

# Stand carbon dynamics in a dry Cambodian dipterocarp forest with seasonally flooded sandy soils

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## មូលនិយសង្ខេប

ដើម្បីអនុវត្តវិធានការ “កំណើន-បាត់បង់” នៃគម្រោងផ្ដួចផ្ដើម “ការកាត់បន្ថយការសាយភាយកាបូន បណ្ដាលមកពីការកាប់និងការបំផ្លាញព្រៃឈើ” យើងផ្តល់ការប៉ាន់ស្មានកំណើនកាបូន ពីការកើនឡើងនៃជីវម៉ាសដើមឈើប្រចាំឆ្នាំ និង ការបាត់បង់ជីវម៉ាសមានជីវិត បណ្ដាលមកពីធម្មជាតិនិងសកម្មភាពមនុស្ស នៅក្នុងព្រៃបោះដីល្បាយខ្សាច់នៃប្រទេសកម្ពុជា។ យើងបានត្រួតពិនិត្យព្រៃបោះដីល្បាយខ្សាច់ ជាព្រៃដែលសម្បូរដោយដើមត្បែង (*Dipterocarpus obtusifolius*) ដែលដុះនៅតំបន់ដីល្បាយខ្សាច់។ យើងបានវិភាគពីអត្រានុកូលសាស្ត្រ និង កំណើនអង្កត់ផ្ចិតកម្ពស់ទ្រូង ដែលមានអង្កត់ផ្ចិត>៥សម ដោយផ្អែកលើការធ្វើជំរឿនដើមឈើអស់រយៈពេល១១ឆ្នាំ(២០០៣ ដល់ ២០១៤)កន្លងមក។ ទីតាំងសិក្សាបានបង្ហាញពីកម្រិតទាបនៃកំណើនកាបូន(០,១៨មក្រ កាបូន/០,២៤ហិចតា/ឆ្នាំ) ចំពោះការស្តុកកាបូនដំបូងមាន(១១,៣មក្រ កាបូន/០,២៤ហិចតា) រៀបរយទៅនឹងប្រភេទព្រៃឈើកម្ពុជាដទៃទៀតដែលត្រូវបានសិក្សាកន្លងមក។ អត្រាដាច់ដើមឈើដែលមានអង្កត់ផ្ចិតកម្ពស់ទ្រូង  $\geq 90$ សម មានកម្រិតទាប(១,០៣%/ឆ្នាំ) ជាហេតុនាំឲ្យមានការបាត់បង់កាបូនតិចតួច(០,១២មក្រ កាបូន/០,២៤ហិចតា) ពីដើមឈើដាច់ដោយធម្មជាតិ ក្នុងអំឡុងពេលមុនកាប់(២០០៣ ដល់ ២០១១)។ ការកាប់ឈើដោយជនអនាមិកបានកាត់បន្ថយការស្តុកកាបូនប្រមាណ៥,៣៧មក្រ កាបូន/០,២៤ហិចតា (៤២,៧% នៃតម្លៃមុនពេលកាប់) ជាមួយនឹងការខូចខាតបន្ទាប់បន្សំ (០,០០៦មក្រ កាបូន/០,២៤ហិចតា) ដែលសមាមាត្រទៅនឹងកំណើនកាបូនក្នុងរយៈពេល ៣០ឆ្នាំកន្លងមក។ កំណើនកាបូនដាច់ខាត កំណើនកាបូនទាប និង ការកាប់ឈើក្នុងទ្រូងទ្រាយធំដែលបានអង្កេតនៅក្នុងទីតាំងសិក្សា បង្ហាញថាព្រៃបោះដុះនៅតំបន់ដីល្បាយខ្សាច់ ចាំបាច់ត្រូវតែមានការបែងចែកជាប្រភេទនៃព្រៃបោះដុះស្លឹកនេះ នៅពេលអនុវត្តវិធានការ “កំណើន-បាត់បង់” នេះ។

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## Abstract

To implement the gain-loss approach from the ‘Reducing Emissions from Deforestation and Forest Degradation’ initiative, we provide estimates of gains from the annual increase in tree biomass and losses in live biomass caused by natural and anthropogenic processes in a sandy dry dipterocarp forest in Cambodia. We examined a sandy dry dipterocarp forest—a form of forest characterised by the strong dominance of *Dipterocarpus obtusifolius*—which was distributed on sites with sandy soils. We analysed the demography and diameter increment of trees with diameters at breast height (DBH) >5 cm based on an 11 year tree census (2003–2014). The study plot showed a low carbon (C) increment (0.18 Mg C 0.24 ha<sup>-1</sup> y<sup>-1</sup>) for the initial C stock (11.3 Mg C 0.24 ha<sup>-1</sup>) compared to other Cambodian forest types that have been studied in the past. The low mortality of trees with DBH ≥10 cm (1.03% y<sup>-1</sup>) resulted in a small C loss from naturally dying trees (0.12 Mg C 0.24 ha<sup>-1</sup>) in the pre-cutting period (2003–2011). Logging by unknown parties decreased C stocks by 5.37 Mg C 0.24 ha<sup>-1</sup> (42.7% of the pre-logging value) with relatively less collateral damage (0.006 Mg C 0.24 ha<sup>-1</sup>); this was equivalent to C increments that had accrued over 30 years. The low absolute C increment, the relatively low C increment, and the intensive logging observed in the study plot suggest that sandy dipterocarp forests need to be stratified into subdivisions of deciduous forests when implementing the gain-loss approach.

## Keywords

Carbon stock, *Dipterocarpus obtusifolius*, forest degradation, mortality, recruitment, Reducing Emissions from Deforestation and Forest Degradation (REDD), tree increment.

## Introduction

Reducing Emissions from Deforestation and Forest Degradation and the role of conservation, sustainable management of forests and enhancement of forest carbon stocks in developing countries (REDD+) is an effort to create financial incentives for developing countries to reduce carbon (C) emissions from forested lands (UNFCCC, 2009). To implement the global climate change mitigation programme, IPCC (2006) presented two methods for calculating changes in C stocks: the gain-loss method and the stock-difference method. The choice of method largely depends on a country’s available data, domestic capacity, and forest transition stage (GOFC-GOLD, 2008; Murdiyarso *et al.*, 2008).

Cambodia has attracted the attention of the REDD+ programme because it is a hotspot for deforestation and forest degradation (FAO, 2010; 2011). In recent years, a several studies have attempted to prepare a full implementation programme for REDD+ activities in Cambodia (Sasaki *et al.*, 2006, 2011, 2012, 2013, 2016; Sasaki & Yoshimoto, 2010). To reduce uncertainties in C estimation for countries experiencing significant forest degradation (Sasaki, 2006), application of the gain-loss method was recently examined in Cambodia (Sasaki *et al.*, 2006, 2012, 2013, 2016; Kiyono *et al.*, 2017). The gain-loss method is built around the gains from annual increases in biomass and the losses in live biomass caused by natural and anthropogenic processes (Murdiyarso *et al.*, 2008). Those estimates must be obtained for each forest type, appropriately stratified by eco-types and degradation

processes (Murdiyarso *et al.* 2008; Pearson *et al.*, 2014; GOFC-GOLD, 2016).

Cambodia has a diversity of forest types (Rollet, 1972; Rundel, 1999) and the extent of their degradation varies, adding a layer of complexity to the task of data collection. The Cambodian Forestry Administration (FA) classified forest cover into four types: evergreen, semi-evergreen, deciduous, and other forests including different types such as forest re-growth, inundated forests, stunted forests, mangrove forests, and forest plantations (FA, 2011). Specific information for each forest-type has been obtained from ground-based studies in Cambodia, and includes data on forest structure (Kimpbat *et al.*, 2000, 2002a; Kao & Iida, 2006; Ouk, 2006; Pin *et al.*, 2013; Toyama *et al.*, 2015; Chheng *et al.*, 2016), biomass (Top *et al.*, 2004a; Kiyono *et al.*, 2010; Khun *et al.*, 2012; Samreth *et al.*, 2012; Chheng *et al.*, 2016; Monda *et al.*, 2016), and biomass increment (FA, 2004; Top *et al.*, 2004a; Kiyono *et al.*, 2017). Despite these, data collection is still fragmented. For example, data on annual increment are relatively limited, possibly because neither the continuous maintenance of permanent sample plots nor frequent tree measurements for forest biomass increment are necessarily straightforward in countries with frequent deforestation and forest degradation (Kiyono *et al.*, 2017).

Positive relationships have been reported between annual above-ground biomass increment and above-ground biomass for Cambodian forests without stratifying forest types (Top *et al.*, 2004a; Kiyono *et al.*, 2017). The coefficients of determination for this relationship

in both previous studies were relatively low. Top *et al.* (2004a) suggested that stand age, soil types, microtopography, or species composition might explain the residuals, whereas Kiyono *et al.* (2017) could not explain these by differing mean annual precipitation or the soil fertility index. The gain-loss method should be built on an ecological understanding of how forests grow (Murdiyarso *et al.* 2008). Additional data on C increment is still required, in addition to data on fundamental forest structure and dynamics for the various forest types.

Deciduous forests comprising dry mixed deciduous forests and dry dipterocarp forests predominate in Cambodia, and cover 24.68% of its land area (FA, 2011). Dry dipterocarp forests are described as *forêt claire* (Rollet, 1972), deciduous dipterocarp forests or woodlands (Rundel, 1999). They exist throughout Indo-Burma (Ashton, 2014) and are scattered among lowland forest areas in Cambodia (JICA, 2002). The name of this community is a result of dominance by a small number of deciduous species of Dipterocarpaceae, such as *Shorea siamensis*, *S. obtusa*, *Dipterocarpus tuberculatus*, *D. intricatus* and *D. obtusifolius* (Rundel, 1999). Dry dipterocarp forests have been further subdivided into four forms, with different combinations of soil type and dominant dipterocarp species (Rollet, 1972).

One form of dry dipterocarp forest is characterised by the strong dominance of *D. obtusifolius* (*Tbeng* in Khmer), which favours sandy soil, gravelly soil or laterite (Smitinand *et al.*, 1980). This forest (hereafter sandy dipterocarp forest) has been referred to as *forêt claire à Dipterocarpus obtusifolius* (Vidal, 1960), *D. obtusifolius* on sand or grey soil (*à D. obtusifolius, sur sable ou terre grise*: Rollet, 1972), *D. obtusifolius* community (Baltzer *et al.*, 2001) and *D. obtusifolius* stand type (Hiramatsu *et al.*, 2007). Sandy dipterocarp forests are most characteristic of areas east of the Mekong River in Cambodia at sites with thin sandy soils over laterites (Rundel, 1999) and are often scattered as forest patches among evergreen forests at sites with deep sandy soils subject to seasonal flooding in Kampong Thom Province, northeast of the Tonle Sap Lake (Hiramatsu *et al.*, 2007).

Sandy dipterocarp forests are often low in species richness (Hiramatsu *et al.*, 2007) and have open structures with 40–70% canopy cover (Rundel, 1999; Hiramatsu *et al.*, 2007; FA, 2011). They are associated with ground fires (Rundel, 1999; Hiramatsu *et al.*, 2007), have nutrient-poor sandy soils (Rollet, 1972; Toriyama *et al.*, 2007a, b), and experience seasonal flood and drought conditions (Rollet, 1972; Rundel, 1999; Baltzer *et al.*, 2001; Araki *et al.*, 2007). Nevertheless the predominant *D. obtusifolius* is ecologically plastic and stress tolerant (Rundel, 1999). Its annual growth is still unknown; in other words, it

is unclear whether sandy dipterocarp forests achieve C increments to the same degree as other deciduous forests (Top *et al.*, 2004a; Kiyono *et al.*, 2017).

There is also a dearth of data related to C emissions due to forest degradation, which is a significant contributor to C emissions in the atmosphere (GOF-C-GOLD 2008). Considerable international variation exists in C emissions from tropical forest degradation caused by selective logging (Pearson *et al.*, 2014). Forest degradation from uncontrolled tree cutting has resulted in significant losses of C stock in Cambodian evergreen forests (Sasaki & Putz, 2009). As such, further data on deciduous forest degradation would contribute to implementation of the gain-loss approach in Cambodia.

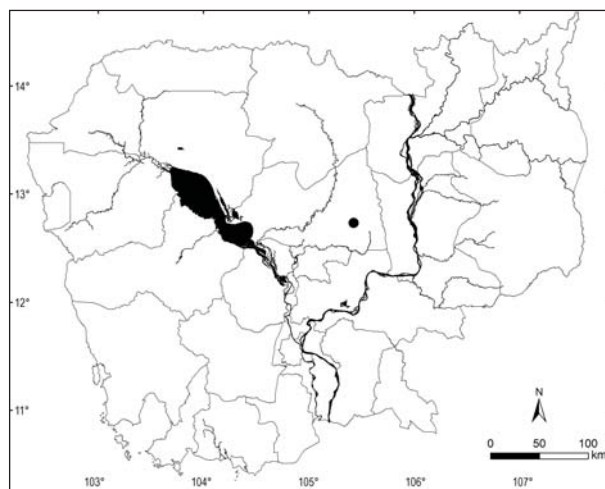
We established a permanent sample plot (30 × 80 m) to investigate stand structure and dynamics in a sandy dipterocarp forest in the Kampong Thom Province of Cambodia. During a chronological tree census (2003–2014), logging by unknown parties occurred in the plot. The plot, while small and isolated, had the potential to provide useful information about sandy dipterocarp forests. The objectives of our study were to clarify the stand dynamics and annual increment in sandy dipterocarp forest based on 11 years of tree census data, and to assess C emission from cutting events and related collateral damage.

## Methods

### Study site

We conducted our study in the Kampong Thom Province in central Cambodia (12.8°N, 105.5°E; elevation: 70 m a.s.l., Fig. 1). The site was positioned on quaternary sedimentary rock and located on a largely flat, slightly undulating alluvial plain (Toriyama *et al.*, 2011). The tropical climate is seasonal, and the months between November and April are dry. The mean annual temperature was 27°C, and the annual rainfall (mean ± SD) was 1,542 ± 248 mm (2000–2010; NIS, 2012).

We established a permanent sample plot (30 × 80 m) for vegetation in a sandy dipterocarp forest with a canopy openness of 50% (Hiramatsu *et al.*, 2007, Fig. 2). The forest includes *D. obtusifolius* (ca. 50% of stand basal area and 60% of stand tree numbers) and *Gluta laccifera* (35% and 6%, respectively) as the dominant species (Hiramatsu *et al.*, 2007). These are the major species in seasonal tropical forests in Asian monsoon areas and are indicative of a dry forest type (Rundel & Boonpragob, 1995; Eiadthong, 2011). The forest lacked auxiliary deciduous species such as *Shorea obtusa*, *Pterocarpus macrocarpus*, and *Xylocarpus*



**Fig. 1** Location of the study site (solid circle) in Kampong Thom Province, Cambodia.

*xylocarpa*, which usually co-occur in dry dipterocarp or deciduous dipterocarp forests (Royal Forest Department, 1962; Tani *et al.*, 2007; Hiramatsu *et al.*, 2007; Eiadthong, 2011; Pin *et al.*, 2013). Edaphic limitation is a potential factor limiting species richness (Hiramatsu *et al.*, 2007). The forest was classified as a deciduous forest using FA (2011); however, the component tree species showed irregular and incomplete leaf shedding (Ito *et al.*, 2007). For example, leaf longevity of *D. obtusifolius* often exceeded one year (Ito *et al.*, unpublished data), a trend which has also been observed in the Thai highlands (Elliott *et al.*, 2006). The soil of the study area was generally sandy and nutrient-poor, similar to other *G. laccifera* habitats (Eiadthong, 2011). The soils have been classified as acrisols (WRB), but with albic and arenic features that suggest a closer relationship with arenosols (WRB) (Toriyama *et al.*, 2007a). The ground surface was waterlogged several times in the middle of the rainy season (August through September: Araki *et al.*, 2007) and the ground vegetation includes *Xyris complanata* R.Br. and insectivorous plants (*Drosera* sp. and *Nepenthes* sp.), which suggest low-nutrient edaphic conditions (Hiramatsu *et al.*, 2007).

#### Data collection

Field surveys were conducted in 2003, 2008, 2009, 2010, 2011, 2012 (pre-logging), and 2014 (post-logging) to investigate tree growth and demography. Censuses in 2003, 2011, and 2014 were conducted in February each year. Censuses in 2009 and 2010 were conducted in December each year. Censuses in 2008 and 2012 were conducted in June and November, respectively. All standing woody stems with a diameter at breast height

(DBH)  $\geq 5$  cm were enumerated and identified to species (except for one specimen which was identified to genus, Appendix 1). We measured stem girth to the nearest 1 mm (1.3 m above ground level) during the tree censuses except in the 2010 census. The height of each tree was measured in 2010 using either a Vertex III clinometer (Hagl f, L ngsele, Sweden) or a telescopic height-measuring pole. We spatially mapped stems with an accuracy  $< 1$  m and measured crown diameters of major and minor axes in 2012 (Fig. 2).

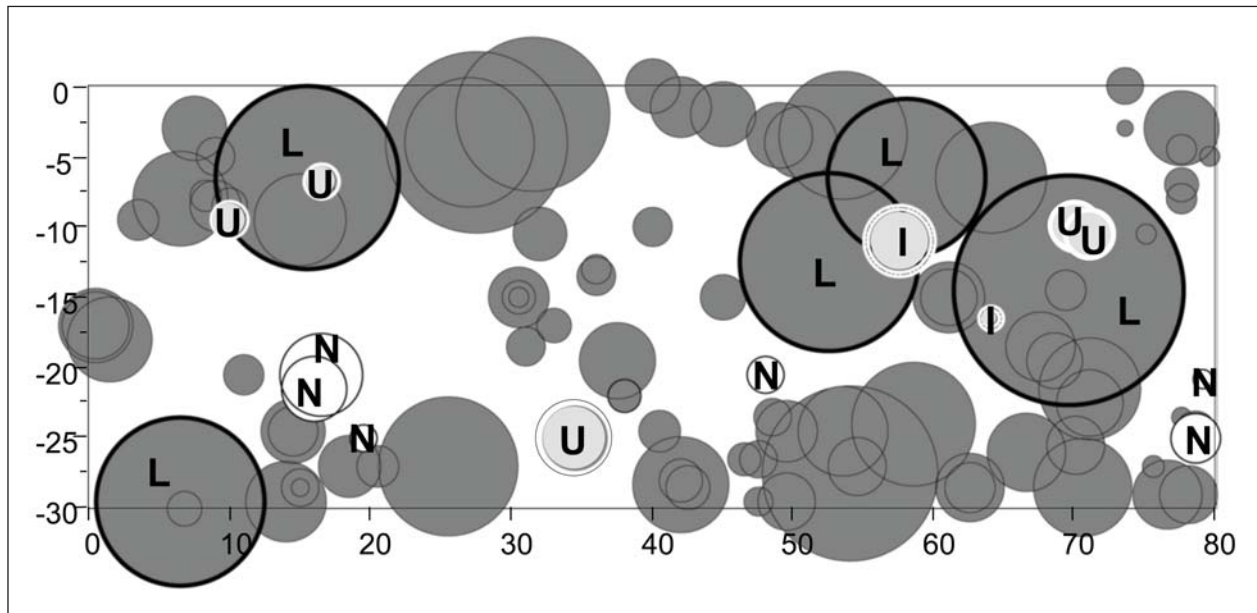
#### Analysis

Annual mortality and recruitment rate were calculated using commonly used logarithmic models (e.g., Swaine *et al.*, 1987; Phillips & Gentry, 1994; Lewis *et al.*, 2004). More specifically, mortality rate ( $\lambda$ ) and recruitment rate ( $k$ ) were calculated as follows:

$$\lambda = (\ln(n_0) - \ln(n_0 - n_d)) / t \quad (\text{Eq. 1}),$$

$$k = (\ln(n_0 + n_r) - \ln(n_0)) / t \quad (\text{Eq. 2}),$$

where  $n_0$  is the number of trees present at the beginning of the census interval, and  $n_d$  and  $n_r$  are the number of trees that died of natural causes and the recruited trees during time ( $t$ ) of the census interval. We used a  $2 \times 2$  contingency table to assess differences in mortality and recruitment rate between individuals with a DBH of 5–10 cm and  $\geq 10$  cm. Given the stems present during the initial 2003 inventory, the numbers of surviving and dying stems at the end of the census interval (2014) provided the values for mortality analysis. Recruited stems were omitted from this analysis. Using the stems present at the end of the 2014 inventory, numbers of existing stems during the initial 2013 inventory and recruited stems during the 11-year census, we were able to identify values for recruitment rate analysis. Dying stems were omitted from this analysis. Hypothesis tests were performed using one-tailed probabilities based on Fisher's exact test. The observed number of dying or recruited trees with DBH  $\geq 5$  cm was compared to the expected number of dying or recruited trees. The expected number was calculated by assuming that there were no mortality or recruitment rate differences during the 11-year census. Significance was tested by the chi-squared test for goodness of fit. To avoid periods with fewer than five expected dying or recruited trees, we divided our observations from all 11 years into three periods: 2003–2008, 2008–2011, and 2011–2014. Numbers of observed and predicted dying or recruited trees for each period were compared to a significance level of  $p=0.05$ . Diameter distributions of the predominant *Dipterocarpus obtusifolius* were evaluated for skewness ( $s$ ) and kurtosis ( $\kappa$ ), and were compared to a normal distribution using the pre-logging 2011 census



**Fig. 2** Individual tree locations and crown sizes within a 30 × 80 m study plot in Kampong Thom Province, Cambodia. Symbol sizes are canopy areas calculated from crown diameters and assume each crown was circular. Letters indicate status changes between 2012 and 2014: L = logged for timber ( $n=5$ ); I = collateral damage from logging ( $n=2$ ); U = cut for unknown reasons ( $n=5$ ); N = natural death ( $n=6$ ).

data and the Shapiro-Wilk test. We used a log-normal distribution to best describe the diameter distribution of *D. obtusifolius*, where we estimated two parameters,  $\mu$  (scale) and  $\sigma$  (shape). A goodness-of-fit test was examined using the Kolmogorov-Smirnov test. We assessed whether the log-normal distribution fitted for *D. obtusifolius* was significantly different from those of associated species using the Kolmogorov-Smirnov test. Four of the tested species were selected based on their basal area in the 2011 census (*G. laccifera*, *Parinari anamensis*, *Syzygium oblatum*, and *Memecylon scutellatum*).

Diameter increments per year were compared between the 2003–2011 census and the 2011–2014 census for trees that had survived since the 2003 (first) census to the 2014 post-logging census ( $n=69$ ) using a Wilcoxon signed rank test. We estimated the total biomass (TB) of the trees using the latest published allometric equations developed in a deciduous dipterocarp forest in Kratie Province, Cambodia (Model 4: Monda *et al.*, 2016):

$$\begin{aligned} \ln(\text{AGB}) &= -2.438 + 2.518 \ln(\text{DBH}) \\ \ln(\text{BGB}) &= -3.734 + 2.521 \ln(\text{DBH}) \end{aligned} \quad (\text{Eq. 3}),$$

where AGB and BGB represent the dry above-ground biomass and dry below-ground biomass of each tree (kg), respectively, and DBH (cm) is the diameter of the stem 1.3 m above-ground. TB was obtained by calculating the

sum of AGB and BGB. Field-measured DBH's of each tree in the 2003, 2011, and 2014 censuses were applied to the equation for evaluating chronological changes in stand C storage, C emissions, and C increment because these three censuses were conducted in the same month of the dry season (February), which avoids DBH swelling in the rainy season. Allometry equations with tree height parameters were not applicable because tree height was measured only during the 2010 census. To evaluate the difference in biomass estimates, we estimated tree biomass for the corresponding DBH dataset from the 2011 census and tree height from the 2010 census using an allometry equation with parameters for tree height (H, m) (Model 2: Monda *et al.*, 2016):

$$\begin{aligned} \ln(\text{AGB}) &= -2.710 + 0.924 \ln(\text{DBH}^2 \times H) \\ \ln(\text{BGB}) &= -4.030 + 0.928 \ln(\text{DBH}^2 \times H) \end{aligned} \quad (\text{Eq. 4}).$$

The difference (%) in the stand TB results between Equations 3 and 4 was calculated as: (stand TB by Eq. 3 – stand TB by Eq. 4) / (stand TB by Eq. 3) × 100.

We found a difference of 6.8% in the study plot, which was considered small, although it suggests relatively low tree height in the study plot compared to the deciduous dipterocarp forest in Kratie where the equations were developed. Besides the TB estimates found using Equation 3, we obtained tree biomass by applying

various equations identical to several previous studies to maintain consistency in the biomass estimates among comparative studies. Top *et al.* (2004a) estimated the AGB of trees with DBH >10 cm using the equation developed by Brown (1997):

$$\text{AGB} = 42.69 - 12.800\text{DBH} + 1.242\text{DBH}^2 \quad (\text{Eq. 5}).$$

Kiyono *et al.* (2017) estimated the ABG of trees with DBH >5 cm using the equation developed by Kiyono *et al.* (2006):

$$\text{AGB} = 11545 \text{BA}^{1.24} \quad (\text{Eq. 6}),$$

where BA is the basal area of a stem at a height of 1.3 m ( $\text{m}^2$ ). Samreth *et al.* (2012) estimated the TB of trees with DBH >7.5 cm using the equation developed by Kiyono *et al.* (2011):

$$\text{TB} = 4.08 \times \text{BA}^{1.25} \times \text{WD}^{1.33} \quad (\text{Eq. 7}),$$

where WD is the basic density ( $\text{kg m}^{-3}$ ) of the stem wood. The species-specific WD data obtained from neighbouring countries used for Equation 7 were selected from a global WD database provided by Chave *et al.* (2009) and Zanne *et al.* (2009). When species-specific data were not available in the database, we used 570, which is the default value for tropical Asian wood (Brown, 1997). The values of WD used for each species are listed in Appendix 1. Kimphat *et al.* (2002b) and Khun *et al.* (2012) presented biomass as standing volume (SV,  $\text{m}^3$ ). We converted AGB to SV similar to Sasaki *et al.* (2016) using the equation developed by Brown (1997):

$$\text{AGB} = \text{SV} \times 0.001 \text{WD} \times \text{BEF} \quad (\text{Eq. 8}),$$

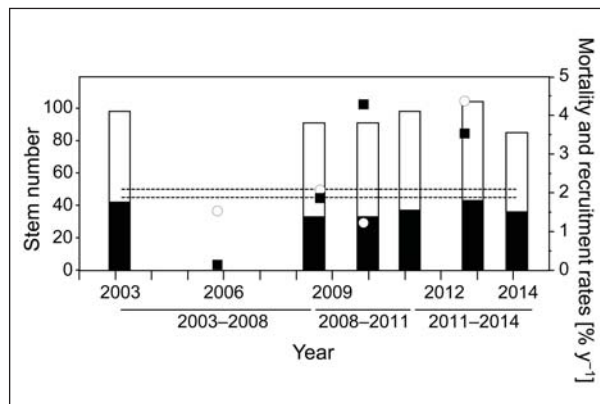
where BEF is the biomass expansion factor (1.74). Stand tree C stock in the study plot was obtained for the 2003, 2011, and 2014 censuses. The C stored in the trees was obtained by multiplying the C content in the dry wood biomass (0.5: IPCC, 2003) by the estimated biomass of each tree. Plot-specific values of tree C emissions by natural causes and C increment without anthropogenic effects were estimated for the 2003–2011 censuses. For stand C emissions estimation, the biomass of all the trees that died during the interval were summed, and the biomass of each tree was estimated from their last measured diameters during the interval. Stand C increment was calculated using a revised method of Clark *et al.* (2001). Increments for surviving trees during the interval were calculated as the difference between their estimated biomass at the beginning (2003) and end of the interval (2011). Increments for recruited trees during the interval were calculated as the difference between their estimated biomass at the end of the interval (2011) and the biomass of a tree of the minimum measured diameter (DBH of 5 or 10 cm). Increments for dying trees during the interval

were calculated as the difference between their estimated biomass at the beginning and end of the interval. For stand C increment, biomass increments were summed for all trees that had survived, were recruited, and were dying. To compare our results with previous studies, the indices of stand structure, biomass, and increment were rescaled per hectare, given that the number of individuals increased linearly with area. A combination of the plot-wise annual AGB increment and the initial AGB in the study plot was compared to previous studies (Top *et al.*, 2004a; Kiyono *et al.*, 2017). These studies were conducted for Cambodian forests without stratifying forest types, which derived positive relationships between annual AGB increment and initial AGB. A logarithmic relationship was obtained for trees with DBH >10 cm using data from 32 plots (four deciduous forest plots, where the details of the forest type were unknown) located in Kampong Thom (Top *et al.*, 2004a). A linear relationship was obtained for trees with DBH >5 cm using data from 49 plots (24 deciduous forest plots, not including sandy dipterocarp forests, Kiyono, pers. comm.) in nine provinces (Kiyono *et al.*, 2017). To maintain consistency in the biomass estimates between the present and previous studies, we used Equations 5 and 6 for biomass estimation and set tree size criteria identical to these particular studies. We recorded the presence of logged trees and collaterally damaged trees from the 2014 census. C loss associated with the cutting procedure was estimated based on DBH from the 2011 census. Tree C emissions by natural and anthropogenic causes were compared during the 2011–2014 censuses. Plot canopy coverages from the 2011 and 2014 censuses were estimated based on crown diameters measured in 2012. We assumed that each crown was circular, and plot canopy coverage was therefore provisionary and calculated as the sum of the crown area within the rectangular plot, with overlapping crown areas excluded.

## Results

### Stand structure and dynamics

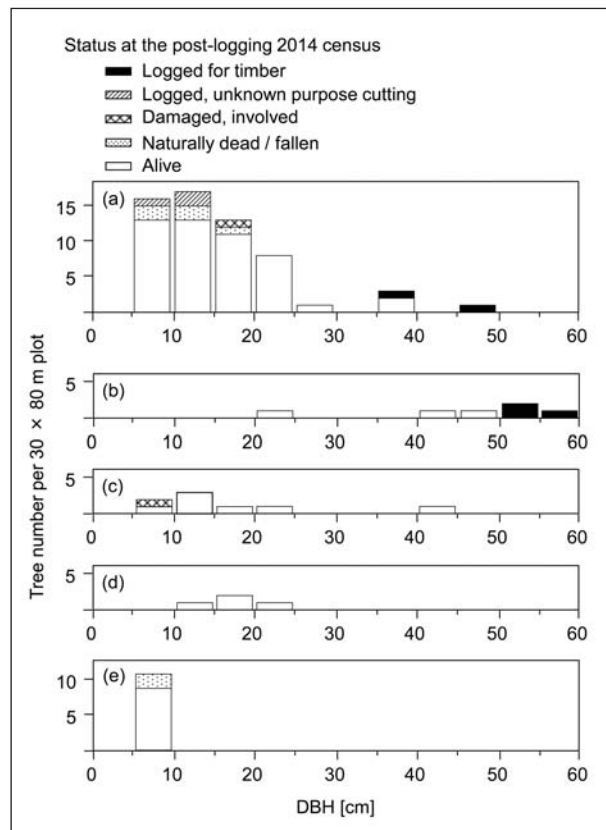
Stand-level tree density ranged 91 to 104 stems  $0.24 \text{ ha}^{-1}$  and 56 to 61 stems  $0.24 \text{ ha}^{-1}$ , for individuals with DBH  $\geq 5$  cm and  $\geq 10$  cm across five pre-logging censuses (2003, 2008, 2009, 2011, 2012) respectively (Fig. 3). During the 11-year census, 121 stems with DBH  $\geq 5$  cm were enumerated, of which 23 died from natural causes and 23 were recruited (Table 1). Sixty-three stems with DBH  $\geq 10$  cm were enumerated, of which six died from natural causes and six were recruited (Table 1). Individuals in the 5–10 cm DBH class that died comprised *M. scutellatum* ( $n=10$ ),



**Fig. 3** Chronological changes in stem density, mortality, and recruitment rate. This is a bar-plot of the number of stems in the study plot (0.24 ha) across five pre-logging censuses (2003, 2008, 2009, 2011, 2012) and one post-logging census (2014). Black and white bars show stems with DBH of 5–10 cm and  $\geq 10$  cm, respectively. Open circles and closed squares indicate mortality and recruitment rates for stems with DBH  $\geq 5$  cm, respectively. Rates were calculated for the periods 2003–2008, 2008–2011, 2011–2014, and 2003–2014 (dotted lines).

*Artocarpus* sp. ( $n=5$ ), and *D. obtusifolius* ( $n=2$ ). Individuals with DBH  $\geq 10$  cm that died comprised *D. obtusifolius* ( $n=3$ ), *Syzygium oblatum* ( $n=1$ ), *Artocarpus* sp. ( $n=1$ ), and *Anneslea fragrans* ( $n=1$ ). Recruited individuals in the 5–10 cm DBH class were *M. scutellatum* ( $n=7$ ), *D. obtusifolius* ( $n=6$ ), *Xylopiella vielana* ( $n=4$ ), *Parinari anamensis* ( $n=3$ ), and *Calophyllum calaba* var. *bracteatum* ( $n=3$ ). Recruited individuals in the DBH  $\geq 10$  cm class were *D. obtusifolius* ( $n=3$ ), *P. anamensis* ( $n=3$ ), and *Symplocos cochinchinensis* ( $n=1$ ). Mortality ( $\lambda$ ) for stems with DBH  $\geq 5$  cm during 2003–2014 was  $2.08\% \text{ y}^{-1}$  (Fig. 3). Significantly higher  $\lambda$  was found for stems of 5–10 cm DBH ( $3.69\% \text{ y}^{-1}$ ) than for stems with DBH  $\geq 10$  cm ( $1.03\% \text{ y}^{-1}$ ) (one-tailed Fisher's exact test,  $p=0.0031$ ). The chi-squared test for goodness of fit indicated that there was a significant difference in the occurrence of dying trees among the different census periods (2003–2008, 2008–2011, 2011–2014) ( $\chi^2=7.242$ ,  $df=2$ ,  $p<0.05$ ) and only the number of dying trees between the 2011 and 2014 censuses were larger than expected values (Fig. 3).

The recruitment rate ( $k$ ) for stems with DBH  $\geq 5$  cm in 2003–2014 was  $1.92\% \text{ y}^{-1}$  (Fig. 3). The recruitment rate for 5–10 cm DBH stems ( $3.98\% \text{ y}^{-1}$ ) significantly exceeded  $\geq 10$  cm DBH stems ( $1.07\% \text{ y}^{-1}$ ) (one-tailed Fisher's exact test,  $p=0.0010$ ). Chi-squared test for goodness of fit showed that the expected number of trees recruited in each period between censuses significantly differed from



**Fig. 4** Frequency distribution of DBH for predominant and associated tree species in the study forest based on pre-logging 2011 census data. Hatched patterns in the bars indicate tree status during the pre-logging 2011 census. A) *Dipterocarpus obtusifolius*; B) *Gluta laccifera*; C) *Parinari anamensis*; D) *Syzygium oblatum*; E) *Memecylon scutellatum*.

the occurrence of period categories within the study plot ( $\chi^2=18.447$ ,  $df=2$ ,  $p<0.05$ ); where the expected figure was greater than their actual occurrence during the 2003–2008 censuses (Fig. 3). Size distributions according to basal area in the 2011 census are shown for five representative tree species in the study plot in Fig. 4. The diameter distribution of *D. obtusifolius* was significantly different from a normal distribution (Shapiro-Wilk test,  $n=59$ ,  $W=0.87$ ,  $p<0.0001$ ). *Dipterocarpus obtusifolius* showed significant positive skewness (coefficient  $s=1.52$ ,  $p<0.05$ ) and large kurtosis (coefficient  $\kappa=2.93$ ,  $p<0.05$ ), with a peak in the 10–15 cm DBH class and a long tail indicating several rare adults (Fig. 4a). The diameter distribution of *D. obtusifolius* did not differ significantly from a log-normal distribution (Kolmogorov-Smirnov test,  $n=59$ ,  $D=0.07$ ,  $p=0.150$ ). The best fitting parameters with a 95% CI were 2.63 (2.50–2.76) and 0.51 (0.43–0.61) for  $\mu$  and  $\sigma$ , respectively. The species-specific diameter

**Table 1** Transition of DBH size classes and conditions over the 11-year study period (2003–2014) for stems in study plot, Kampong Thom Province, Cambodia.

Stem size class in 2014	Condition in 2014	Stem size class in 2003			Total
		<5 cm DBH <sup>a</sup>	5–10 cm DBH	≥10 cm DBH	
5–10 cm DBH	Alive	16	20		58
	Dieback <sup>b</sup>	0	1		
	Dead	3	14		
	Cut	3	0		
	Collateral damage	1	0		
≥10cm DBH	Alive		6	43	63
	Dieback		0	0	
	Dead		0	6	
	Cut		1	6	
	Collateral damage		0	1	
<b>Total</b>		<b>23</b>	<b>42</b>	<b>56</b>	<b>121</b>

<sup>a</sup>Not enumerated in 2003; <sup>b</sup> Dieback of primary stems reduced the height of the stem by less than 1.3 m.

distributions of associated species were significantly different from *D. obtusifolius* (*G. laccifera*,  $n=6$ ,  $D=0.85$ ,  $p=0.010$ , Fig. 4b; *S. oblatum*,  $n=4$ ,  $D=0.42$ ,  $p=0.015$ , Fig. 3d; *M. scutellatum*,  $n=11$ ,  $D=0.93$ ,  $p=0.010$ , Fig. 3e), except for *P. anamensis* ( $n=8$ ,  $D=0.23$ ,  $p=0.150$ , Fig. 4c). Visual inspection suggested that *G. laccifera* had a distinct distribution skewed to the larger size class (Fig. 4b), and *M. scutellatum* had a distinct distribution limited to the 5–10 cm DBH class (Fig. 4e). Detailed structure data for each species are given in Appendix 2.

#### Size increment and C emissions

Annual diameter increments during the 2003–2014 censuses averaged  $0.14 \pm 0.12$  cm  $y^{-1}$  and  $0.11 \pm 0.08$  cm  $y^{-1}$  for all of the specimens ( $n=69$ ) and the *D. obtusifolius* ( $n=48$ ) trees that survived over the course of the censuses. Diameter increments for trees that survived the 2003–2014 censuses were significantly higher between the 2011 and 2014 censuses ( $0.18 \pm 0.16$  cm  $y^{-1}$ ) than between the 2003 and 2011 censuses ( $0.12 \pm 0.12$  cm  $y^{-1}$ ) (Wilcoxon signed rank test,  $p<0.0001$ ). Plotwise and species-specific diameter increments for each size class are described in Appendix 3. Visual inspection suggested that *P. anamensis* and *C. calaba* var. *bracteatum* showed relatively high increments. The bark of *M. scutellatum* was often peeling, which resulted in highly variable increments. Basal areas of stems with DBH  $\geq 5$  cm and  $\geq 10$  cm increased from 11.24 to 12.31  $m^2 ha^{-1}$  and from 10.54 to 11.74  $m^2 ha^{-1}$  between the 2003 and 2011 pre-logging

censuses, respectively (Appendix 2). Emissions of C for dying individuals with DBH  $\geq 5$  cm and  $\geq 10$  cm during the 2003–2014 census were 0.36 Mg C  $0.24ha^{-1}$  and 0.25 Mg C  $0.24ha^{-1}$ , respectively (Table 2). The DBH classes for dying trees of five representative tree species in the study plot during the 2011–2014 censuses are described in Fig. 4. Tree C increments were larger than C emissions from dead trees from 2003 to 2011; thus, tree C stock in the stand slightly increased (from 11.26 to 12.60 MgC  $0.24 ha^{-1}$  for trees with DBH  $\geq 5$  cm, Table 2). Above-ground tree C stock estimates derived from several equations are also shown in Table 2. Annual above-ground biomass increments in the study plot were lower than estimated values from previously reported regression relationships between the annual above-ground biomass increment and the above-ground biomass (Fig. 5). The annual above-ground biomass increment in this study plot ( $1.61$  Mg  $ha^{-1} y^{-1}$ , estimated using Eq. 5) was 48% of the expected value derived from the logarithmic relationship developed by Top *et al.* (2004a) ( $3.38$  Mg  $ha^{-1} y^{-1}$ ) given an initial above-ground biomass of 113.4 Mg  $ha^{-1}$  (estimated using Eq. 5). The annual above-ground biomass increment ( $1.08$  Mg  $ha^{-1} y^{-1}$ , estimated using Eq. 6) was 32% of the expected value derived from the linear relationship reported by Kiyono *et al.* (2017) ( $3.34$  Mg  $ha^{-1} y^{-1}$ ), given an above-ground biomass of 69.2 Mg  $ha^{-1}$  (estimated using Eq. 6). Estimates of stand structure and tree biomass are summarised and compared to previous studies of Cambodian forest in Table 3.



**Table 2** Plot-wise tree carbon (C) dynamics in study plot, Kampong Thom Province, Cambodia.

Item (MgC 0.24 ha <sup>-1</sup> )	Census year	DBH size criteria (cm)	Total biomass		Above-ground biomass	
			Eqs. 3 <sup>a</sup>	Eqs. 3 <sup>a</sup>	Eq. 5 <sup>b</sup>	Eq. 6 <sup>c</sup>
C stock	2003	≥5	11.26	8.8	14.0	8.3
		≥10	10.93	8.6	13.6	8.0
	2011	≥5	12.60	9.87	15.53	9.27
		≥10	12.32	9.65	15.24	9.05
	2014	≥5	7.56	5.9	9.6	5.6
		≥10	7.28	5.7	9.4	5.4
C emissions from dead trees	2003–2011	≥5	0.12	0.10	0.14	0.09
		≥10	0.06	0.05	0.07	0.05
	2011–2014	≥5	0.24	0.19	0.29	0.18
		≥10	0.19	0.15	0.24	0.14
C emissions from logging and collateral damage	2011–2014	≥5	5.37	4.21	6.33	3.90
		≥10	5.36	4.19	6.30	3.88
C increment	2003–2011	≥5	1.42	1.12	1.66	1.04
		≥10	1.31	1.02	1.54	0.95

<sup>a</sup> Monda *et al.* (2016); <sup>b</sup> Brown (1997) used in Top *et al.* (2004a); <sup>c</sup> Kiyono *et al.* (2011) used in Kiyono *et al.* (2017).

### Cutting operations in sandy dipterocarp forests

Logging by unknown parties occurred at the study site between November 2012 and February 2014, likely in late 2013 or early 2014, judging from the freshness of stumps. Ten logged trees were scattered within the 0.24 ha plot (Fig. 2). Five large logged stems were either removed from the plot or left behind partially sawn. Another five small fallen trunks were left behind; their locations were not related to visible skid trails, which indicated normal removal operations. The average DBH of the former was 50.1 cm (35.9 and 46.9 cm for *D. obtusifolius*,  $n=2$ ; 54.3–57.8 cm for *G. laccifera*,  $n=3$ ) in the 2011 census (Fig. 4a, b). The average DBH of the unlogged trees of these two species was 16.4 cm (range: 5.3–39.0 cm for *D. obtusifolius*,  $n=54$ ; 23.4–47.1 cm for *G. laccifera*,  $n=3$ ). The average DBH of the latter was 8.2 cm (range: 5.5–13.8 cm for *D. obtusifolius*,  $n=3$ ; 5.9 cm for *C. calaba* var. *bracteatum*,  $n=1$ ; 4.9 cm for *P. anamensis*,  $n=1$ ) in the 2011 census (Fig. 4a, c; *C. calaba* not shown). In addition to the logged trees ( $n=10$ ), logging operations caused collateral damage to remaining individuals (Figs 2 & 4). Broken-stemmed trees ( $n=2$ ) occurred in the vicinity of logged tree stumps; a form of damage directly attributable to cutting operations. From 2011 to 2014, densities of trees with DBH ≥5 cm and ≥10 cm fell 87.6% (from 97 to 85 stems 0.24 ha<sup>-1</sup>) and 80.3% (from 61 to 49 stems 0.24 ha<sup>-1</sup>), respectively (Fig. 3). Basal areas of individuals with DBH ≥5 cm and

≥10 cm declined to 67.3% (from 12.31 to 8.29 m<sup>2</sup> ha<sup>-1</sup>) and 65.7% (from 11.74 to 7.71 m<sup>2</sup> ha<sup>-1</sup>), respectively (Appendix 2). Basal area depletion as a result of cutting and collateral damage was 34.4% of the initial area (4.23 of 12.31 m<sup>2</sup> ha<sup>-1</sup>). Total tree C stock for trees with DBH ≥5 cm was 12.60 Mg C 0.24 ha<sup>-1</sup> in the 2011 census, where 5.37 Mg C 0.24 ha<sup>-1</sup>, 0.006 Mg C 0.24 ha<sup>-1</sup> and 0.24 Mg C 0.24 ha<sup>-1</sup> were lost to logging, damage and natural mortality until 2014, respectively (Table 2). Logging intensity and collateral damage associated with cutting are summarised and compared to previous tropical forest studies in Table 4.

## Discussion

### Stand structure and dynamics

Sandy dipterocarp forests are characterised by the strong dominance of *D. obtusifolius*, with poor associated species richness (Appendix 1; Hiramatsu *et al.*, 2007; Tani *et al.*, 2007). Generally, numbers of dying and recruited trees of *D. obtusifolius* were similar in our study, suggesting a stable dynamic, resulting in a positively skewed log-normal distribution (Fig. 4a). These results are not inconsistent with previous reports of the species adapting well to edaphic and meteorological conditions specific to sandy dipterocarp forests (Norisada & Kojima, 2005a, 2007; Miyazawa *et al.*, 2014a, 2014b). However, it remains

**Table 3** Stand structure and tree biomass estimates reported in previous studies of Cambodian deciduous forests.

Index (unit)	This study (pre-logging)	Previous studies	Forests and measurement details in previous studies <sup>a</sup>	References
Tree density (trees ha <sup>-1</sup> )	379–433	626	Mixed deciduous forest in Kampong Thom- Sandan; trees with DBH >5 cm; tree components lacking <i>Do</i> , <i>Di</i> , <i>Dt</i> , <i>Ss</i> , and <i>Ta</i>	Kimphat <i>et al.</i> (2002a)
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	11.2–12.3	32.0		
Standing volume (m <sup>3</sup> ha <sup>-1</sup> )	74.1–83.0	179.2		
Aboveground biomass (Mg ha <sup>-1</sup> )	113.4–127.0	189	Deciduous forest in Kampong Thom; trees with DBH >10 cm; forest details unknown	Top <i>et al.</i> (2004)
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	11.2–12.3	24.8	Deciduous forest in Mondulkiri-Seima; trees with DBH >5 cm; dominated by <i>Dt</i>	Khun <i>et al.</i> (2012), Sasaki <i>et al.</i> (2016)
Standing volume (m <sup>3</sup> ha <sup>-1</sup> )	74.1–83.0	192.1		
Above-ground C stock (Mg C ha <sup>-1</sup> )	36.8–41.1	95.1		
Total (above-ground + below-ground) biomass (Mg ha <sup>-1</sup> )	131.7–147.6	257.8 ± 92.0 <sup>b</sup>	Deciduous forest in Preah Vihear, Kratie-Snoul, Kratie-Sandan; trees with DBH >5 cm; dominated by <i>Dt</i> , <i>Di</i> , <i>So</i> , and <i>Ta</i>	Kiyono <i>et al.</i> (2010)
Total tree C stock (Mg C ha <sup>-1</sup> )	66.7–74.8	55.2 ± 6.9 <sup>c</sup> , 56.2 ± 6.7 <sup>d</sup>	Deciduous forest in Ratanakiri, Siem Reap, Kampong Thom, Kratie; trees with DBH >7.5 cm; common species are <i>Do</i> , <i>Dt</i> , <i>Ss</i> , <i>So</i> , and <i>Ta</i>	Samreth <i>et al.</i> (2012)
Total biomass (Mg ha <sup>-1</sup> )	93.9–105.0	32.2–158.9	Deciduous dipterocarp forest in Kratie; trees with DBH >5 cm; forest details unknown	Monda <i>et al.</i> (2016)
Annual diameter increment (cm y <sup>-1</sup> )	0.14 ± 0.12 <sup>e</sup> 0.12 ± 0.08 <sup>f</sup> 0.19 ± 0.15 <sup>g</sup>	0.32	Deciduous forest in Kampong Thom; trees with DBH > 3 cm; commercial species; forest details unknown	FA (2014)
		0.45	Same; in Kratie	
		0.56	Same; in Siem Reap	
		0.14	Same; in Ratanakiri	

<sup>a</sup> *Do* = *Dipterocarpus obtusifolius*; *Di* = *D. intricatus*; *Dt* = *D. tuberculatus*; *Ss* = *Shorea siamensis*; *So* = *S. obtusa*; *Ta* = *Terminalia alata*. <sup>b</sup> Mean ± SD. <sup>c</sup> 1998 census, Mean ± SE. <sup>d</sup> 2000–2001 census, Mean ± SE. <sup>e</sup> All species, 2003–2014, Mean ± SD. <sup>f</sup> *D. obtusifolius*, 2003–2014, Mean ± SD. <sup>g</sup> Trees with DBH >30 cm, *D. obtusifolius* and *G. laccifera*, 2003–2011, Mean ± SD.

unclear why *D. obtusifolius* did not expand to occupy ground spaces which lacked tree canopy occupants (Fig. 2) and this is unlikely to be related to low-light conditions or a lack of flowering trees. Flowering was observed in much smaller trees (minimum diameter for flowering 11.8 cm; Ito *et al.*, 2016) than other dipterocarps (≥50 cm, Sist *et al.*, 2003b). Mycorrhizal limitation is a potential factor limiting recruitment, as symbiotic fungi promote the survival and growth of juveniles (Alexander *et al.*, 1992). As adult dipterocarps are a source of mycorrhizal colonisers that infect juvenile plants, logging of adult trees reduces the size of the fungal source pool.

The average mortality of trees with DBH ≥10 cm in the tropics is well documented (1.81 ± 0.16% y<sup>-1</sup>, mean ± 95% CI; Lewis *et al.*, 2004). Our study site had very low tree mortality for these individuals over the 11-year

census (1.03% y<sup>-1</sup>). High mortality for trees in the 5–10 cm DBH class (3.69% y<sup>-1</sup>) was mainly due to high turnover of some shrubby species (e.g., *M. scutellatum*; Fig. 4e). Numbers of recruited trees were balanced with the number of dying trees for trees with DBH ≥5 cm and ≥10 cm. Plotwise stem density was consequently relatively stable until the 2012 census (Fig. 3). This implies that the study forest is likely to be sustained in the absence of anthropogenic disturbance. Over the course of the study, we found that plot-wise mortality and recruitment rates were relatively high between the 2011–2014 censuses, followed by the 2008–2011 censuses and the 2003–2008 censuses (Fig. 3). Diameter increments for trees that survived during the course of the study were also higher during 2011–2014 than 2003–2011 (Appendix 3). The casual relationship underlying these trends in stand

**Table 4** Collateral damage associated with forest logging reported in previous studies.

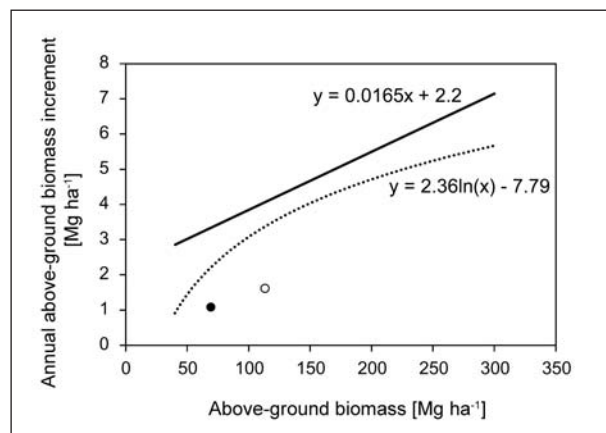
Index of collateral damage (unit)	This study	Previous studies	Conditions of forests and logging operations in previous studies	References
No. of collaterally damaged trees per felling of a single tree (tree tree <sup>-1</sup> )	<1	ca. 10	Closed-canopy neotropical forests with DBH 60–140 cm harvested	Jackson <i>et al.</i> (2002), Feldpausch <i>et al.</i> (2005)
Ratio of carbon stock, collateral trees to logged trees (%)	3.2	110	Amazonian humid tropical forest	Feldpausch <i>et al.</i> (2005)
Carbon stock loss to collateral tree damage (Mg C ha <sup>-1</sup> )	0.7	3.2	Amazonian humid tropical forest	Feldpausch <i>et al.</i> (2005)
Cutting intensity normalised by proportion of damaged trees (2.5% of original tree population) (trees ha <sup>-1</sup> )	20.8	<4	East Kalimantan forest	Sist <i>et al.</i> (1998)
Proportion of canopy lost at cutting intensity of 50 m <sup>3</sup> ha <sup>-1</sup> (%)	20.8	39.1	Regression from 11 previous studies including a Brazilian moist tropical forest, conventional cutting operations	Pereira <i>et al.</i> (2002)
		22.7	Same, reduced-impact logging operations	Pereira <i>et al.</i> (2002)
Ratio of skidding damage of original stand area (%)	Not measured	25	Dense evergreen forest in Indonesian Borneo	Sist <i>et al.</i> (2003a)

dynamics are unknown, but they may reflect changing climatic or edaphic conditions.

#### Stand C storage and increments

Sandy dipterocarp forests are characterised by an open structure (Rundel, 1999; Hiramatsu *et al.*, 2007; FA, 2011). This is consistent with lower plot-wise C storage and its relating forest structure indices found in the study plot compared with various Cambodian deciduous forests (Table 3). Given the positive relationship between annual above-ground biomass increment and above-ground biomass (Top *et al.*, 2004a; Kiyono *et al.*, 2017), the biomass increment in sandy dipterocarp forests is expected to be lower than other types of deciduous forests. The mean increment for above-ground stand biomass for the average initial above-ground stand biomass has been estimated to be 4.59 Mg ha<sup>-1</sup> y<sup>-1</sup> for deciduous forests (Top *et al.*, 2004a), and 4.79 Mg ha<sup>-1</sup> y<sup>-1</sup> for unstratified forest categories (Kiyono *et al.*, 2017). These estimates are fairly high compared to the values estimated in our study (1.61 Mg ha<sup>-1</sup> y<sup>-1</sup> and 1.08 Mg ha<sup>-1</sup> y<sup>-1</sup>, using Eqs. 5 and 6, respectively). The latest application of the gain–loss method nationally in Cambodia assumed that a more conservative mean annual increment would be identical to all of the forest categories (1.5 MgC ha<sup>-1</sup> y<sup>-1</sup>, Sasaki *et al.*, 2016), which was twice our study estimate (0.74 MgC ha<sup>-1</sup> y<sup>-1</sup>, using Eq. 3). It is also noteworthy that the above-ground biomass increments in our study plot were 48% and 32%

of the expected values for initial above-ground biomass using regression relationships (Fig. 5). The absolute and relative low C increment in our study plot suggests that sandy dipterocarp forests might need to be stratified into



**Fig. 5** Relationship between plot-wise annual above-ground biomass increment and initial above-ground biomass. Dotted and solid lines represent regression lines of the relationships reported by Top *et al.* (2004a) and Kiyono *et al.* (2017), respectively. Circles indicate a combination of annual above-ground biomass increment and initial above-ground biomass in study plot. Open and closed circles indicate biomass estimation using equations identical to Top *et al.* (2004a) and Kiyono *et al.* (2017), respectively.

subdivisions of deciduous forests when implementing the gain–loss approach. Given the low mortality and balanced recruitment of our study plot, the relatively low increment suggests that tree growth was limited. Though seemingly lower diameter increments were found at our study site than those reported for Cambodian deciduous forests (FA, 2004), lack of detailed information for the latter prevent meaningful comparisons (Table 3; Appendix 3). We still do not know why sandy dipterocarp forest has a relatively low increment, although this is not related to light availability. *Dipterocarpus obtusifolius* physiologically adapts to seasonal flood and drought conditions (Miyazawa *et al.*, 2014a, 2014b), high irradiance levels (Norisada & Kojima, 2005a), and high temperatures (Norisada & Kojima, 2007). The nutritional responses of the species are also similar to other canopy-dominating dipterocarp species in sandy soils (Norisada & Kojima, 2005b). Acrisols underlying sandy dipterocarp forests are generally nutrient-poor soils compared to more nutrient-rich plinthite in dry dipterocarp forests on the east bank of Mekong (Toriyama *et al.*, 2007a, 2010). Thus, growth of *D. obtusifolius* might be limited by the nutrient-poor edaphic conditions of our study site.

#### Logging and its impact on C stock

The four logged and fallen tree species in our study are often targets for both timber and fuel extraction (Top *et al.*, 2004b; San *et al.*, 2012). The wood of *D. obtusifolius* is graded as durable (Grade II: MAFF, 2005) and subject to commercial exploitation (Kim Phat *et al.*, 1999). Large logged trees of *D. obtusifolius* and *G. laccifera* in the studied plot were possibly used for timber, while the small trunks (<30 cm DBH) left behind may have been felled for fuel (Top *et al.*, 2004b) or used to test chainsaw performance. Over-exploitation of forest resources has been reported in the region (KimPhat *et al.*, 2001; Top *et al.*, 2004c). Basal area depletion from logging in our study plot (34.4%) was above the indicative criteria for sustainable logging operations (<15%) proposed in East Kalimantan (Sist & Nguyen-Thé, 2002). For Cambodian mixed forests, Kimphat *et al.* (2002a) tentatively proposed a sustainable harvest potential as selective felling of 30% of the stand volume during a 30-year cutting cycle. Logging in the study plot removed substantial C stocks (5.37 MgC 0.24 ha<sup>-1</sup>, 42.6% of the pre-logging value), which is equivalent to a C increment of 30 years (accrual rate 1.42 Mg C 0.24 ha<sup>-1</sup> 8y<sup>-1</sup>; Table 2). Notably, the annual tree C stock increment would decline after cutting operations. A sustainable cutting cycle prediction should be based on the remaining basal area after felled trees are deducted (Sist *et al.*, 2003c; Kimphat *et al.*, 2004).

Selective logging, particularly in operations without a sustainable management plan, is frequently associated with serious collateral forest damage (Pereira *et al.*, 2002; Sasaki & Putz, 2009). The extent of collateral damage in our study plot, however, appeared to be less than that reported for logging operations in other tropical forests (Table 4). This is obviously due to the low tree density of our study plot. Tree density and basal area for individuals with <10 cm DBH values in previous studies were ca. 525 trees ha<sup>-1</sup> and 57 m<sup>2</sup> ha<sup>-1</sup>, respectively (Sist *et al.*, 1998; Pereira *et al.*, 2002; Feldpausch *et al.*, 2005; Table 4). The respective values for our study plot were rescaled to 254 trees ha<sup>-1</sup> and 11.7 m<sup>2</sup> ha<sup>-1</sup>, respectively. Such low tree densities and basal areas are found in other sandy dipterocarp forests (e.g., 235 trees ha<sup>-1</sup> and 5.5 m<sup>2</sup> ha<sup>-1</sup>: FA, unpublished data). Directional felling without collateral damage to other trees is greatly simplified in sparse forests (Feldpausch *et al.*, 2005). Skid damage could also be minimised with basic requirements for logging roads in sparse forests compared to dense forests (Sist *et al.*, 2003a).

How intensive logging alters stand dynamics in sandy dipterocarp forests is still unknown. Logging has the potential to accelerate the growth of surviving trees (Putz *et al.*, 2001), as light conditions improve when a dense forest is thinned (Kao *et al.*, 2011). However, our open-canopied sandy dipterocarp forest likely had unlimited light availability. Along increasing environmental stress gradients, sandy dipterocarp forests become increasingly open in structure and lower in stature, grading eventually into savanna woodlands with decreasing woody cover (Rundel, 1999). Further studies are necessary to clarify whether over-exploitation increases environmental stress and leads to further forest degradation.

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## Appendix 1 List of component species in study plot, Kampong Thom Province, Cambodia.

Family (APG III)	Species <sup>a</sup>	Khmer name <sup>a</sup>	Basic density <sup>b</sup> (kg m <sup>-3</sup> )	Data source <sup>c</sup>
Anacardiaceae	<i>Gluta laccifera</i> (Pierre) Ding Hou	Krouel	689	Cambodia
Annonaceae	<i>Xylopiya vielana</i> Pierre	Kray Krahom	570	Default
Calophyllaceae	<i>Calophyllum calaba</i> L. var. <i>bracteatum</i> (Wight) P.F.Stevens	Phaong	570	Default
Chrysobalanaceae	<i>Parinari anamensis</i> Hance	Thlok	641	Cambodia
Dipterocarpaceae	<i>Dipterocarpus obtusifolius</i> Teijsm. ex Miq.	Tbeng	650	Vietnam
Melastomataceae	<i>Memecylon scutellatum</i> (Lour.) Hook. & Arn.	Phlorng	570	Default
Moraceae	<i>Artocarpus</i> sp.	Kroung	570	Default
Myrtaceae	<i>Syzygium oblatum</i> (Roxb.) Wall. ex A.M.Cowan & Cowan	Pring	570	Default
Pentaphylacaceae	<i>Anneslea fragrans</i> Wall.	Sorphy	634	Myanmar
Rubiaceae	<i>Catunaregam tomentosa</i> (Blume ex DC.) Tirveng.	Ror Veang	570	Default
Symplocaceae	<i>Symplocos cochinchinensis</i> subsp. <i>laurina</i> (Retz.) Nooteboom	Luot	538	Cambodia

<sup>a</sup> Scientific names and Khmer names refer to Toyama *et al.* (2013); <sup>b</sup> Chave *et al.* (2009) and Zanne *et al.* (2009) were used for data selection; <sup>c</sup> Country name indicates place where original data were obtained, while default indicates the default value for tropical Asia (Brown, 1997).



Appendix 2 Species-specific basal area and stem density per DBH class in the first (2003), pre-logging (2011), and post-logging (2014) censuses at study plot, Kampong Thom Province, Cambodia.

2003 (first) census. Basal area is given as  $\text{m}^2 \text{ha}^{-1}$  and stem density (in parentheses) is given as trees  $0.24 \text{ha}^{-1}$ . Only genus names are shown (see Appendix 1 for full scientific names).

Genus	DBH class (cm)												Total	
	5–10		10–20		20–30		30–40		40–50		50–60			
<i>Gluta</i>	–	(–)	–	(–)	0.15	(1)	–	(–)	2.07	(3)	1.81	(2)	4.03	(6)
<i>Xylopi</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Calophyllum</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Parinari</i>	0.07	(3)	0.06	(1)	0.44	(2)	–	(–)	–	(–)	–	(–)	0.57	(6)
<i>Dipterocarpus</i>	0.34	(18)	2.06	(28)	1.31	(8)	1.36	(3)	0.69	(1)	–	(–)	5.76	(58)
<i>Memecylon</i>	0.16	(13)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.16	(13)
<i>Artocarpus</i>	0.07	(5)	0.03	(1)	–	(–)	–	(–)	–	(–)	–	(–)	0.10	(6)
<i>Syzygium</i>	–	(–)	0.33	(4)	0.17	(1)	–	(–)	–	(–)	–	(–)	0.50	(5)
<i>Anneslea</i>	–	(–)	0.06	(1)	–	(–)	–	(–)	–	(–)	–	(–)	0.06	(1)
<i>Catunaregam</i>	0.03	(2)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.03	(2)
<i>Symplocos</i>	0.03	(1)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.03	(1)
<b>Total</b>	<b>0.70</b>	<b>(42)</b>	<b>2.54</b>	<b>(35)</b>	<b>2.07</b>	<b>(12)</b>	<b>1.36</b>	<b>(3)</b>	<b>2.76</b>	<b>(4)</b>	<b>1.81</b>	<b>(2)</b>	<b>11.24</b>	<b>(98)</b>

2011 (pre-logging) census. Basal area is given as  $\text{m}^2 \text{ha}^{-1}$  and stem density (in parentheses) is given as trees  $0.24 \text{ha}^{-1}$ .

Genus	DBH class (cm)												Total	
	5–10		10–20		20–30		30–40		40–50		50–60			
<i>Gluta</i>	–	(–)	–	(–)	0.18	(1)	–	(–)	1.38	(2)	2.90	(3)	4.46	(6)
<i>Xylopi</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Calophyllum</i>	0.04	(3)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.04	(3)
<i>Parinari</i>	0.03	(2)	0.20	(4)	0.20	(1)	0.41	(1)	–	(–)	–	(–)	0.84	(8)
<i>Dipterocarpus</i>	0.30	(16)	2.30	(30)	1.52	(9)	1.39	(3)	0.71	(1)	–	(–)	6.22	(59)
<i>Memecylon</i>	0.14	(12)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.14	(12)
<i>Artocarpus</i>	0.03	(2)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.03	(2)
<i>Syzygium</i>	–	(–)	0.27	(3)	0.18	(1)	–	(–)	–	(–)	–	(–)	0.46	(4)
<i>Anneslea</i>	–	(–)	0.06	(1)	–	(–)	–	(–)	–	(–)	–	(–)	0.06	(1)
<i>Catunaregam</i>	0.03	(2)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.03	(2)
<i>Symplocos</i>	–	(–)	0.04	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.04	(1)
<b>Total</b>	<b>0.57</b>	<b>(36)</b>	<b>2.87</b>	<b>(39)</b>	<b>2.08</b>	<b>(12)</b>	<b>1.8</b>	<b>(4)</b>	<b>2.09</b>	<b>(3)</b>	<b>2.9</b>	<b>(3)</b>	<b>12.31</b>	<b>(97)</b>

## Appendix 2 Cont'd

2014 (post-logging) census. Basal area is given as m<sup>2</sup> ha<sup>-1</sup> and stem density (in parentheses) is given as trees 0.24 ha<sup>-1</sup>.

Genus	DBH class (cm)												Total	
	5–10		10–20		20–30		30–40		40–50		50–60			
<i>Gluta</i>	–	(–)	–	(–)	0.19	(1)	–	(–)	1.45	(2)	–	(–)	1.64	(3)
<i>Xylopia</i>	0.04	(4)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.04	(4)
<i>Calophyllum</i>	0.06	(3)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.06	(3) <sup>a</sup>
<i>Parinari</i>	0.02	(1)	0.24	(4)	0.21	(1)	0.44	(1)	–	(–)	–	(–)	0.91	(6)
<i>Dipterocarpus</i>	0.31	(16)	1.92	(23)	1.74	(10)	0.98	(2)	–	(–)	–	(–)	4.95	(51)
<i>Memecylon</i>	0.12	(10)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.12	(10)
<i>Artocarpus</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Syzygium</i>	–	(–)	0.16	(2)	0.33	(2)	–	(–)	–	(–)	–	(–)	0.49	(4)
<i>Anneslea</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Catunaregam</i>	0.03	(2)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.03	(2)
<i>Symplocos</i>	–	(–)	0.05	(1)	–	(–)	–	(–)	–	(–)	–	(–)	0.05	(1)
<b>Total</b>	<b>0.58</b>	<b>(36)</b>	<b>2.37</b>	<b>(30)</b>	<b>2.47</b>	<b>(14)</b>	<b>1.42</b>	<b>(3)</b>	<b>1.45</b>	<b>(2)</b>	–	(–)	<b>8.29</b>	<b>(85)</b>

<sup>a</sup> One tree was cut higher than 1.3 m, but still alive.

### Appendix 3 Species-specific diameter increments per DBH class for the first (2003), pre-logging (2011), and post-logging(2014) censuses in study plot, Kampong Thom Province, Cambodia.

2003–2011 (first to pre-logging) census. Diameter increments are given as mean  $\pm$ SD, (cm year<sup>-1</sup>). Sample sizes are given in parenthesis. Only genus names are shown (see Appendix 1 for full scientific names).

Genus	DBH class (cm)												Total	
	5–10		10–20		20–30		30–40		40–50		50–60			
<i>Gluta</i>	–	(–)	–	(–)	0.22	(1)	–	(–)	0.29 $\pm$ 0.09	(3)	0.33 $\pm$ 0.04	(2)	0.29 $\pm$ 0.07	(6)
<i>Xylopia</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Calophyllum</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Parinari</i>	0.33 $\pm$ 0.14	(3)	0.38	(1)	0.52 $\pm$ 0.27	(2)	–	(–)	–	(–)	–	(–)	0.40 $\pm$ 0.18	(6)
<i>Dipterocarpus</i>	0.10 $\pm$ 0.09	(17)	0.11 $\pm$ 0.07	(28)	0.08 $\pm$ 0.05	(8)	0.05 $\pm$ 0.08	(3)	0.07	(1)	–	(–)	0.10 $\pm$ 0.07	(57)
<i>Memecylon</i>	0.04 $\pm$ 0.12	(7)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.04 $\pm$ 0.12	(7)
<i>Artocarpus</i>	-0.01	(1)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	-0.01	(1)
<i>Syzygium</i>	–	(–)	0.01 $\pm$ 0.02	(3)	0.13	(1)	–	(–)	–	(–)	–	(–)	0.04 $\pm$ 0.06	(4)
<i>Anneslea</i>	–	(–)	-0.01	(1)	–	(–)	–	(–)	–	(–)	–	(–)	-0.01	(1)
<i>Catunaregam</i>	0.02 $\pm$ 0.00	(2)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.02 $\pm$ 0.00	(2)
<i>Symplocos</i>	0.24	(1)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.24	(1)
<b>Total</b>	<b>0.11</b> <b><math>\pm</math>0.13</b>	<b>(31)</b>	<b>0.11</b> <b><math>\pm</math>0.09</b>	<b>(33)</b>	<b>0.17</b> <b><math>\pm</math>0.19</b>	<b>(12)</b>	<b>0.05</b> <b><math>\pm</math>0.08</b>	<b>(3)</b>	<b>0.24</b> <b><math>\pm</math>0.13</b>	<b>(4)</b>	<b>0.33</b> <b><math>\pm</math>0.04</b>	<b>(2)</b>	<b>0.12</b> <b><math>\pm</math>0.13</b>	<b>(85)</b>

## Appendix 3 Cont'd

2011–2014 (pre-logging to post-logging) census.

Genus	DBH class (cm)												Total	
	5–10		10–20		20–30		30–40		40–50		50–60			
<i>Gluta</i>	–	(–)	–	(–)	0.24	(1)	–	(–)	0.38 ±0.22	(2)	–	(–)	0.33 ±0.17	(3)
<i>Xylopia</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Calophyllum</i>	0.48 ±0.13	(3)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.48 ±0.13	(3)
<i>Parinari</i>	0.24 ±0.23	(2)	0.39 ±0.24	(4)	0.34	(1)	0.40	(1)	–	(–)	–	(–)	0.35 ±0.19	(8)
<i>Dipterocarpus</i>	0.10 ±0.17	(14)	0.20 ±0.14	(24)	0.17 ±0.15	(9)	0.06 ±0.08	(2)	–	(–)	–	(–)	0.16 ±0.15	(49)
<i>Memecylon</i>	0.10 ±0.15	(9)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.10 ±0.15	(9)
<i>Artocarpus</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Syzygium</i>	–	(–)	0.15 ±0.06	(3)	0.39	(1)	–	(–)	–	(–)	–	(–)	0.21 ±0.13	(4)
<i>Anneslea</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Catunaregam</i>	0.10 ±0.06	(2)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.10 ±0.06	(2)
<i>Symplocos</i>	–	(–)	0.32	(1)	–	(–)	–	(–)	–	(–)	–	(–)	0.32	(1)
<b>Total</b>	<b>0.15</b> <b>±0.19</b>	<b>(30)</b>	<b>0.23</b> <b>±0.16</b>	<b>(32)</b>	<b>0.21</b> <b>±0.15</b>	<b>(12)</b>	<b>0.17</b> <b>±0.21</b>	<b>(3)</b>	<b>0.38</b> <b>±0.22</b>	<b>(2)</b>	–	(–)	<b>0.20</b> <b>±0.17</b>	<b>(79)</b>

2003–2014 (first to post-logging) census.

Genus	DBH class (cm)												Total	
	5–10		10–20		20–30		30–40		40–50		50–60			
<i>Gluta</i>	–	(–)	–	(–)	0.22	(1)	–	(–)	0.29 ±0.01	(2)	–	(–)	0.26 ±0.04	(3)
<i>Xylopia</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Calophyllum</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Parinari</i>	0.34 ±0.17	(3)	0.39	(1)	0.48 ±0.21	(2)	–	(–)	–	(–)	–	(–)	0.39 ±0.16	(6)
<i>Dipterocarpus</i>	0.10 ±0.09	(15)	0.14 ±0.08	(23)	0.10 ±0.05	(8)	0.02 ±0.00	(2)	–	(–)	–	(–)	0.12 ±0.08	(48)
<i>Memecylon</i>	0.07 ±0.06	(5)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.07 ±0.06	(5)
<i>Artocarpus</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Syzygium</i>	–	(–)	0.05 ±0.03	(3)	0.20	(1)	–	(–)	–	(–)	–	(–)	0.09 ±0.08	(4)
<i>Anneslea</i>	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)
<i>Catunaregam</i>	0.04 ±0.01	(2)	–	(–)	–	(–)	–	(–)	–	(–)	–	(–)	0.04 ±0.01	(2)
<i>Symplocos</i>	–	(–)	0.26	(1)	–	(–)	–	(–)	–	(–)	–	(–)	0.26	(1)
<b>Total</b>	<b>0.12</b> <b>±0.12</b>	<b>(26)</b>	<b>0.14</b> <b>±0.09</b>	<b>(27)</b>	<b>0.18</b> <b>±0.16</b>	<b>(12)</b>	<b>0.02</b> <b>±0.00</b>	<b>(2)</b>	<b>0.29</b> <b>±0.01</b>	<b>(2)</b>	–	(–)	<b>0.14</b> <b>±0.12</b>	<b>(69)</b>