ORIGINAL ARTICLE

Effects of large aboveground biomass loss events on the deadwood and litter mass dynamics of seasonal tropical forests in Cambodia

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Received: July 1, 2018 Accepted: August 15, 2018

ABSTRACT Dead organic matter (DOM), which includes deadwood (DW) and litter (LT), plays an important role in forest ecosystem functions. To date, little DOM data have been collected in the seasonal forests of Indochina. We monitored DW and LT masses in Cambodian seasonal forests during a period of 10 years at intervals of 1–2 years in 22 permanent sample plots (PSPs) in evergreen forest (EF, $n = 10$) and deciduous forest (DF, $n = 12$) deployed across Cambodia. We found that large aboveground biomass (AGB) loss events, which were probably caused by logging, increased DW mass and DOM carbon stock. However, such AGB loss events did not necessarily affect LT masses (i.e., coarse LT [CLT] and fine LT including partly decomposed roots to a soil depth of 5 cm [FLT]). The mean DOM carbon stock and masses of DW, LT, CLT, and FLT during the study period had no significant relationships with AGB in either EF or DF. DOM and its components exhibited large spatial variations, suggesting that additional sampling is required for greater precision. The Cambodian seasonal forest was characterized by a relatively small DW mass, possibly due to anthropogenic removal of DW and dying trees.

Key words: carbon, country level, DOM, Indochina, nationwide scale

INTRODUCTION

Dead organic matter (DOM), including deadwood (DW) and litter (LT), plays an important role in nutrient and carbon cycling in forest ecosystems (Sayer 2005, Palace et al. 2012). For residents relying on forests as a resource, medium- to large-diameter DW is an important source of fuel due to its high caloric content (Chambers et al. 1999, Yan et al. 2007) and the edible wood-rotting fungus mushrooms that are available over protracted periods. Improved understanding of the magnitude and spatio-temporal variation (Hopkins 1966, Yoneda et al. 1990) in DOM is crucial for sustainable forest management in regions subjected to environmental disturbance.

Most DOM studies have been conducted in the Americas (Powers et al. 2009, Palace et al. 2012). The DW mass of Malaysian tropical rainforests has been compared to that of the Amazon (Sato et al. 2016). However, few DOM data have been collected in seasonal tropical forests (Vogt et al. 1986, Yoneda et al. 1991, Kiyohara et al. 2004,

Palace et al. 2012). Data on DOM dynamics are scarce (Kiyono et al. 2010, Ito et al. 2014); in particular, long-term LT mass trends have been little studied (Hopkins 1966, Spain 1984, Wieder and Wright 1995). Countrywide DOM estimates have never been calculated for the compilation of national carbon accounts or sustainable forest management in the seasonal forests of Indochinese countries.

Thus, we examined the effects of disturbance and the resultant large aboveground biomass (AGB) losses on DOM dynamics in seasonal forests of Cambodia that are subjected to anthropogenic influences. The components of our study were as follows. (i) We monitored forest DOM dynamics in permanent sample plots (PSPs) deployed on a nationwide scale. (ii) To estimate the influence of large AGB loss events on temporal changes in DOM, we compared PSPs that experienced large AGB loss events with those that did not. (iii) We calculated the mean $\pm$ standard deviation (SD) of DW and LT masses and DOM carbon stocks in the PSPs during the study period and compared them with values obtained in other seasonal

Fig. 1. Locations of permanent sample plots (PSPs) in Cambodia (modified from Kiyono et al. 2017).

Evergreen forest (EF) includes semi-evergreen forest (SEF). Circles represent EF. Squares represent deciduous forest (DF). The forest cover map was modified from data available at <http://www.opendevdevelopmentcambodia.net/>. Non-forested areas comprised cropland, grassland, wetlands, settlements, and other land uses (National Institute for Environmental Studies et al. 2005). Dashed lines (based on the descriptions in Akinaga 1943) indicate the boundaries of three main forest-cover regions: the Mekong Basin, the coast of Tonlé Sap Lake, and the Krâvanh (Cardamom) Mountains.

tropical forests.

STUDY SITES AND METHODS

Cambodian forest types

Forests in Cambodia (Fig. 1) include three main forest-cover regions: the Mekong Basin, the coast of Tonlé Sap Lake, and the Krâvanh (Cardamom) Mountains (Akinaga 1943). They can be divided into lowland forests, montane forests, and azonal forest formations (Rundel 1999). Cambodian forests comprise evergreen forest (EF), semi-evergreen forest (SEF), and deciduous forest (DF) (Samreth et al. 2012). All forests are subject to a tropical monsoon climate, with a pronounced rainy season from about May to October, and a dry season from November to around April (World Bank Group 2015). The mean annual temperature is 26.5–30°C, except at high altitudes on mountains. The geology is mainly sandy alluvium, shale and other impermeable rock, sandstone, and conglomerates in hilly regions and clayish and silty alluvium in the lowlands (Crocker 1962). The mean annual precipitation ranged from 1,400 to >4,000 mm, depending on the region, during 1990–2012 (World Bank Group 2015). Monthly precipitation in

Cambodia during the study period (2003–2012) is shown in Fig. 2. For the purposes of the United Nations Framework Convention on Climate Change (UNFCCC), Cambodia defines a forest as having a minimum tree crown cover of 10 %, a minimum area of 0.5 ha, and a minimum tree height of 5 m (<http://cdm.unfccc.int/DNA/index.html>). The mean carbon stocks of four carbon pools (AGB, belowground biomass, DW, and LT) per unit land area were estimated in a previous study (Kiyono et al. 2010) using the PSP data from the Ministry of Environment, Cambodia (MoE-PSP) for the three main forest types (EF including SEF, DF, and secondary forest). Using Forestry Administration PSP data, the mean carbon stocks of two carbon pools (AGB and belowground biomass) of trees per unit land area were estimated for two main forest types (EF including SEF and DF) (Samreth et al. 2012). EF had a larger carbon stock than DF in terms of biomass (Kiyono et al. 2010, 2017; Samreth et al. 2012) and soils within the same geological formations (Toriyama et al. 2011).

PSP data

We selected 22 MoE-PSPs (Table 1) from the 49 PSPs listed in Kiyono et al. (2017). The 22 PSPs were distributed

Fig. 2. Historical monthly precipitation (World Bank Group 2015).

The values are for all of Cambodia and are based on a model output spatially disaggregated and downscaled to a minimum 50-km resolution. The annual rainfall in the period April 2010–March 2011 (1568 mm year⁻¹, i.e., rainfall in two different years, including one year before the litter (LT) mass survey in March 2012) was the lowest in the period April 2003 to March 2015 (12-year average: 1933 ± 294 mm, mean ± SD). The annual rainfall during the period April 2011–March 2012 (2128 mm year⁻¹ in the year before the LT mass survey in March 2012) was the second largest within the same 12-year period.

Table 1. General description of the permanent sample plots (PSPs) used in this study.

PSP no.	Province	Forest type ¹	Dominant sp. ²	Elevation m	MAP ³ mm	Dead organic matter census ⁴ Year
1	Siem Reap	EF	Dd	23	1486	2005, 2006, 2008 ⁵ , 2010, 2011, 2012, 2013, 2014, 2015
2	Siem Reap	EF	Dd	28	1486	2005, 2006, 2008 ⁵ , 2010, 2011, 2012, 2013, 2014, 2015
3	Kratie	EF	Im	111	1748	2005, 2006, 2008 ⁵ , 2010, 2011, 2012
4	Kratie	EF	Im	89	1748	2005, 2006
5	Kratie	EF	Dc	100	1748	2010, 2011, 2012, 2013
6	Kampot	EF	Le	688	2530	2005, 2006, 2008 ⁵ , 2010, 2011, 2012, 2013, 2014, 2015
7	Kampot	EF	Sl	675	2530	2005, 2006, 2008 ⁵ , 2010, 2011, 2012, 2013, 2014, 2015
8	Sihanoukville	EF	At	31	3013	2005, 2006
9	Koh Kong	EF	Nh	80	3100	2011, 2012, 2013, 2014, 2015
10	Koh Kong	EF	Im	65	3100	2011, 2012, 2013, 2014, 2015
11	Preah Vihear	DF	Di	76	1745	2005, 2006, 2008 ⁵ , 2010, 2011, 2012, 2013, 2014, 2015
12	Preah Vihear	DF	So	73	1745	2005, 2006, 2008 ⁵ , 2010, 2011, 2012, 2013, 2014, 2015
13	Kratie	DF	Dt	68	1748	2005, 2006
14	Kratie	DF	So	77	1796	2010, 2011, 2012, 2013, 2014, 2015
15	Kratie	DF	Ss	74	1796	2010, 2011, 2012, 2013, 2014, 2015
16	Sihanoukville	DF	Eu	29	3013	2005, 2006
17	Kampong Speu	DF	So	128	2176	2008 ⁵ , 2010, 2011, 2012, 2013, 2014, 2015
18	Kampong Speu	DF	So	163	2176	2008 ⁵ , 2010, 2011, 2012, 2013, 2014, 2015
19	Kampong Chhnang	DF	So	150	1710	2011, 2012, 2013, 2014, 2015
20	Kampong Chhnang	DF	Pf	160	1710	2011, 2012, 2013, 2014, 2015
21	Pursat	DF	So	230	2117	2011, 2012, 2013, 2014, 2015
22	Pursat	DF	So	225	2117	2011, 2012, 2013, 2014, 2015

¹ Evergreen forest (EF) including semi-evergreen forest (SEF) and deciduous forest (DF). ² At, *Albizia thorelli*; Dc, *Dipterocarpus costatus*; Dd, *Dipterocarpus dyeri*; Im, *Irvingia malayana*; Le, *Lithocarpus elephantum*; Sl, *Syzygium lineatum*; Nh, *Nephelium hypoleucum*; Di, *Dipterocarpus intricatus*; So, *Shorea obtusa*; Dt, *Dipterocarpus tuberculatus*; Ss, *Shorea siamensis*; Eu, *Eugenia* sp.; Pf, *Peltophorum ferrugineum*. ³ Mean annual precipitation. ⁴ Measured during the dry season (February–April). ⁵ Also measured in the rainy season (September 2008).

among all of the three main forest-cover regions (Akinaga 1943) at 23–688 m a.s.l.: (i) three PSPs in EF and another three in DF in the Mekong Basin; (ii) two PSPs in EF and six PSPs in DF along the coast of Tonlé Sap Lake; (iii) six PSPs in EF and two PSPs in DF in the Krâvanh (Cardamom) Mountains (Fig. 1). Each PSP contained nested plots measuring 20×100 m and 5×40 m. Botanical name and diameter at breast height (DBH) were recorded for trees (including standing dead trees) with a DBH ≥ 30 cm in the 20×100 -m plots and with a DBH ≥ 5 cm in the 5×40 -m plots. DBH was measured using a measuring tape at a height of 1.3 m, except in cases of trunk irregularity or branching, in which case diameter was measured just below or above that height. Tree height was measured using a handheld clinometer (Suunto, Finland). Nomenclature followed Pauline (2000). Common tree species included *Albizia thorelli*, *Dipterocarpus costatus*, *Irvingia malayana*, *Lithocarpus elephantum*, *Nephelium hypoleucum*, and *Syzygium lineatum* in EF; *D. intricatus*, *D. tuberculatus*, *Eugenia* sp., *Peltophorum ferrugineum*, *Shorea obtusa*, *S. siamensis*, *Terminalia tomentosa*, and *Xylia dolabriformis* in DF; and *D. dyeri* and *Lagerstroemia cochinchinensis* in SEF. Although no history of anthropogenic intervention in the PSP forests has been recorded, some evidences of selective logging and firewood extraction were found. Judging from the composition of the dominant species (e.g., fewer *P. dasyrrhachis*, a pioneer species in EF and SEF), the PSP forests were not used for slash-and-burn farming. The tree census was repeated irregularly two to nine times per PSP during the dry seasons between 2005 and 2015. Although no National Forest Inventory (NFI) has been performed in Cambodia, the projected area of the studied PSPs (0.2 ha) was within the 0.1–0.5 ha often used in the NFIs of other countries (Sato 2012). For simplification, we included SEF in the EF category in this paper, based on previous studies (Kiyono et al. 2010, 2017; Samreth et al. 2012), given that the tree biomasses of these two forest types were similar. The MoE-PSPs included some secondary forests, which were considered EF or DF according to their tree composition. Edaphic conditions (Clark et al. 2002) such as the topography of the PSP forests were ignored.

Aboveground DW mass (hereafter DW mass) and LT mass were repeatedly measured in the 22 PSPs at 1–2-year intervals for periods of 2–10 years (Table 1). We adopted the DOM measurement techniques of Hairiah et al. (2001) and Kiyono et al. (2010). To estimate DW volume, we recorded the diameter and length of woody debris on the ground (dead trees and stumps) with a diameter >5 cm and length >0.5 m in the 5×40 -m plot. In five of the 0.5×0.5 -

m subplots systematically arranged within each 5×40 -m plot, we collected coarse LT (CLT), defined as woody debris ≤ 5 cm in diameter and/or ≤ 0.5 m in length and all of the undecomposed and unburned leaves and branches. We also collected fine LT (FLT), defined as dark-colored LT including leaves, branches and all woody roots that had partly decomposed and passed through a 2-mm mesh sieve, to a soil depth of 5 cm.

DW in the diameter range of 2–5 cm was included in CLT in this study, which also included other plant organs, such as leaves. DW as defined in many other studies (i.e., debris with diameters >2 cm or >2.5 cm; Jaramillo et al. 2003, Palace et al. 2012) falls between DW and DW plus CLT in the present study. LT mass defined in many other studies (diameter <2 cm or <2.5 cm; Wieder and Wright 1995, Jaramillo et al. 2003) falls roughly between the FLT and FLT plus CLT masses in this study.

Some trees were lost during the study period. In forests with stand AGB losses amounting to 5–20 % of the initial values, the missing trees were mostly timber species with large DBHs, suggesting that logging and collateral damage were the main causes of tree death (Kiyono et al. 2017). In our study, stand AGB losses ≥ 5 % year⁻¹ of initial stand values of ≥ 100 Mg ha⁻¹ were defined as large-stand AGB losses and were probably caused by logging; few large trees died in PSPs with initial stand values <100 Mg ha⁻¹.

LT data collection in the rainy season

Field surveys were conducted in the dry season as fieldwork in the rainy season was difficult; however, in 2008, surveys were conducted in both the dry and rainy seasons to enable comparison between seasons.

As described above, EF data were collected from 10 PSPs; these data included 60 censuses of trees, DW, and LT during the dry season, and 5 LT censuses during the rainy season (5–27 September 2008) (Table 1). DF data were collected from 12 PSPs and included 68 censuses of trees, DW, and LT during the dry season, and 4 LT censuses during the rainy season (1–30 September 2008) (Table 1).

Estimating tree AGB, DW mass, LT mass, and DOM carbon stock

Tree AGB was estimated using DBH data and the following generic allometry equation for tropical and subtropical trees (Kiyono et al. 2006, 2017): $Tree\ AGB = 11545\ ba^{1.24}$ ($n = 515$, $R^2 = 0.963$, $P < 0.0001$), where *Tree*

AGB is the sum of the aboveground organ (e.g., leaf, branch, stem) mass (kg), and *ba* is the basal area of a stem at a height of 1.3 m (m^2). The equation is derived from data for trees with $1 \leq \text{DBH} \leq 51$ cm.

The dry matter weight of standing dead trees was assumed to be 80 % of the weight of living trees (4.3.3.5.3 in IPCC 2003). Although the density of woody debris significantly varies (Keller et al. 2004), we assumed a basic density of 0.45 Mg m^{-3} (value for Laos in Kiyono et al. 2007) in the conversion of volume to dry matter weight: $Wd = 0.45 Vd$, where *Wd* is the weight of DW (Mg) and *Vd* is the volume of woody debris on the ground and in stumps (m^3). The tree species common in Cambodian forests were considered to have a wood basic density of $0.68 \pm 0.10 \text{ Mg m}^{-3}$ (mean $\pm$ SD ; range $0.55\text{--}0.86 \text{ Mg m}^{-3}$) in EF, including SEF, and $0.64 \pm 0.08 \text{ Mg m}^{-3}$ (range $0.55\text{--}0.77 \text{ Mg m}^{-3}$) in DF (IPCC 2006, Uji 1998). The extent of decay is generally divided into several classes (Palace et al. 2012). For example, $0.36\text{--}0.74 \text{ Mg m}^{-3}$ (Eaton and Lawrence 2006) and $0.22\text{--}0.54 \text{ Mg m}^{-3}$ (medians of decay classes calculated using the values in Harmon et al. 1995) have been used for dry tropical forests. However, we did not collect samples of decayed matter in the PSPs, instead using a value of 0.45 Mg m^{-3} , which is within the range of decay classes described by Harmon et al. (1995), and represents approximately 70 % of the wood density of common species in the study area. Fresh CLT and FLT samples were collected, and a set of fresh composite subsamples was immediately taken for weighing and subsequently air-dried by sunlight. Each sample was weighed regularly until it became constant. The air-dried subsamples were brought to the laboratory for oven drying at 70°C for at least 72 h. The value of LT stock in the dry season was tentatively used as the annual mean value in this study. LT stock is typically larger in the dry season than in the rainy season in the tropics (Wieder and Wright 1995, Kiyono et al. 2007). The tree AGB and DW, CLT, and FLT masses per unit land area were summed for each plot.

Assuming that carbon fractions account for 0.50 of the biomass and DW mass and 0.37 of the LT mass (IPCC 2003), we summed the carbon stock in the two carbon pools (DW and LT) for each plot.

To examine the influence of large AGB loss events on temporal changes in AGB, DW, and LT masses, we distinguished PSPs that had experienced large AGB loss events over the study period (hereafter, $\text{PSP}_{\text{w/s}}$) from those that had not (hereafter, $\text{PSP}_{\text{w/o/s}}$).

DOM residence time

We defined the mean residence times (year) of DW and DOM carbon as stock (Mg ha^{-1}) divided by input ($\text{Mg ha}^{-1} \text{ year}^{-1}$), following previous studies (Baker et al. 2007, Palace et al. 2007, Sato et al. 2016). In Cambodian forests with AGB within the ranges $17.7\text{--}293.3 \text{ Mg ha}^{-1}$ for EF and $64.4\text{--}254.1 \text{ Mg ha}^{-1}$ for DF, AGB gain (annual increase in biomass due to biomass growth, $\text{Mg ha}^{-1} \text{ year}^{-1}$) was positively correlated with AGB (Mg ha^{-1} , $\text{AGB gain} = 0.0165 \text{ AGB} + 2.20$, Kiyono et al. 2017). However, AGB loss (annual decrease due to wood removal and losses due to disturbances) in $\text{PSP}_{\text{w/o}}$ was not significantly correlated with AGB (Kiyono et al. 2017). These results indicate that as AGB becomes large, Cambodian forests experience increased AGB gain, but also lose a certain amount of AGB, with some losses due to selective logging. AGB loss is equivalent to DOM input and was estimated at 1.34 ± 3.58 (mean $\pm$ SD) $\text{Mg ha}^{-1} \text{ year}^{-1}$ in EF and $1.22 \pm 1.96 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in DF (calculated using the data in Fig. 6 of Kiyono et al. 2017).

Calculating the number of sample plots required for precise DW mass, LT mass, and DOM carbon stock estimates

The UNFCCC has provided a Clean Development Mechanism (CDM) afforestation and reforestation (A/R) methodological tool for calculating the number of sample plots required for precise estimations in A/R CDM projects (http://cdm.unfccc.int/Reference/tools/ar/methAR_tool03_v01.pdf). This tool is appropriate for carbon-stock monitoring purposes; it estimates the number of PSPs per stratum needed to monitor changes in (i) carbon pools at a desired level of precision and (ii) the cost of sample plot establishment. Using this tool, we estimated the reasonable numbers of sample plots required to obtain accurate values for DW mass, LT mass, and DOM carbon stock in EF and DF. Costs were *ca.* US\$800 per EF plot and US\$700 per DF plot (Kiyono et al. 2010).

Applying the UNFCCC tool to field data collected in this study (10 PSPs in EF and 12 PSPs in DF), we calculated the number of samples required to obtain mean values of DW elements at a precision level of 0.05 at a confidence level of 95 %. We then calculated the current precision level and the confidence range of the means from the 22 PSP datasets.

Fig. 3. Annual changes in aboveground biomass (AGB) (a, b), deadwood (DW) mass (c, d), and dead organic matter (DOM) carbon stock (e, f) in each permanent sample plot (PSP).

a, c, e: ■ PSP 1, ◆ PSP 2, ▲ PSP 3, × PSP 4, □ PSP 7, * PSP 8, — PSP 9, ● PSP 10, PSPs without large AGB loss events; △ PSP 5, ◇ PSP 6, PSPs with large AGB loss events. b, d, f: ■ PSP 12, ◆ PSP 13, ▲ PSP 14, × PSP 15, * PSP 16, □ PSP 19, — PSP 22, PSPs without large AGB loss events; △ PSP 11, ◇ PSP 17, □ PSP 18, ○ PSP 20, ◇ PSP 22, PSPs with large AGB loss events. Large symbols represent years with large AGB loss events.

Statistical analysis

The differences in DOM values between forests with and without large AGB loss events and between forest types were analyzed with an unbalanced two-way analysis of variance (ANOVA) that included interaction terms using R3.3.1 software (R Development Core Team 2011). Simple main effects were tested via *post hoc* analysis when the effects and the interaction were statistically significant.

RESULTS

Components significantly related to large AGB loss events

AGB (Fig. 3a, b) tended to increase in most PSP_{wo}s. However, AGB sometimes decreased in PSP_{wi}s (Fig. 3, large symbol). The observed period-mean AGB range in the PSPs was 17.7–293.3 Mg ha⁻¹ in EF (180.6 ± 83.5 Mg ha⁻¹ [mean $\pm$ SD], $n = 10$) and 64.4–254.1 Mg ha⁻¹ in DF (136.2 ± 50.3 Mg ha⁻¹, $n = 12$). The difference in means between EF and DF was not significant (*t*-test, $P = 0.162$).

DW mass (Fig. 3c, d) and DOM carbon stock (Fig. 3e, f) were largest in the years of the large AGB loss events

Fig. 4. Changes in size distribution of deadwood (DW) components before and after large aboveground biomass (AGB) loss events in PSPs that experienced a large biomass loss (PSP_{wi}s).

Black and crosshatched bars: DW on the ground and in stumps, respectively. Open bar: DW in standing dead trees. a: PSP_{wi}, EF (PSP 6, Table 1) in 2008 before the large AGB loss event (black bar) and in 2010 after the event (crosshatched and open bars). b: PSP_{wi}, DF (PSP 11, Table 1) in 2006 before the large AGB loss event (black bar) and in 2008 after the event (crosshatched and open bars). c: PSP_{wo}, EF (PSP 7, Table 1) in 2008 and 2010. d: PSP_{wo}, DF (PSP 12, Table 1) in 2006 and 2008.

Table 2. Deadwood (DW) mass, litter (LT) mass, and dead organic matter carbon (DOM C) stock in seasonal tropical forests of Cambodia.

Mass and ratio of dead organic matter element	Forest type								<i>P</i> between forest type		
	EF				DF				PSP _{wo}	PSP _{wi}	PSP _{all}
	PSP _{wo} (<i>n</i> = 8)	PSP _{wi} (<i>n</i> = 2)	<i>P</i>	PSP _{all} (<i>n</i> = 10)	PSP _{wo} (<i>n</i> = 7)	PSP _{wi} (<i>n</i> = 5)	<i>P</i>	PSP _{all} (<i>n</i> = 12)			
DW mass (Mg ha ⁻¹)	5.3 ± 4.9	49.5 ± 3.9	*	12.8 ± 17.8	2.8 ± 2.4	12.2 ± 12.9	*	6.7 ± 9.3	*	*	n/s
CLT mass (Mg ha ⁻¹)	9.0 ± 2.0	8.5 ± 3.6	*	8.9 ± 2.2	5.1 ± 1.7	3.9 ± 0.5	*	4.6 ± 1.5	n/s	n/s	*
FLT mass (Mg ha ⁻¹)	8.9 ± 4.2	7.1 ± 2.1	n/s	8.6 ± 3.9	9.2 ± 3.8	7.8 ± 1.9	n/s	8.6 ± 3.1	n/s	n/s	n/s
LT mass (Mg ha ⁻¹)	18.0 ± 5.2	15.7 ± 5.7	n/s	17.5 ± 5.0	14.3 ± 3.7	11.7 ± 2.4	n/s	13.2 ± 3.3	n/s	n/s	*
DOM C stock (Mg C ha ⁻¹)	9.1 ± 3.8	29.1 ± 4.0	*	13.1 ± 9.1	6.6 ± 1.4	10.1 ± 6.6	*	8.0 ± 4.5	*	*	n/s
DW mass/AGB (%)	9 ± 19	23 ± 4	n/s	12 ± 18	2 ± 2	9 ± 9	n/s	5 ± 6	n/s	n/s	n/s
CLT mass/AGB (%)	13 ± 22	4 ± 1	n/s	11 ± 20	5 ± 4	3 ± 1	n/s	4 ± 3	n/s	n/s	n/s
FLT mass/AGB (%)	10 ± 15	3 ± 0.3	n/s	9 ± 13	8 ± 5	6 ± 2	n/s	7 ± 4	n/s	n/s	n/s
LT mass/AGB (%)	23 ± 37	7 ± 1	n/s	20 ± 33	13 ± 7	9 ± 3	n/s	11 ± 5	n/s	n/s	n/s
DOM/AGB C stock (%)	27 ± 48	28 ± 3	n/s	27 ± 42	12 ± 5	16 ± 8	n/s	14 ± 7	n/s	n/s	n/s

Observed period-mean ± SD. PSP_{wi}, forest that experienced stand AGB loss of ≥5 % year⁻¹ from an initial stand AGB of ≥100 Mg ha⁻¹, PSP_{wo}, forest that did not experience such a stand AGB loss. DW: deadwood; CLT: coarse litter; FLT: fine litter; LT: CLT + FLT; DOM C: dead organic matter (DW + LT) carbon; AGB: aboveground biomass. *, *P* ≤ 0.05.

(Fig. 3, large symbol). A large AGB loss event increased larger diameter DW, including standing dead trees (Fig. 4a, b). Each of the observed period-mean DW masses and DOM carbon stocks was significantly (ANOVA, $P < 0.001$) larger in PSP_{wi} than in PSP_{wo}, and larger in EF than in DF (Table 2). The large AGB loss $\times$ forest type interaction term was significant (ANOVA, $P < 0.001$); DW mass and DOM carbon stock in the PSP_{wi} were far greater in EF than in DF. However, when PSP_{wi} and PSP_{wo} were combined (hereafter, PSP_{all}) (Table 2), the difference between EF and DF was not significant (t -test, $P = 0.284$ for DW mass, and $P = 0.133$ for DOM carbon stock) because the within-forest type variances of DW mass and DOM carbon stock were greatly increased by combining PSP_{wi} and PSP_{wo}.

The proportions of standing dead tree mass in DW mass were 0.012 ± 0.017 in PSP_{wi} and 0.18 ± 0.37 (mean $\pm$ SD) in PSP_{wo} in EF, and they were 0.08 ± 0.07 in PSP_{wi} and 0.09 ± 0.08 in PSP_{wo} in DF. The ratio of standing dead trees/DW mass was not significantly different between PSP_{wi} and PSP_{wo}, or between forest types (ANOVA, $P = 0.091$ – 0.830). The proportions of DW mass in dead trees with diameters ≥ 10 cm (hereafter, DW _{≥ 10 cm}, i.e. referring to the DBHs of standing dead trees and diameters at the midpoint of fallen trees) in DW mass were 0.91 ± 0.05 in PSP_{wi} and 0.65 ± 0.30 in PSP_{wo} for EF, and they were 0.75 ± 0.10 in PSP_{wi} and 0.58 ± 0.23 in PSP_{wo} for DF.

Fig. 5. Annual changes in coarse litter (CLT) mass (a, b), fine litter (FLT) mass (c, d), and litter (LT, CLT + FLT) mass (e, f) in each permanent sample plot (PSP).

See legend to Fig. 3 for an explanation of symbols.

Components not significantly related to large AGB loss events

Temporal changes in CLT (Fig. 5a, b), FLT (Fig. 5c, d), and LT (Fig. 5e, f) mass were not significantly related to large AGB loss events.

Within six PSPs (Numbers 1, 2, 6, and 7 in EF; Numbers 11 and 12 in DF; Table 1) that were continually monitored for the 10-year study period, CLT mass frequently fell, reaching a minimum in 2012 in EF (Fig. 5a); FLT (Fig. 5c, d) and LT (Fig. 5e, f) fell to minima in 2012 in both EF and DF. The maximum decrease rate ($-2.2 \pm 4.5 \text{ Mg ha}^{-1} \text{ year}^{-1}$, mean $\pm$ SD) in FLT mass occurred between 2011 and 2012 in EF.

The observed period-mean CLT mass was significantly (ANOVA, $P < 0.0001$) larger in PSP_{wi} than in PSP_{wo} in both EF and DF. Forest type (EF vs. DF) (ANOVA, $P = 0.267$, Table 2) and the large AGB loss $\times$ forest type interaction term (ANOVA, $P = 0.647$) had no significant effects. The observed period-mean FLT mass was not significantly different between PSP_{wi} and PSP_{wo} (ANOVA, $P = 0.820$) or between EF and DF (ANOVA, $P = 0.389$) (Table 2). The large AGB loss $\times$ forest type interaction term was not significant (ANOVA, $P = 0.894$).

LT mass in the rainy season

The CLT mass in 2008 was significantly smaller during the rainy season than during the dry season in EF (paired t -test, $P = 0.003$, $n = 5$) (Table 3). In DF, the CLT mass was significantly smaller during the dry season than during the rainy season (paired t -test, $P = 0.005$, $n = 4$) (Table 3). FLT mass and total (LT mass) were not significantly different between seasons (paired t -test, $P = 0.105$ – 0.834 , $n = 4$ – 5) (Table 3).

Table 3. Litter (LT) mass during the dry and rainy seasons in 2008.

Forest type	DOM element	Dry season Mg ha^{-1}	Rainy season Mg ha^{-1}	P	n
EF	CLT	14.3 ± 4.0	6.8 ± 3.2	*	5
EF	FLT	10.9 ± 5.9	9.9 ± 5.2	n/s	5
EF	LT	25.2 ± 9.0	16.7 ± 4.4	n/s	5
DF	CLT	4.0 ± 1.5	8.7 ± 1.4	*	4
DF	FLT	7.9 ± 4.3	6.4 ± 7.9	n/s	4
DF	LT	11.9 ± 5.1	15.1 ± 7.9	n/s	4

Mean $\pm$ SD. *, $P \leq 0.05$. The abbreviations of the DOM elements are explained in Table 2.

DOM residence time

The mean residence times of DW mass, DW + CLT mass, and DOM carbon stock for PSP_{wo} were 4.0 ± 3.7 years (mean $\pm$ SD), 10.7 ± 4.9 years, and 6.8 ± 2.8 years, respectively, in EF, and they were 2.7 ± 1.9 years, 6.3 ± 1.7 years, and 4.9 ± 1.1 years, respectively, in DF. In PSP_{all} , the respective mean residence times were 10.6 ± 14.3 years, 17.2 ± 14.5 years, and 9.8 ± 6.8 years in EF, and 5.2 ± 6.9 years, 8.8 ± 6.6 years, and 6.0 ± 3.3 years in DF. The mean residence times of DW mass and DOM carbon stock did not differ significantly between EF and DF in either PSP_{wo} (t -test, $P = 0.436$ for DW mass, and $P = 0.120$ for DOM carbon stock, $n = 7$ – 8) or PSP_{all} (t -test, $P = 0.265$ for DW mass and $P = 0.105$ for DOM carbon stock, $n = 10$ – 12). However, the residence time of DW + CLT mass was longer in EF than in DF for both PSP_{wo} (t -test, $P = 0.041$, $n = 7$ – 8) and PSP_{all} (t -test, $P = 0.087$, $n = 10$ – 12).

Relationships of AGB with DW mass, CLT mass, FLT mass, and DOM carbon stock

The observed period-mean AGB was not significantly correlated with DW mass, CLT mass, FLT mass, or DOM (DW + LT) carbon stock in PSP ($r = 0.075$ – 0.384 , $P = 0.218$ – 0.816) (Fig. 6a–j). None of the observed period-mean ratios of DW mass, CLT mass, FLT mass, or LT mass to AGB, or the ratio of DOM carbon stock to AGB carbon stock (DOM/AGB carbon stock) differed significantly between PSP_{wi} and PSP_{wo} (ANOVA, $P = 0.298$ – 0.823) or between EF and DF (ANOVA, $P = 0.440$ – 0.834) (Table 2). The large AGB loss $\times$ forest type interactions were not significant (ANOVA, $P = 0.565$ – 0.900). In PSPs with the smallest AGBs (16.4 Mg ha^{-1} for EF and 62.0 Mg ha^{-1} for DF; Fig. 6i, j), the DOM/AGB carbon stock ratio reached 1.45 in EF and 0.31 in DF.

Number of samples required for precise measurement of DW mass, LT mass, and DOM carbon stock

The estimated number of samples required to obtain a mean DW mass value with a precision level of 0.05 and a confidence level of 95 % was 1878 for EF and 1226 for DF (3103 in total, Table 4b). These same numbers for CLT mass, FLT mass, LT mass, and DOM carbon stock were 122, 263, 114, and 639, respectively.

Fig. 6. Observed period-mean of aboveground biomass (AGB) and deadwood (DW) mass (a, b), coarse litter (CLT) mass (c, d), fine litter (FLT) mass (e, f), litter (LT) mass (g, h), and dead organic matter (DOM) carbon stock (i, j).
 ○, PSPs with large AGB loss events; ●, PSPs without large AGB loss events.

Table 4. Means and confidence intervals of deadwood (DW) mass, litter (LT) mass, and dead organic matter carbon (DOM C) stock, and numbers of samples required to obtain a precision level of 0.05 and a confidence level of 95 %.

DOM element	Level of precision	Numbers of samples in this study (a) and those required (b)			Mean and confidence interval of mass, Mg ha ⁻¹		
	<i>p</i>	EF	DF	Total	Min	Mean	Max
a							
DW	0.59	10	12	22	3.9	9.6	15.2
CLT	0.12	10	12	22	5.8	6.6	7.4
FLT	0.17	10	12	22	7.2	8.8	10.3
LT	0.11	10	12	22	13.4	15.2	16.9
DOM C	0.37	10	12	22	6.4	10.1	13.8
b							
DW	0.05	1878	1226	3103	–	–	–
CLT	0.05	60	61	122	–	–	–
FLT	0.05	120	143	263	–	–	–
LT	0.05	60	54	114	–	–	–
DOM C	0.05	385	255	639	–	–	–

Means and confidence intervals of deadwood (DW) mass, litter (LT) mass, and dead organic matter carbon (DOM C) stock (a), and numbers of samples required to obtain a precision level of 0.05 and a confidence level of 95 % (b). The abbreviations of the DOM elements are explained in Table 2.

The precision levels of means for DW mass, LT mass, and DOM carbon stock in this study

When we used 10 plots in EF and 12 plots in DF, the achieved precision level of the mean was 0.59 for DW mass, 0.11–0.17 for LT mass, and 0.27 for DOM carbon stock (Table 4a). The errors for DW mass and DOM carbon stock were larger than the LT mass error.

DISCUSSION

Can DOM data compiled from our samples be extrapolated to represent Cambodian forests across the nation?

The 22 PSPs from which we obtained the DOM data were located in the three main forest-cover regions of Cambodia (Fig. 1). Hence, these data were national in scope. However, the confidence intervals of the DOM element means were broad, particularly in the case of DW mass and DOM carbon stock (Table 4a). Larger sample sizes will be required to increase confidence in these estimates.

DW mass dynamics and the influence of large AGB loss events

Large AGB loss events sometimes greatly increased DW mass (Figs. 3c, d; 4c, d). The mean of the observed period-mean of DW mass in both EF and DF was significantly larger when large AGB loss events occurred (Table 2), suggesting that logging had increased the DW mass (Carlson et al. 2017). DW_{≥10cm} mass accounted for the largest proportion of DW mass (≥0.58).

LT mass dynamics and the influence of large AGB loss events

CLT mass in DF was influenced more strongly by environmental conditions, such as rainfall and ground fires, than by large AGB loss events. Forest floor LT mass is generally greater during the dry season than during the rainy season in seasonal forests (Hopkins 1966, Scott et al. 1992, Wieder and Wright 1995). However, we found that this was not the case in the DF we studied, where lower CLT mass was estimated during the dry season in 2008 (Table 3). LT mass depends on the balance among the quantity of litterfall (input), decomposition and combustion (output), movement (both), and other parameters (Wieder

and Wright 1995, Powers et al. 2009). The quantities of litterfall and leaf decomposition rates did not significantly differ between young secondary and mature seasonal forests studied by Ewel (1976). Ground fires occur frequently in Cambodian DF (Wood 2012), and these appeared to reduce CLT mass in DF.

We commonly observed LT mass decreases during 2012 (Fig. 5). Reduced leaf litterfall and an increase in the decomposition rate from April 2011 to March 2012 probably explain the decreased FLT mass in EF during the period 2011–2012. Reduced rainfall during April 2010–March 2011 (Fig. 2) likely reduced dry matter production, thereby reducing leaf litterfall in the following year. Abundant rainfall between April 2011 and March 2012 (Fig. 2) may have increased the LT decomposition rate (Wieder and Wright 1995, Powers et al. 2009). The decrease in LT mass during 2011–2012 was $4.7 \pm 8.2 \text{ Mg ha}^{-1} \text{ year}^{-1}$ (mean $\pm$ SD) in EF and $0.2 \pm 5.2 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in DF; these values were lower than the mean LT supply rate in seasonal tropical forests ($9.4 \pm 2.5 \text{ Mg ha}^{-1} \text{ year}^{-1}$) calculated from Table 1 in Vogt et al. (1986).

Difference in DOM traits between EF and DF

Differences in the life forms of evergreen and deciduous canopy trees probably account for the difference in DOM mass between EF and DF. We found no clear difference in AGB ranges between EF and DF. However, DF had significantly lower DW and rainy-season CLT mass than did EF. In DF, the abundance of fallen leaves likely increased the frequency of ground fires in the dry season (Wood 2012), which burned a proportion of the DW.

DOM carbon stock dynamics

AGB values appeared to have little influence on DW mass, LT mass, or DOM carbon stocks (Fig. 6). The mean residence times of DW mass and DW + CLT mass in PSP_{all} were 10.6 ± 14.3 (mean $\pm$ SD) and 17.2 ± 14.5 years, respectively, in EF, and 5.2 ± 6.9 and 8.8 ± 6.6 years, respectively, in DF. The values in EF were similar to the mean residence time of DW mass in Malaysian primary rainforests (16.6 ± 3.7 years; Sato et al 2016), but the residence times for DF were generally shorter. The DW turnover rate in Cambodian DF forests probably exceeded the turnover rate in Malaysian primary rainforests. The DOM/AGB carbon stock ratio can become large in forests with small AGB. We cannot ignore the roles of DOM in

forest structure and function, particularly in heavily disturbed forests (Pfeifer et al. 2015).

DOM mass value characteristics of Cambodian seasonal forests in a global context

The period-mean mass of DW larger than 2 cm diameter ($\text{DW}_{>2\text{cm}}$) in the PSP_{all} will fall between 14.2 ± 19.2 and $23.1 \pm 19.5 \text{ Mg ha}^{-1}$ in EF ($n = 10$), and between 6.7 ± 9.3 and $11.3 \pm 9.0 \text{ Mg ha}^{-1}$ in DF ($n = 12$) (Table 5). This $\text{DW}_{>2\text{cm}}$ mass in Cambodian EF was similar to the mean $\text{DW}_{>2\text{cm}}$ mass in a Chinese seasonal tropical forest (Lü et al. 2010). The period-mean $\text{DW}_{>2\text{cm}}$ masses in EF and DF were smaller than the mean $\text{DW}_{>2\text{cm}}$ or $\text{DW}_{>2.5\text{cm}}$ masses in the Americas (Table 5, $31.4 \pm 10.8 \text{ Mg ha}^{-1}$, Jaramillo et al. 2003; $44.4 \pm 42.6 \text{ Mg ha}^{-1}$, Palace et al. 2012).

Reductions in the dead tree production rate due to harvesting of standing trees, DW removal by residents, and ground fires likely account for the relatively small quantity of DW mass in Cambodia. Selective logging of old trees before the establishment of the PSPs may explain the small numbers of dead trees remaining in the forest during our study period. The effects of human intervention cannot be accurately estimated because the volume of timber removed prior to the study is unknown. Nevertheless, the effects of logging are undoubtedly long lasting in these forests (Top et al. 2004). In PSP_{wo}, the proportion of standing dead trees in DW mass was ≤ 0.18 , and the proportion in AGB was even less. These proportions are smaller than those for undisturbed tropical forests in the Americas (Palace et al. 2012) (i.e., ≥ 0.3 of DW mass; calculated from Fig. 2 in Palace et al. 2012). Baker et al. (2007) reported low DW mass values in an intact southwestern Amazonian forest, likely the result of rapid carbon cycling. The AGB values of the Cambodian forests in the present study were increasing (Fig. 3) (Kiyono et al. 2017), suggesting that some living trees had been harvested in recent years and that the forests are still immature. Ground fires frequently occur in DF (Wood 2012), and these may explain the small numbers of dead trees in DF. However, fire was rare in EF, and the DW masses were also relatively low. Therefore, fire cannot explain the low DW mass values in EF. Young fallow forests are also sometimes almost devoid of DW because DW produced during slash-and-burn farming is removed as fuelwood (Kiyono et al. 2007). However, the 22 PSP forests used in this study were probably not affected by slash-and-burn farming.

LT masses measured in this study (8.6 ± 3.9 – $17.5 \pm$

Table 5. Comparison of dead organic matter (DOM) value characteristics of Cambodian seasonal forests with those of seasonal tropical forests globally.

DOM element	Country or region	DOM mass Mg ha ⁻¹	<i>n</i>	AGB Mg ha ⁻¹	Source and remarks
DW _{>5 cm}	Cambodia	14.2 ± 19.2	10	180.6 ± 83.5	EF, PSP _{all} , this study
DW _{>5 cm} + CLT _{<5 cm}	Cambodia	23.1 ± 19.5	10	180.6 ± 83.5	EF, PSP _{all} , this study
DW _{>5 cm}	Cambodia	6.7 ± 9.3	12	136.2 ± 50.3	DF, PSP _{all} , this study
DW _{>5 cm} + CLT _{<5 cm}	Cambodia	11.3 ± 9.0	12	136.2 ± 50.3	DF, PSP _{all} , this study
DW _{>2 cm}	China	18.0 ± 20.0	25	403.6 ± 104.6	Lü et al. 2010. CF ³ , 0.5 of AGB and DW mass.
DW _{>2 cm}	The Americas (Mexico, Jamaica, Venezuela, and Brazil)	44.4 ± 42.6	18	158.4 ± 87.2	Palace et al. 2012
DW _{>2.5 cm}	Mexico	31.4 ± 10.8	16	69.7 ± 24.0	Jaramillo et al. 2003.
DW _{>10 cm}	Costa Rica	6.45 (0–32) ¹	18	50–500	Kissing and Powers 2010
DW _{>10 cm}	Congo Republic	8.9 ± 5.8–20.0 ± 8.7	4	n/a	Ekoungoulou et al. 2018. CF ³ , 0.5 of DW mass.
DW _{>10 cm}	Gabon	65 (0.06–254) ¹	47	293.7 ± 119.9	Carlson et al. 2017
DW	Mexico	14.9 ± 3.0 ² –25.3 ± 2.8 ²	n/a	38.1 ± 5.1 ² – 72.4 ± 3.4 ²	Lucia et al. 2017. CF ³ , 0.5 of AGB and DW mass.
FLT	Cambodia	8.6 ± 3.9	10	180.6 ± 83.5	EF, PSP _{all} , this study
FLT + CLT _{<5 cm}	Cambodia	17.5 ± 5.0	10	180.6 ± 83.5	EF, PSP _{all} , this study
FLT	Cambodia	8.6 ± 3.1	12	136.2 ± 50.3	DF, PSP _{all} , this study
FLT + CLT _{<5 cm}	Cambodia	13.2 ± 3.3	12	136.2 ± 50.3	DF, PSP _{all} , this study
LT _{<2 cm}	Cambodia	8.3 ± 3.0	12	n/a	EF, Ito et al. 2014. CF ³ , 0.37 of LT mass.
LT _{<2 cm}	China	3.8 ± 0.0	25	403.6 ± 104.6	Lü et al. 2010. CF ³ , 0.5 of AGB and 0.37 of LT mass.
LT _{<2.5 cm}	Mexico	11.1 ± 6.2	16	69.7 ± 24.0	Jaramillo et al. 2003.
LT _{<2 cm}	Costa Rica	3–9 ¹	24	n/a	Schilling et al. 2016. LT values were read from Fig. 1 in Schilling et al. (2016).
LT _{<2 cm}	Panama	6.76 ± 1.25–10.05 ± 2.46	20	n/a	Dry season, Wieder and Wright 1995
LT	Mexico	12.3 ± 1.8 ² –14.4 ± 2.9 ²	n/a	38.1 ± 5.1 ² – 72.4 ± 3.4 ²	Lucia et al. 2017. CF ³ , 0.5 of AGB and 0.37 of LT mass.
LT	Mexico	5.4 ± 1.3 ² –14.2 ± 1.1 ²	3–7	n/a	Gavito et al. 2017.

Mean ± SD. ¹Range. ²Mean ± SE. ³Carbon fraction assuming that accounts for 0.5 of AGB and 0.37 of LT mass (IPCC 2003). Subscripts denote the low- or high-end cutoff size; cutoff size was not reported for DW and LT without subscript. The abbreviations of DOM element are the same as in Table 2.

5.0 Mg ha⁻¹ in EF and 8.6 ± 3.1–13.2 ± 3.3 Mg ha⁻¹ in DF) were not markedly different from most values reported for other seasonal tropical forests (Table 5).

CONCLUSIONS

Disturbances that caused large AGB loss increased DW mass and DOM carbon stock. However, their influence

on LT (CLT and FLT) mass was not clear. The Cambodian seasonal forest was characterized by relatively low DW masses, likely due to the removal of DW and dying trees from the forest by local residents. These findings will be useful for sustainable forest management in the region. However, larger sample sizes are required to increase the precision of parameter estimates. We do not have estimates of biomass removal (proportion of the biomass removed in an AGB loss event; Pearson et al. 2014) or of DOM remain-

ing in the soil. Future studies should quantitatively evaluate the impacts of biomass removal.

ACKNOWLEDGEMENTS This research was conducted as part of the A-0802 and B-072 programs supported by the Global Environment Research Fund of the Ministry of the Environment, Japan and was funded in part by “Forestation: basic data collection aiming at small scale afforestation/reforestation CDM in environmental planting” and “the Emergency project to develop the structure of promoting REDD action” funded by the Forestry Agency, Japan. The datasets for 2005 and 2006 were collected through the project “Capacity Building for Greenhouse Gas Inventory Development in Asia-Pacific Developing Countries” implemented by National Institute for Environmental Studies, Japan, with the collaboration from the Ministry of Environment of Cambodia. Funding support for the project was provided by the Asia-Pacific Network for Global Change Research (APN) through its CAPaBLE Programme.

LITERATURE

- Akinaga K. 1943. *Futsu-In Ringyo Kiko* (Traveller's journal of forestry in French Indo-China). Narumi-shoten, Tokyo. (In Japanese)
- Baker TR, Coronado ENH, Phillips OL, Martin J, van der Heijden GMF, Garcia M, Espejo JS. 2007. Low stocks of coarse woody debris in a southwest Amazonian forest. *Oecologia* 152: 495–504.
- Carlson BS, Koerner SE, Medjibe VP, White LJT, Poulsen JR. 2017. Deadwood stocks increase with selective logging and large tree frequency in Gabon. *Global Change Biology*, 23 (4): 1648–1660.
- Chambers JQ, Higuchi N, Schimel JP, Ferreira LV, Melack JM. 1999. Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon. *Oecologia* 122: 380–388.
- Clark DB, Clark DA, Brown S, Oberbauer SF, Veldkamp E. 2002. Stocks and flows of coarse woody debris across a tropical rain forest nutrient and topography gradient. *Forest Ecology and Management* 164: 237–248.
- Crocker CD. 1962. *The soils of Cambodia, Exploratory survey*. Royal Cambodian Government Soil Commission and USAID Joint Publication, Phnom Penh.
- Eaton JM, Lawrence D. 2006. Woody debris stocks and fluxes during succession in a dry tropical forest. *Forest Ecology and Management* 232: 46–55.
- Ekoungoulou R, Niu S, Folega F, Nzala D, Liu X. 2018. Carbon stocks of coarse woody debris in central African tropical forests. *Sustainability in Environment* 3 (2): 142–160.
- Ewel JJ. 1976. Litter fall and leaf decomposition in a tropical forest succession in eastern Guatemala. *Journal of Ecology* 64 (1): 293–308.
- Gavito ME, Sandoval-Pérez AL, del Castillo K, Cohen-Salgado D, Colarte-Avilés ME, Mora F, Santibáñez-Rentería A, Siddique I, Urquijo-Ramos C. 2017. Resilience of soil nutrient availability and organic matter decomposition to hurricane impact in a tropical dry forest ecosystem. *Forest Ecology and Management*, DOI: 10.1016/j.foreco.2017.08.041
- Hairiah K, Sitompul SM, Van Noordwijk M, Palm C. 2001. *Methods for Sampling Carbon Stocks Above and Below Ground*. ASB Lecture Note 4B, International Centre for Research in Agroforestry. Bogor. https://www.researchgate.net/publication/255628087_Methods_for_sampling_carbon_stocks_above_and_below_ground (cited 2018 April 2).
- Harmon ME, Whigham DF, Sexton J, Olmsted I. 1995. Decomposition and mass of woody detritus in the dry tropical forests of the northern Yucatan peninsula, Mexico. *Biotropica* 27 (3): 305–316.
- Hopkins B. 1966. Vegetation of the Olokemeji Forest Reserve, Nigeria. IV. The litter and soil with special reference to their seasonal changes. *Journal of Ecology* 54: 687–703.
- [IPCC] Intergovernmental Panel on Climate Change. 2003. *Good Practice Guidance for Land Use, Land Use Change, and Forestry*. the National Greenhouse Gas Inventories Programme, Penman J, Gytarsky M, Hiraishi T, Krug T, Kruger D, Pipatti R, Buendia L, Miwa K, Ngara T, Tanabe K, Wagner F (eds), IGES, Hayama.
- [IPCC] Intergovernmental Panel on Climate Change. 2006. *2006 IPCC Guidelines for National Greenhouse Gas Inventories*. the National Greenhouse Gas Inventories Programme, Eggleston HS, Buendia L, Miwa K, Ngara T, Tanabe K (eds), IGES, Hayama
- Ito E, Toriyama J, Araki M, Kiyono Y, Kanzaki M, Tith B, Keth S, Chandraratna L, Chann S. 2014. Physiochemical surface-soil properties after litter-removal manipulation in a Cambodia lowland dry evergreen forest. *JARQ* 48 (2): 195–211.
- Jaramillo VJ, Kauffman JB, Rentería-Rodríguez L, Cummings DL, Ellingson LJ. 2003. Biomass, carbon, and nitrogen pools in Mexican tropical dry forest landscapes. *Ecosystems* 6: 609–629.
- Keller M, Palace M, Asner GP, Pereira JR R, Silva JNM. 2004. Coarse woody debris in undisturbed and logged forests in the eastern Brazilian Amazon. *Global Change Biology* 10: 784–795.
- Kissing LB, Powers JS. 2010. Coarse woody debris stocks as a function of forest type and stand age in Costa Rican tropical dry forest: long-lasting legacies of previous land use. *Journal of Tropical Ecology* 26 (4): 467–471.
- Kiyohara S, Kanzaki M, Ohta S, Kajiwarra T, Wacharinrat C, Sahunulu P. 2004. The role of coarse woody debris dynamics in carbon sequestration of tropical dry evergreen forest, northeast Thailand. *The 51st Annual Meeting of the Ecological Society of Japan*, Kushiho, P1-058c, <http://doi.org/10.14848/esj.E5J51.0.143.0> (In Japanese) (cited 2017 December 8).
- Kiyono Y, Prajadinata S, Oo MZ, Oosumi Y. 2006. *Baiomasutanso-chikuseki no kan'i-na keisoku, yosoku-shuho no*

- kaihatsu* (Development of the simplified methodologies for measuring and predicting biomass carbon stock). In: *CDM Shoku-rin Kiso Deta Seibi 2005* (Fiscal report of forestation basic data collection aiming at small-scale environmental planting, CDM project, 2005). Forestry and Forest Products Research Institute, Tsukuba, 8–41. (In Japanese)
- Kiyono Y, Furuya N, Sum T, Umemiya C, Ito E, Araki M, Matsumoto M. 2010. Carbon Stock Estimation by Forest Measurement contributing to sustainable forest management in Cambodia. *JARQ* 44 (1): 81–92.
- Kiyono Y, Ito E, Monda Y, Toriyama J, Saito H, Furuya N, Sum T, Tith B, Keth N, Keth S, Chandararity L, Phallaphearaoth, Chann S, Sokh H. 2017. A feasibility study for determining the mean annual aboveground biomass gain of tropical seasonal forests in Cambodia. *TROPICS* 25 (4): 127–138.
- Kiyono Y, Ochiai Y, Chiba Y, Asai H, Saito K, Shiraiwa T, Horie T, Songnouxhai V, Navongxai V, Inoue Y. 2007. Predicting chronosequential changes in carbon stocks of *Pachymorph* bamboo communities in slash-and-burn agricultural fallow, northern Lao People's Democratic Republic. *Journal of Forest Research* 12: 371–383.
- Lü Xiao-Tao, Yin Jiang-Xia, Jepsen MR, Tang Jian-Wei. 2010. Ecosystem carbon storage and partitioning in a tropical seasonal forest in Southwestern China. *Forest Ecology and Management* 260: 1798–1803.
- Lucia Nevescanin-Moreno, Yépez Enrico A., Kristofer J, Jaime Garatuza-Payan, Rodrigo V. 2017. Carbon stocks in two successional stages of a dry tropical forest for the establishment of an intensive carbon monitoring site in Northwestern Mexico. *2017 Joint NACP and Ameriflux Principal Investigators Meeting*, poster. (https://www.nacarbon.org/cgi-bin/web/investigations/inv_pgp.pl?pgid=728)
- National Institute for Environmental Studies (Japan), Ministry of Environment of Cambodia (Cambodia), Joint Graduate School of Energy & Environment, King Mongkut's University of Technology Thonburi (Thailand). 2005. *Capacity Building for Greenhouse Gases Inventory Development in Asia-Pacific Developing Countries*. Final Report for APN 3-year CAPaBLE Project: 2003-CB03; 2004-CB05CMY, 2005-CB05CMY, Asia-Pacific Network for Global Change Research, www.apn-gcr.org.
- Palace M, Keller M, Asner GP, Natalino J, Silva M, Passos C. 2007. Necromass in undisturbed and logged forests in the Brazilian Amazon. *Forest and Ecology and Management* 238: 309–318.
- Palace MW, Keller M, Hurtt GC, Frolking S. 2012. A review of above ground necromass in tropical forests. 215–252 In: Sudarhana P, Nageswara-Rao M, Soneji JR (eds) *Tropical Forests*. Intech (online publisher). Published online at: <http://www.intechopen.com/books/tropical-forests>.
- Pauline DP. 2000. *Plants used in Cambodia*. Imprimerie Olympic, Phnom Penh
- Pearson TRH, Brown S, Casarim FM. 2014. Carbon emissions from tropical forest degradation caused by logging. *Environmental Research Letters* 9:034017. DOI:10.1088/1748-9326/9/3/034017
- Pfeifer M, Lefevre V, Turner E, Cusack J, Khoo M, Chey VK, Peni M, Ewers RM. 2015. Deadwood biomass: an underestimated carbon stock in degraded tropical forests? *Environmental Research Letters* 10:044019. DOI:10.1088/1748-9326/10/4/044019
- Powers JS, Montgomery RA, Adair EC, Brearley FQ, DeWalt SJ, Castanho CT, Chave J, Deinert E, Ganzhorn JU, Gilbert ME, González-Iturbe JA, Bunyavejchewin S, Grau HR, Harms KE, Hiremath A, Iriarte-Vivar S, Manzane E, De Oliveira AA, Poorter L, Ramanamanjato JB, Salk C, Varela A, Weiblen GD, Lerdau MT. 2009. Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. *Journal of Ecology* 97 (4): 801–81.
- R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0, URL <http://www.r-project.org/> (cited 2017 August 14).
- Rundel PW. 1999. *Conservation Priorities in Indochina-WWF Desk Study Forest habitats and flora in Lao PDR, Cambodia, and Vietnam*. World Wide Fund for Nature, Indochina Programme Office, Hanoi.
- Samreth V, Chheng K, Monda Y, Kiyono Y, Toriyama J, Saito S, Saito H, Ito E. 2012. Tree biomass carbon stock estimation using permanent sampling plot data in different types of seasonal forests in Cambodia. *JARQ* 46 (2): 187–192.
- Sato T. 2012. Measurement of permanent sample plots. In: Hirata Y, Takao G, Sato T, Toriyama J (eds) *REDD-plus Cookbook*, REDD Research and Development Center, Forestry and Forest Products Research Institute, Tsukuba, 116–119.
- Sato T, Yagihashi T, Niiyama K, Abd Rahman K, Azizi R. 2016. Coarse woody debris stocks and inputs in a primary hill dipterocarp forest, peninsular Malaysia. *Journal of Tropical Forest Science* 28 (Special Issue): 382–391.
- Sayer EJ. 2005. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews* 80: 1–31.
- Schilling EM, Waring BG, Schilling JS, Powers JS. 2016. Forest composition modifies litter dynamics and decomposition in regenerating tropical dry forest. *Oecologia* 182: 287–297.
- Scott DA, Proctor J, Thompson J. 1992. Ecological studies on a lowland evergreen rain forest on Maracá Island, Roraima, Brazil. II. Litter and nutrient cycling. *Journal of Ecology* 80: 705–717.
- Spain AV. 1984. Litterfall and the standing crop litter in three tropical Australian rainforests. *Journal of Ecology* 72: 947–961.
- Top N, Mizoue N, Kai S. 2004. Estimating forest biomass increment based on permanent sample plots in relation to woodfuel consumption: a case study in Kampong Thom Province, Cambodia. *Journal of Forest Research* 9 (2): 117–123.
- Toriyama J, Ohta S, Ohnuki Y, Ito E, Kanzaki M, Araki M, Chann S, Tith B, Keth S, Hirai K, Kiyono Y. 2011. Soil carbon stock in Cambodian monsoon forests. *JARQ* 45 (3): 309–316.
- Uji, T. 1998. *Nephelium L.* In: Sosef MSM, Hong LT,

- Prawirohatmodjo S (eds) Plant Resources of South-East Asia No. 5 (3). *Timber trees: Lesser-known timbers*. Backhuys Publishers, Leiden. 404–406.
- Vogt KA, Grier CC, Vogt DJ. 1986. Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. *Advances in Ecological Research* 15: 303–377.
- Wieder RK, Wright SJ. 1995. Tropical Forest Litter Dynamics and Dry Season Irrigation on Barro Colorado Island, Panama. *Ecology* 76 (6): 1971–1979.
- Wood TF. 2012. Fire ecology of the dry dipterocarp forests of South West Cambodia. *Cambodian Journal of Natural History* 1: 64–74.
- World Bank Group. 2015. *Climate change knowledge portal for development practitioners and policy makers*. http://sdwebx.worldbank.org/climateportal/index.cfm?page=country_historical_climate&ThisRegion=Asia&ThisCCode=KHM# (cited 2017 August 14).
- Yan ER, Wang XH, Huang JJ, Zeng FR, Gong L. 2007. Long-lasting legacy of forest succession and forest management: Characteristics of coarse woody debris in an evergreen broad-leaved forest of Eastern China. *Forest and Ecology and Management* 252: 98–107.
- Yoneda T, Tamin R, Ogino K. 1990. Dynamics of aboveground big woody organs in a foothill dipterocarp forest, West Sumatra, Indonesia. *Ecological Research* 5: 111–130.
- Yoneda T, Sahunalu P, Dhanmanonda P, Tanpibal V, Puriyakorn B. 1991. Decomposition of woody litter in Thailand. In: Yoda K, Sahunalu P (eds) *Improvement of Biological Productivity of Tropical Wastelands in Thailand*. Department of Biology, Osaka City University, Osaka. 161–183.