<i>Vatica harmandiana</i> Pierre	8.3	0.10	16.8
	<i>Vatica odorata</i> (Griff.) Symington	275.0	4.04	26.5
Ebenaceae	<i>Diospyros filipendula</i> Pierre ex Lecomte	12.5	0.19	20.2
	<i>Diospyros montana</i> Roxb.	4.2	0.02	8.6
	<i>Diospyros undulata</i> Wall.	75.0	0.29	10.6
	<i>Diospyros venosa</i> Wall. ex A.DC.	145.8	0.92	15.4
Euphorbiaceae	<i>Croton poilanei</i> Gagnep.	8.3	0.12	18.5
	<i>Suregada glomerulata</i> Baill.	8.3	0.02	5.6
Fabaceae	<i>Albizia corniculata</i> (Lour.) Druce	4.2	0.05	12.7
	<i>Sindora siamensis</i> Teijsm. ex Miq.	29.2	2.23	70.4

Annex 1 Cont'd

Family	Species	Tree density (trees ha ⁻¹)	Basal Area (m ² ha ⁻¹)	Maximum DBH (cm)
Fagaceae	<i>Lithocarpus harmandii</i> (Hickel & A.Camus) A.Camus	4.2	0.02	8.5
Irvingiaceae	<i>Irvingia malayana</i> Oliver ex A.Benn.	4.2	0.46	37.4
Lauraceae	<i>Beilschmiedia inconspicua</i> Kosterm.	12.5	0.10	13.8
Malvaceae	<i>Microcos tomentosa</i> Sm.	12.5	0.05	8.2
Melastomataceae	<i>Memecylon caeruleum</i> Jack	37.5	0.31	24.0
	<i>Memecylon lilacinum</i> Zoll. & Moritzi	12.5	0.05	8.8
	<i>Memecylon</i> sp.1	16.7	0.08	11.1
	<i>Memecylon</i> sp.2	41.7	0.17	8.9
Myristicaceae	<i>Knema globularia</i> (Lam.) Warb.	4.2	0.02	8.1
Myrtaceae	<i>Syzygium albiflorum</i> (Duthie ex Kurz) Bahadur & R.C.Gaur	12.5	0.08	10.5
	<i>Syzygium angkae</i> (Craib) Chantaran. & J.Parn	12.5	0.21	21.2
	<i>Syzygium chanlos</i> (Gagnep.) Merr. & L.M.Perry	54.2	1.02	22.5
	<i>Syzygium grande</i> (Wight) N.P.Balacr.	8.3	0.15	19.5
	<i>Syzygium oblatum</i> (Roxb.) Wall. ex Cowan & Cowan	54.2	1.00	35.0
	<i>Syzygium syzygioides</i> (Miq.) Merr. & L.M. Perry	75.0	2.33	38.0
	<i>Syzygium zeylanicum</i> (L.) DC.	16.7	0.07	9.7
Ochnaceae	<i>Ochna integerrima</i> (Lour.) Merr.	12.5	0.03	5.4
Pentaphragaceae	<i>Ternstroemia wallichiana</i> Ridl.	33.3	0.28	15.7
Peraceae	<i>Chaetocarpus castanocarpus</i> Thwaites	16.7	0.24	21.1
Phyllanthaceae	<i>Antidesma puncticulatum</i> Miq.	4.2	0.02	8.7
	<i>Aporosa ficifolia</i> Baill.	29.2	0.24	14.4
	<i>Aporosa planchoniana</i> Baill. ex Müll.Arg.	8.3	0.02	5.5
	<i>Aporosa tetrapleura</i> Hance	8.3	0.03	6.3
	<i>Hymenocardia punctata</i> Wall. ex Lindl.	4.2	0.02	6.9
Polygalaceae	<i>Xanthophyllum flavescens</i> Roxb.	95.8	1.80	35.0
Rhizophoraceae	<i>Carallia brachiata</i> (Lour.) Merr.	4.2	0.01	5.8
Rutaceae	<i>Clausena excavata</i> Burm.f.	4.2	0.01	5.0
Sapindaceae	<i>Nephelium hypoleucum</i> Kurz	12.5	0.11	14.0
	<i>Xerospermum laevigatum</i> Radlk. ssp. <i>laevigatum</i>	4.2	0.01	6.3
Schoepfiaceae	<i>Schoepfia fragrans</i> Wall.	8.3	0.03	6.9
Stemonuraceae	<i>Gomphandra</i> sp.	4.2	0.02	8.7
Symplocaceae	<i>Symplocos cochinchinensis</i> S.Moore ssp. <i>laurina</i> (Retz.) Noot.	8.3	0.11	17.4
Unknown	Unidentified sp.01	4.2	0.05	12.7
	Unidentified sp.02	4.2	0.04	11.2
	Unidentified sp.03	4.2	0.04	11.7
	Unidentified sp.04	4.2	0.02	8.7

Annex 1 Cont'd

Family	Species	Tree density (trees ha ⁻¹)	Basal Area (m ² ha ⁻¹)	Maximum DBH (cm)
	Unidentified sp.05	4.2	0.02	7.1
	Unidentified sp.06	4.2	0.10	17.7
	Unidentified vein sp.01	12.5	0.03	6.4
	Unidentified vein sp.02	8.3	0.04	9.2
	Total	1817	42.3	129.8