COARSE WOODY DEBRIS STOCKS AND INPUTS IN A PRIMARY HILL DIPTEROCARP FOREST, PENINSULAR MALAYSIA

T Sato[1, *], T Yagihashi[2], K Niiyama[3, 1], K Abd Rahman[4] & R Azizi[5]

[1]*Department of Forest Vegetation, Forestry and Forest Products Research Institute, Tsukuba, Ibaraki 305-8687, Japan*
[2]*Tohoku Research Center, Forestry and Forest Products Research Institute, Morioka, Iwate 020-0123, Japan*
[3]*Bureau of International Partnership, Forestry and Forest Products Research Institute, Tsukuba, Ibaraki 305-8687, Japan*
[4]*Forest Research Institute Malaysia, 52109 Kepong, Selangor, Malaysia*
[5]*Green Forest Resources, Rawang 48000, Selangor, Malaysia*

**satoo@affrc.go.jp*

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. Hill dipterocarp forests are a major forest type within the tropical lowland evergreen rainforests of Peninsular Malaysia. However, the coarse woody debris(CWD) dynamics of these forests remain poorly understood. To improve our understanding of CWD dynamics in hill dipterocarp forests, we investigated stocks and inputs of CWD under different topographical conditions in Semangkok Forest Reserve, Selangor, Malaysia. The total CWD (mean ± standard error of the mean) was 81.7 ± 17.0 Mg ha^{-1} with a range of 0.1 to 379.7 Mg ha^{-1}. Although we found no significant differences in total CWD among topographies, the large CWD stock may have resulted from the relatively large amount of aboveground biomass in this hill dipterocarp forest. Downed CWD (fallen logs and uproots) was higher than standing CWD (standing dead and snaps) regardless of slope position. The mean CWD input from tree mortality was 8.2 ± 2.2 Mg ha^{-1} year^{-1} over 18 years. Assuming the long-term equilibrium of stocks and inputs, the turnover time was 16.6 ± 3.7 years, with no significant differences among topographies. Thus, our study demonstrated the importance of large tree mortality to CWD dynamics in hill dipterocarp forests using long-term tree census data.

Keywords: Standing and fallen deadwood, necromass flux, topography, large tree, long-term ecological plot, tropical forest

INTRODUCTION

Coarse woody debris (CWD) is an important component of carbon stocks and other ecological services in forest ecosystems (Franklin et al. 1987). CWD consists of fallen and standing dead wood and contributes anywhere from less than 10% to more than 40% of the aboveground biomass (AGB) in these systems (Brown 2002, Palace et al. 2012). CWD stock and its input (addition) vary spatially and temporally within and across forests (Harmon et al. 1986, Gale 2000).

Hill dipterocarp forests, dominated by *Shorea curtisii* are a major forest type within the tropical lowland evergreen rainforests of Peninsular Malaysia (Whitmore 1984). Hill dipterocarp forests make up approximately 43% of the tropical lowland evergreen rainforests (Hamdan et al. 2015) in Peninsular Malaysia. Hamdan et al. (2015) quantified the AGB of dipterocarp forests in Peninsular Malaysia using satellite data and found that 72% of the forest area contained AGB of more than 300 Mg ha^{-1}. AGB estimates have been conducted in other dipterocarp forests using sampling plot data (Okuda et al. 2004, Jeyanny et al. 2014). Since surveys of live biomass alone are insufficient to determine carbon pools and their dynamics (Rice et al. 2004), many studies have been conducted for analysis of carbon stocks, including CWD (Saner et al. 2012, Ngo et al. 2013) and CWD dynamics (Yoneda et al. 1977, Yoneda et al. 1990, Pfeifer et al. 2015) in dipterocarp forests in South-East Asia. However, comparative studies of CWD stocks across topographical types are limited (Gale 2000, Gale & Hall 2001).

The abundance of CWD data from Amazonian forests makes it possible to compare the broad range of CWD stocks and their dynamics to develop an overall understanding of forest carbon stocks (Baker et al. 2007, Chao et al.

2009). However, more studies of CWD dynamics (i.e stocks and inputs) are required to understand the role of carbon cycles in hill dipterocarp forest ecosystems.

In the present study, we investigated CWD in a primary hill dipterocarp forest in Peninsular Malaysia using a 6-ha permanent plot that had several topographical conditions. We also calculated AGB using long-term (18 years) tree census data from the same plot. Collectively, these data allowed us to assess the dynamics of CWD in a hill dipterocarp forest. The aims of the study were to estimate: (1) CWD stocks under different topographical conditions in a primary hill dipterocarp forest and (2) the input rate and turnover time of CWD.

MATERIALS AND METHODS

Study site

This study was conducted in a primary hill dipterocarp forest in Semangkok Forest Reserve, which is near Fraser's Hill and approximately 60 km north of Kuala Lumpur (Figure 1). Semangkok Forest Reserve is a 28-ha virgin jungle reserve surrounded by secondary forest that was selectively logged in the 1980s. The average annual rainfall is 2414 mm, and the average annual minimum and maximum temperatures are 21.9 and 33.0 °C respectively (Saifuddin et al. 1991).

The study plot was a 6-ha (300 m × 200 m) long-term monitoring plot (3° 37' N, 101° 44' E) established within the virgin jungle reserve in 1992. The elevation at the study site was 400–515 m above sea level (asl) with a narrow ridge in the north–south direction and aspects facing the steep east and west slopes (Figure 1). The bedrock of the 6-ha plot is granitic acid volcanic rock, and the soils are classified as Acrisol (Tange et al. 1998).

The plot was divided into 150 quadrats measuring 20 m × 20 m and forest dynamics monitored since 1993. In that first census all trees greater than 5 cm in diameter at breast height (dbh) in each quadrat were tagged, measured and identified (Niiyama et al. 1999). The 1993 census recorded a total of 455 tree species, with a basal area of 42.9 m^2 ha^{-1}, of which *S. curtisii* comprised 29% (Niiyama et al. 1999). Seven more tree censuses were conducted in 1995, 1997, 1999, 2001, 2003, 2007 and 2011, giving a total of 8 censuses during this 18-year study (see Niiyama et al. 1999 and Abd Rahman et al. 2002).

CWD stock estimation

We used a sample plot inventory method to estimate CWD stock. Seven 20 m × 100 m transects, which consisted of five 20 m × 20 m sample quadrats, were placed in the plot. Each quadrat was a sampling unit, and all 35 were used for analysis (Figure 1). All CWD components

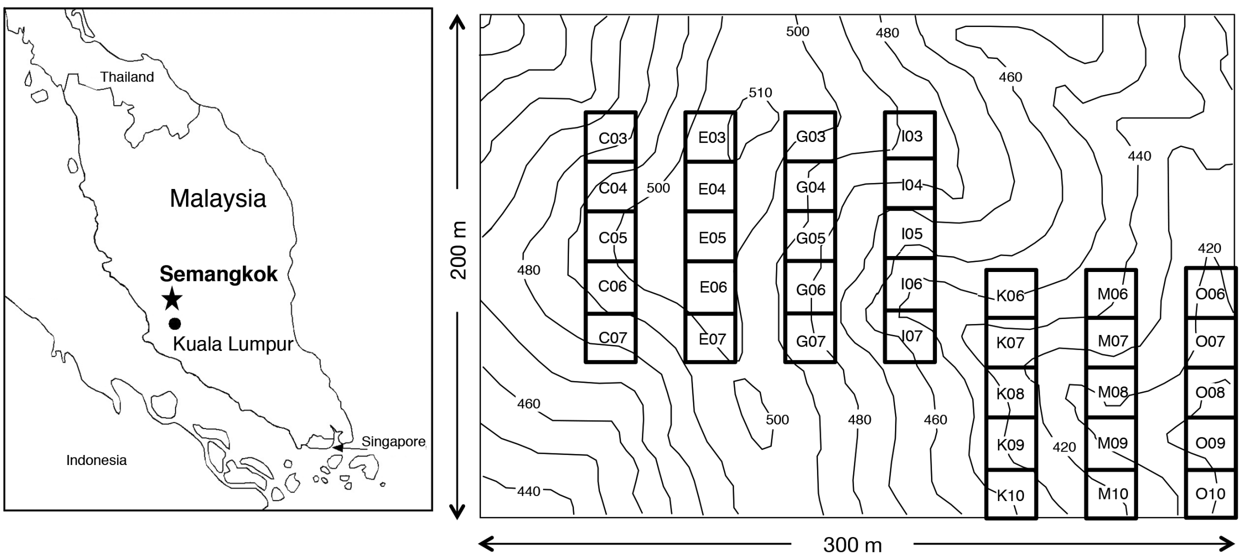

Figure 1 Location of Semangkok Forest Reserve (left) and layout of quadrats in the 6-ha plot (right); the contour interval is 10 m

with an end diameter of 10 cm or more were measured in each sampling quadrat from August to September of 2009 and 2010. This debris was classified by mode of tree death as: standing dead, snaps (broken stems), uproots (uprooted trees) or fallen logs (adapted from Chao et al. 2009). We used the measurement procedure described by Siitonen et al. (2000) as follows: a dead tree was measured and included in a sample quadrat if the center of the trunk at the root end was situated inside the quadrat. Thus, fallen trees that extended partly outside the quadrat were measured completely, whereas fallen trees projecting into the quadrat from outside were not measured. We recorded the dbh of standing dead trees and calculated the stem biomass using allometric equations developed by Chave et al. (2014). For snaps, we recorded the diameter of the midpoint of broken boles if possible. In the case of high midpoints, we measured dbh instead of the midpoint diameter. We recorded the diameter at both ends, length, position, and decay class for fallen and uprooted logs. CWD volume was calculated with the Smalian formula for logs and with the Huber formula for snaps (Harmon & Sexton 1996). The decay classes are show in Table 1.

Wood densities were determined by the water-displacement method, using small samples of wood collected from the plot. The dry weight was determined by multiplying the volume of each decay class by wood density (Table 1). In the present study, we combined classes 0 and 1 owing to the scarcity of CWD of class 0.

Topographic categories

We calculated elevation and slope in each 20 m × 20 m quadrat in the plot. The elevation of a quadrat was calculated as the mean value of its four corners, using the method described by Harms et al. (2001). The slope was calculated as the rate of the maximum change in elevation from the quadrat to each of its eight surrounding quadrats using the method described by Burrough and McDonnell (1998). For quadrats at the edge of the 6-ha plot, at least three surrounding quadrats did not contain elevation data. These surrounding quadrats were assigned the elevation of the focal quadrat.

Using the threshold of the first and third quartiles of elevation (445 and 487 m respectively) and the third quartile of the slope (32°), the quadrats were divided into four topographic categories as follows: steep slope (slope ≥ 32°), upper slope (elevation ≥ 487 m, slope < 32°), middle slope (445 m ≤ elevation < 487 m, slope < 32°) and lower slope (elevation < 445 m, slope < 32°). Since the 6-ha plot contained two steep slopes (Tange et al. 1998), we separated regions with a steep slope from the other three topographic categories. The number of CWD sampling quadrats in each category was as follows: 9 for the steep slope, 7 for the upper slope, 8 for the middle slope and 11 for the lower slope (Table 2). Findings by Tange et al. (1998) have suggested that soil thickness and soil moisture tend to increase from the upper slope to the lower slope.

Table 1 Mean densities of coarse woody debris (CWD) pieces in six decay classes in Semangkok Forest Reserve

Decay class	Criteria	Wood density ($g\ cm^{-3}$ ± SEM)	No. of samples
0	Recently dead, withered leaves remain on baranches	0.64 ± 0.04	6
1	Cambial zone rotting, big branches remain	0.61 ± 0.03	4
2	Sapwood rotting, big branches remain	0.52 ± 0.07	6
3	Heartwood rotting, only bole remains	0.46 ± 0.04	4
4	Sapwood lost, only heartwood remains	0.40 ± 0.03	4
5	Almost completely decomposed, turning into a mass of amorphous organic matter	0.38 ± 0.04	6

SEM = standard error of mean; decay classes defined by Yoneda et al. (1977)

Table 2 Aboveground biomass (AGB) and coarse woody debris (CWD) mass in different topographic categories at the plot

Topography	No. of quadrats	AGB ($Mg\ ha^{-1} \pm SEM$)		CWD ($Mg\ ha^{-1} \pm SEM$)	CWD input from 1993–2011 ($Mg\ ha^{-1}\ year^{-1} \pm SEM$)	Turnover time (year ± SEM)
		1993	2011			
Steep slope	9	380.4 ± 82.9	309.0 ± 66.8	119.3 ± 41.5	9.3 ± 4.3	25.4 ± 10.9
Upper slope	7	642.5 ± 135.4	674.9 ± 139.3	86.9 ± 36.4	6.9 ± 2.4	12.4 ± 4.0
Middle slope	8	505.2 ± 131.3	430.2 ± 124.2	83.5 ± 45.0	12.0 ± 8.1	20.9 ± 9.6
Lower slope	11	289.7 ± 51.8	275.3 ± 84.2	46.4 ± 15.3	5.3 ± 1.7	9.0 ± 2.4
Overall mean		432.9 ± 51.3	399.3 ± 54.7	81.7 ± 17.0	8.2 ± 2.2	16.6 ± 3.7
Kruskal–Wallis test		p = 0.1289	p = 0.0669	p = 0.4341	p = 0.7661	p = 0.6798

SEM = standard error of the mean

AGB and CWD inputs

All trees measuring 10 cm or greater in dbh in all sampling quadrats were evaluated during the eight tree censuses. We also developed equations describing the relationship between dbh (D) and total height (H) in the plot using a Weibull function (Yang et al. 1978). The samples were collected from 98 trees with dbh values ranging from 2.5 to 130.3 cm. The equation was as follows:

$$H = 69.592 \times (1 - \exp(-0.03673 \times D^{0.7109})$$

where D is in cm and H is in m.

The AGB values of living plants were calculated using the allometric equations developed by Chave et al. (2014) as follows:

$$AGB = 0.0673 \times (\rho D^2 H)^{0.976}$$

where ρ = wood density, D is in cm, H is in m and AGB is in kg dry mass. Each species was assigned a wood density value obtained from the comprehensive global wood density database (Chave et al. 2009, Zanne et al. 2009). We also calculated the ratio of AGB from large trees (dbh ≥ 70 cm) to the total AGB in each sample quadrat (Appendix).

The CWD inputs due to tree mortality were similarly counted in each of the eight tree censuses. The stock for each tree that died was determined using the same allometric equation applied to AGB (Chave et al. 2014) and employed the last measured dbh prior to death. Assuming equilibrium conditions, the turnover time of the CWD pool was calculated as follows (Baker et al. 2007, Palace et al. 2007):

$$\text{Turnover time} = M / I$$

where M = total stock of the CWD ($Mg\ ha^{-1}$) and I = the CWD input rate ($Mg\ ha^{-1}\ year^{-1}$).

Statistical analyses

The differences in CWD stock and other parameters relating to CWD dynamics among topographic categories were tested using the nonparametric Kruskal–Wallis test. Kruskal–Wallis tests were also conducted to examine the CWD stock across the four modes of tree death for each slope position. Multiple comparisons were performed with a Steel–Dwass test. All statistical analyses were carried out using R software version 3.2.3 (2015).

RESULTS AND DISCUSSION

CWD stock in the primary hill dipterocarp forest

We measured 545 pieces of dead wood in the sample quadrats from August till September of 2009 and 2010 and found 7 standing dead, 46 snap, 470 fallen logs and 22 uproots. Total CWD values for individual quadrats ranged from 0.1 to 379.7 $Mg\ ha^{-1}$ (n = 35, Appendix), giving a mean CWD value (± SEM) per quadrat of 81.7 ± 17.0 $Mg\ ha^{-1}$ (Table 2). This value was higher than that previously reported for undisturbed dipterocarp forests in South-East Asia (Yoneda et al. 1977, Yoneda et al. 1990, Ngo et al. 2013, Pfeifer et al. 2015).

Contrary to the large variability in previous reports, the AGB in this plot was relatively high compared with that in other undisturbed lowland dipterocarp forests (Saner et al. 2012) and hill dipterocarp forests (Ngo et al. 2013). Since the large amount of AGB is one of the drivers for enhancement of CWD stocks (Iwashita et al. 2013), the large CWD stock may result from the relatively large amount of AGB in this hill dipterocarp forest.

CWD stocks in different topographies

Mean CWD stocks showed a decreasing trend downslope, with the highest mass on the steep slope (119.3 ± 41.5 Mg ha^{-1}) and lowest mass on the lower slopes (46.4 ± 15.3 Mg ha^{-1}), but no significant difference in CWD among topographies was detected (Kruskal–Wallis test, $p > 0.05$; Table 2). Many large *S. curtisii* trees (dbh ≥ 70 cm) are distributed around ridges in Semangkok Forest Reserve (Niiyama et al. 1999, Tange et al. 1998), and they dominate the top canopy layer (40–50 m in height). Some quadrats (e.g. C04 and E03; Appendix) held these large trees thus yielded relatively high AGB values in the plot. The high AGB represented by large trees could be a source of high CWD stock, especially in the upper and steep slope areas.

The larger CWD deposits on the upper slope as compared with that on downslope areas is inconsistent with studies (e.g. Rubino & McCarthy 2003) showing that CWD pieces found on steep slopes may be redistributed to lower slope positions. It is noted that insufficient sample size in the present study may have contributed to the non-significant differences among topographies. CWD was found to exhibit wide variation in sample areas smaller than 0.1 ha in a boreal forest (Karjalainen & Kuuluvainen 2002). Future work quantifying movement of CWD material from the upper slope to downslope areas could clarify how CWD pieces are redistributed on topographies characteristic of hill dipterocarp forests in Peninsular Malaysia.

Mode of tree death

Downed CWD (fallen logs and uproots combined; 58.8 ± 13.9 Mg ha^{-1}) was greater than standing CWD (standing dead and snaps combined; 22.9 ± 7.5 Mg ha^{-1}) in the plot (Welch's t-test, $p > 0.05$). Forty six per cent of the fallen logs (n = 470) were pieces in the 10–20 cm diameter range; these pieces contributed only 8% of its total stock. Uprooted logs showed relatively high CWD stock despite their small number and were more frequently observed in the middle and steep slope positions (Figure 2).

Standing CWD made up 28% of total stock in the plot, and this proportion was similar to that found in another lowland (Yoneda et al. 1977) and hill dipterocarp forest (Yoneda et al. 1990) (Table 3). Since we did not observe any severe disturbances such as fire, windstorms or drought in the plot during the study period (Sato et al. 2013), snap tree numbers, which can be increased by storms (Toledo et al. 2012), showed little variation in CWD stock among topographies. In contrast to our results, Ngo et al. (2013) reported relatively high standing CWD in a hill dipterocarp forest, probably caused by lightning strikes. In our plot, one standing dead tree (near the ridge) that contributed to the increased CWD stock, was thought to have died after lightning struck it. Lightning could be one factor that results in standing dead trees, and may enhance CWD stock in hill dipterocarp forests.

CWD dynamics in the plot

Mean CWD input across all topographies, estimated from tree mortality, was 8.2 ± 2.2 Mg ha^{-1} $year^{-1}$ (Table 2). We found no significant differences among topographies for either CWD input or turnover time (Kruskal–Wallis test, $p < 0.05$; Table 2). Assuming long-term equilibrium of stocks and inputs, mean turnover time across all topographies was 16.6 ± 3.7 years, as calculated from the ratio of the mean CWD stock to the above-mentioned mean CWD input. Although comparison of estimated input rates is difficult owing to the use of different methodologies, researchers have estimated the annual inputs of CWD to be 3.8 Mg ha^{-1} $year^{-1}$ in the Peruvian Amazon of the Neotropical zone (Baker et al. 2007), 4.8 Mg ha^{-1} $year^{-1}$ in the Brazilian Amazon (Rice et al. 2004) and 4.9 Mg ha^{-1} $year^{-1}$ at La Selva, Costa Rica (Clark et al. 2002). Relatively few studies have been performed in dipterocarp forests in South-East Asia; the annual inputs of CWD are 3.3–20.5 Mg ha^{-1} $year^{-1}$ (average 9.3 Mg ha^{-1} $year^{-1}$) in lowland dipterocarp forests (Yoneda et al. 1977). Our estimates used census

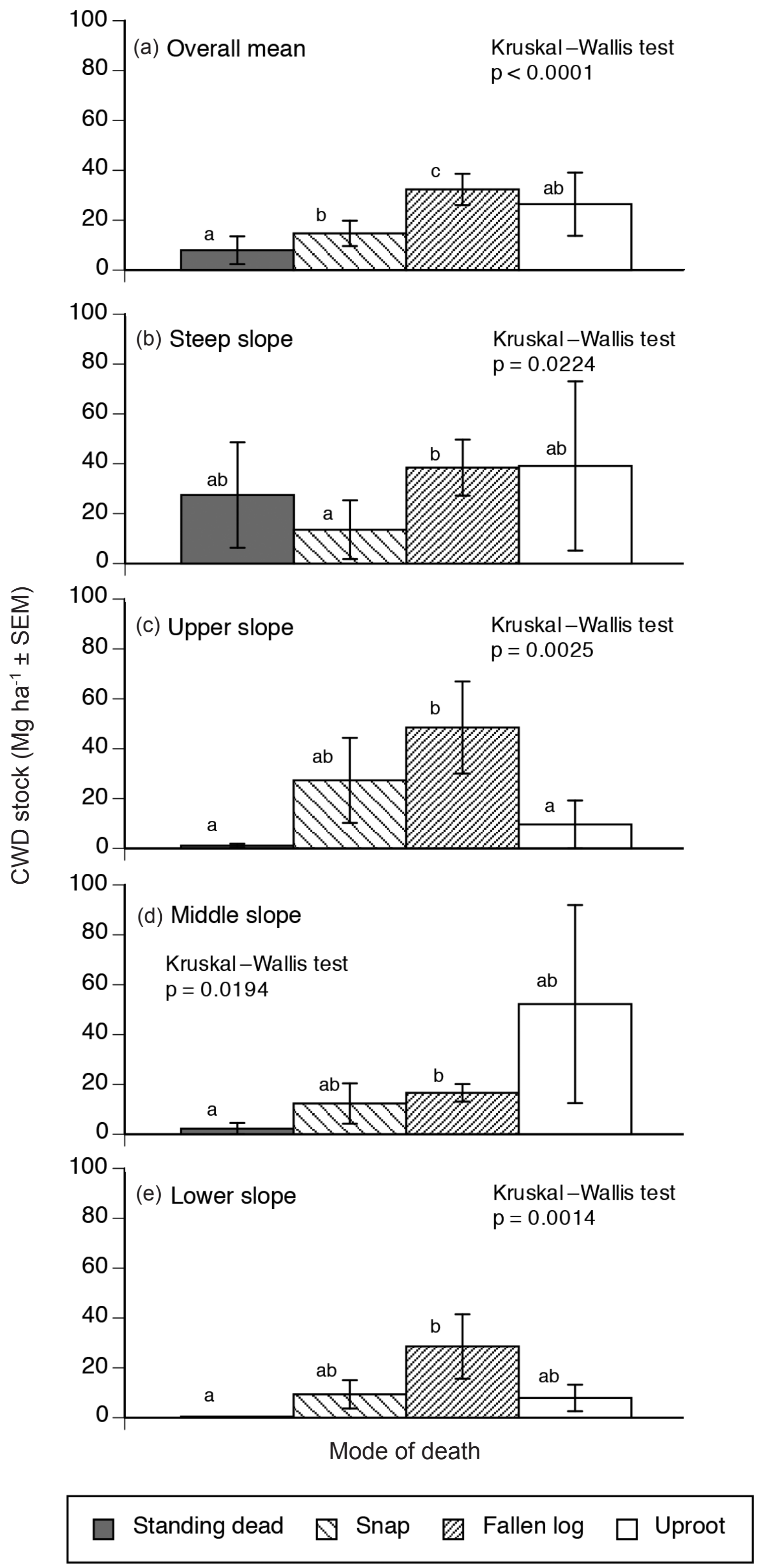

Figure 2 Mean coarse woody debris (CWD) in different topographical categories at Semangkok Forest Reserve based on mode of death; means with different letters are significantly different (Steel–Dwass test: $p < 0.05$); SEM = standard error of mean

Table 3 Coarse woody debris (CWD) measured in undisturbed tropical forests in South-East Asia

Country	Site	Standing CWD ($Mg\ ha^{-1}$)	Downed CWD ($Mg\ ha^{-1}$)	Total CWD ($Mg\ ha^{-1}$)	Total CWD/ AGB ratio	References
Malaysia	Semangkok	22.9	58.8	81.7	0.21	This study
Malaysia	Pasoh	14.0	35.0	49.0	0.12	Yoneda et al. (1977)
Indonesia	Pinang Pinang	16.0	39.0	55.0	0.13	Yoneda et al. (1990)
Malaysia	OG1_SAFE, Sabah	–		10.2	0.04	Pfeifer et al. (2015)
	OG2_SAFE, Sabah	–		27.0	0.14	
Singapore	Bukit Timah	18.9	12.3	31.2	0.09	Ngo et al. (2013)

Standing CWD = standing dead trees and snaps, Downed CWD = fallen logs and uproot trees; Aboveground biomass (AGB) was calculated from all living trees with dbh > 10 cm using an equation developed by Chave et al. (2014), OG1 and OG2 are primary forest blocks in the Stability of Forest Ecosystems (SAFE) project in Sabah

mortality data and were on the higher end of those in these studies.

The mortality of large-size trees played an important role in the enhancement of CWD input (Figure 3). Since we had conducted eight tree censuses between 1993 and 2011, we could identify some dead wood from this period, as well as prior to 1993, in each sampling quadrat. In some quadrats such as G03 and G04 (Figure 3a), CWD mass was greater than the CWD input over 18 years, implying that CWD accumulated prior to 1993 had contributed to CWD stock in those quadrats. On the other hand, large tree input due to mortality during the study period would also enhance CWD stock in the plot (Figures 3c and d). Rice et al. (2004) explained that high mortality prior to establishing a study plot would cause a relatively high CWD stock and low turnover in Amazonian forests. Woods (2014) suggested that CWD input rates fluctuate greatly due to occasional mortality of large canopy trees. Such "legacy" (cf. Yan et al. 2007) wood may be one of the reasons why this forest had high CWD stock and input.

CONCLUSIONS

Our study showed high CWD stocks in a primary hill dipterocarp forest of Peninsular Malaysia. CWD stocks among topographies were not found to be significantly different, as were CWD inputs. This non-significant result could be due to small sample sizes. From tree census data taken over 18 years, our study showed the importance of mortality of large trees to CWD dynamics in hill dipterocarp forests. Since the chance of reduction in AGB and subsequent CWD input depends largely on disturbance frequency further observation of forest dynamics would provide insights into CWD dynamics in hill dipterocarp forest ecosystems.

ACKNOWLEDGEMENTS

We appreciate the field assistance provided by K Kimura, S Iida, T Igarashi, K Miyamoto, T Yagi, K Tanaka and M Noguchi. This study was conducted under the programme of the NIES/FRIM/UPM/UTM/FDNS Joint Research Project. This study was supported by the 'Global Environment Research Account for National Institutes', Ministry of the Environment, Government of Japan.

REFERENCES

Abd Rahman K, Niiyama K, Azizi R, Appanah S & Iida S. 2002. Species assembly and site preference of tree species in a primary seraya-ridge forest of Peninsular Malaysia. *Journal of Tropical Forest Science* 14: 287–303.

Baker TR, Coronado ENH, Phillips OL et al. 2007. Low stocks of coarse woody debris in a southwest Amazonian forest. *Oecologia* 152: 495–504.

Brown S. 2002. Measuring carbon in forests: current status and future challenges. *Environmental Pollution* 116: 363–372.

Burrough PA & McDonell RA. 1998. *Principles of Geographical Information Systems*. Oxford University Press, New York.

Chao K-J, Phillips OL, Monteagudo A, Torres-Lezama A & Martínez RV. 2009. How do trees die? Mode of death in northern Amazonia. *Journal of Vegetation Science* 20: 260–269.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG & Zanne AE. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12: 351–366.

Chave J, Réjou-Méchain M, Búrquez A et al. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* 20: 3177–3190.

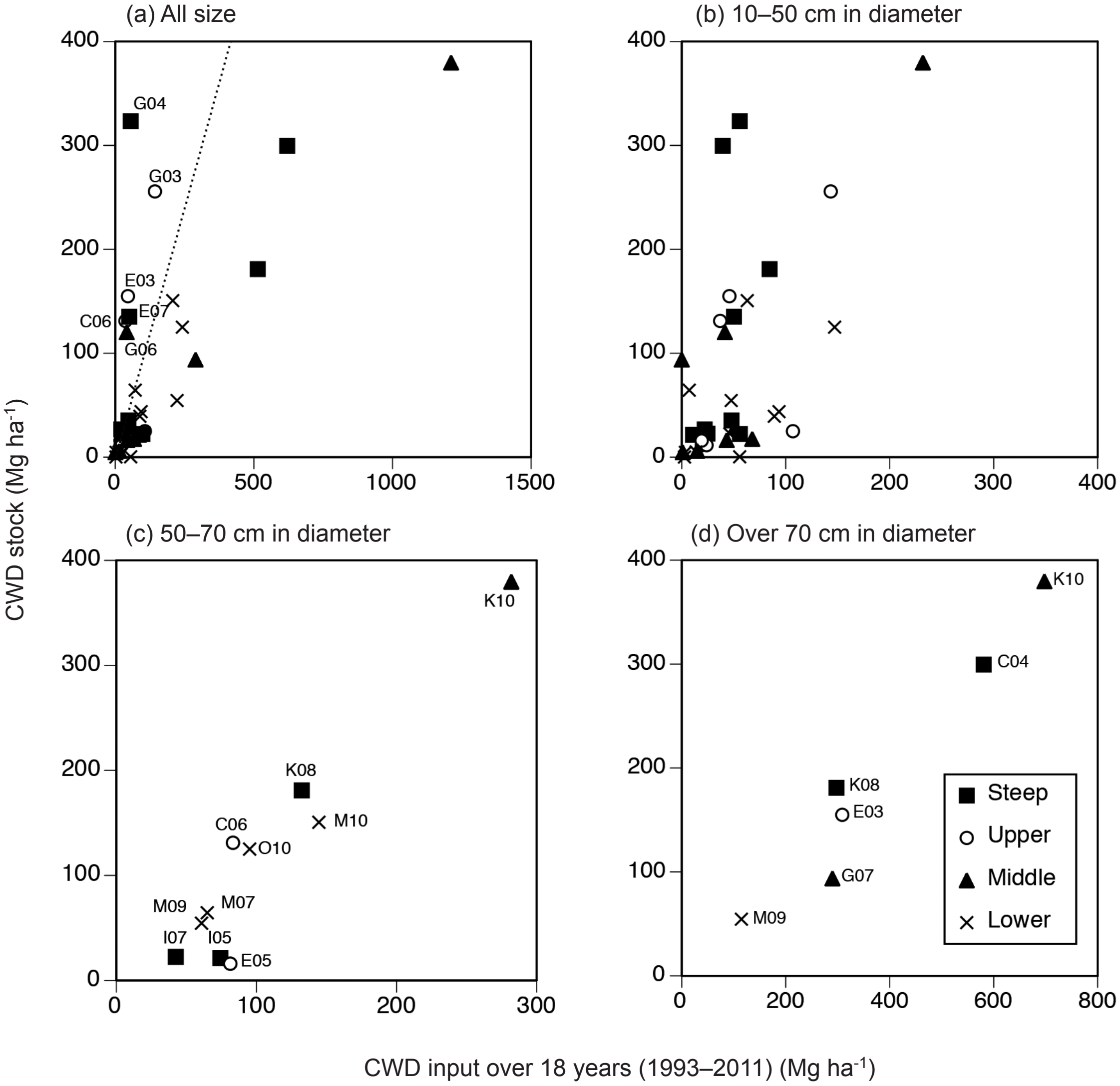

Figure 3 Relationships between CWD input over 18 years and CWD stock in each diameter class of CWD; the dotted line in (a) shows the 1:1 values between CWD stock and input, each plotted point represents a quadrat (identified by alphabet-number codes); CWD = coarse woody debris

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.

Franklin JF, Shugart HH & Harmon ME. 1987. Tree death as an ecological process *BioScience* 37: 550–556.

Gale N. 2000. The aftermath of tree death: coarse woody debris and the topography in four tropical rain forests. *Canadian Journal of Forest Research* 30: 1489–1493.

Gale N & Hall P. 2001. Factors determining the modes of tree death in three Bornean rain forests. *Journal of Vegetation Science* 12: 337–348.

Hamdan O, Hasmadi IM, Aziz Hk, Norizah K & Zulhaidi MSH. 2015. L-band saturation level for aboveground biomass of dipterocarp forests in Peninsular Malaysia. *Journal of Tropical Forest Science* 27: 388–399.

Harmon ME & Sexton J. 1996. *Guidelines for Measurements of Woody Detritus in Forest Ecosystems*. US LTER Publication No. 20. University of Washington, Seattle.

Harmon ME, Franklin JF, Swanson FJ et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133–302.

Harms KE, Condit R, Hubbell SP & Foster RB. 2001. Habitat associations of tree and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89: 947–959.

Iwashita DK, Litton CM & Giardina CP. 2013. Coarse woody debris carbon storage across a mean annual temperature gradient in tropical montane wet forest. *Forest Ecology and Management* 291: 336–343.

Jeyanny V, Husni MHA, Rasidah KW, Kumar BS, Arifin A & Hisham MK. 2014. Carbon stocks in different carbon pools of a tropical lowland forest and a montane forest with varying topography. *Journal of Tropical Forest Science* 26: 560–571.

Karjalainen L & Kuuluvainen T. 2002. Amount and diversity of coarse woody debris within a boreal forest landscape dominated by *Pinus sylvestris* in Vienansalo wilderness, eastern Fennoscandia. *Silva Fennica* 36: 147–167.

Niiyama K, Abd Rahman K, Iida S, Kimura K, Azizi R & Appanah S. 1999. Spatial patterns of common tree species relating to topography, canopy gaps and understory vegetation in a hill dipterocarp forest at Semangkok Forest Reserve, Peninsular Malaysia. *Journal of Tropical Forest Science* 11: 731–745.

Ngo KM, Turner BL, Muller-Landau HC et al. 2013. Carbon stocks in primary and secondary tropical forests in Singapore. *Forest Ecology and Management* 296: 81–89.

Okuda T, Suzuki M, Numata S et al. 2004. Estimation of aboveground biomass in logged and primary lowland rainforests using 3-D photogrammetric analysis. *Forest Ecology and Management* 203: 63–75.

Palace M, Keller M, Asner GP, Silva JNM & Passos C. 2007. Necromass in undisturbed and logged forests in the Brazilian Amazon. *Forest Ecology and Management* 238: 309–318.

Palace M, Keller M, Hurtt G & Frolking S 2012. A review of above ground necromass in tropical forests. Pp 215–252 in Sudarshana P, Nageswara-Rao M & Soneji JR (eds) *Tropical Forests*. InTech, Rijeka.

Pfeifer M, Lefebvre 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.

Rice AH, Pyle EH, Saleska SR et al. 2004. Carbon balance and vegetation dynamics in an old-growth Amazonian forest. *Ecological Applications* 14: s55–s71.

Rubino DL & McCarthy BC. 2003. Evaluation of coarse woody debris and forest vegetation across topographic gradients in a southern Ohio forest. *Forest Ecology and Management* 183: 221–238.

Saifuddin S, Abdul Rahim N & Muhammad Farid AR. 1991. *Watershed Research in Forest Plantation: I. Establishment and Physical Characteristics of Bukit Tarek Watershed.* Research Pamphlet No. 110. Forest Research Institute Malaysia, Kepong.

Saner P, Loh YY, Ong RC & Hecto A. 2012. Carbon stocks and fluxes in tropical lowland dipterocarp rainforests in Sabah, Malaysian Borneo. *PLOS ONE* 7: e29642.

Sato T, Niiyama K, Yagihashi T, Noguchi M, Abd Rahman K & Azizi R. 2013. Comparison of forest carbon stocks between canopy conditions in two typical dipterocarp forest types in Peninsular Malaysia. *Bulletin of Forestry and Forest Products Research Institute* 12: 155–156.

Siitonen J, Martikainen P, Punttila P & Rauh J. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management* 128: 211–225.

Tange T, Yagi H, Sasaki S, Niiyama K & Abd Rahman K. 1998. Relationship between topography and soil properties in a hill dipterocarp forest dominated by *Shorea curtisii* at Semangkok Forest Reserve, Peninsular Malaysia. *Journal of Tropical Forest Science* 10: 398–409.

Toledo JJ, Magnusson WE, Castilho CV & Nascimento HEM. 2012. Tree mode of death in Central Amazonia: Effects of soil and topography on tree mortality associated with storm disturbances. *Forest Ecology and Management* 263: 253–261.

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 Ecology and Management* 252: 98–107.

Yang RC, Kozak A & Smith JHG. 1978. The potential of Weibull-type functions as flexible growth curves. *Canadian Journal of Forest Research* 8: 424–431.

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, Yoda K & Kira T. 1977. Accumulation and decomposition of big wood litter in Pasoh Forest, West Malaysia. *Japanese Journal of Ecology* 27: 53–60.

Whitmore TC. 1984. *Tropical Rain Forests of the Far East.* Oxford University Press, Oxford.

Woods KD. 2014. Multi-decade biomass dynamics in an old-growth hemlock-northern hardwood forest, Michigan, USA. *PeerJ* 2: e598.

Zanne AE, Lopez-Gonzalez G, Coomes DA et al. 2009. Towards a worldwide wood economics spectrum. Dryad Digital Repository. http://dx.doi.org/10.5061/dryad.234.

Appendix Aboveground biomass (AGB) and coarse woody debris (CWD) stock per sampling quadrat (Mg ha^{-1})

Sample quadrat code	Topography	AGB in 1993 (Mg ha^{-1})	AGB in 2011 (Mg ha^{-1})	CWD input due to mortality (Mg ha^{-1} year^{-1})	CWD (Mg ha^{-1})
C03	Steep slope	209.5 (0)	237.7 (0)	2.7	35.5
C04	Steep slope	762.2 (71)	229.4 (0)	34.5	304.8
E07	Steep slope	272.8 (38)	429.5 (51)	2.8	136.1
G04	Steep slope	143.1 (0)	165.3 (0)	3.1	323.2
G05	Steep slope	680.3 (27)	804.6 (57)	1.2	26.6
105	Steep slope	272.2 (59)	240.9 (72)	3.9	21.4
106	Steep slope	143.8 (0)	229.3 (0)	1.4	22.7
107	Steep slope	272.0 (0)	262.6 (0)	5.5	22.7
K08	Steep slope	668.2 (52)	182.0 (0)	28.6	180.9
C05	Upper slope	817.8 (63)	1068.7 (64)	1.1	11.5
C06	Upper slope	319.6 (0)	339.6 (0)	6.7	131.1
E03	Upper slope	970.8 (60)	1006.2 (50)	19.9	157.4
E04	Upper slope	420.7 (0)	505.3 (34)	1.3	11.5
E05	Upper slope	1191.6 (75)	1030.4 (76)	5.6	16.0
E06	Upper slope	542.7 (22)	628.8 (51)	5.9	25.0
G03	Upper slope	234.7 (0)	145.6 (0)	7.7	255.7
C07	Middle slope	318.7 (0)	349.7 (0)	2.9	29.2
G06	Middle slope	197.1 (0)	260.6 (0)	2.3	120.3
G07	Middle slope	645.8 (53)	594.9 (26)	16.1	93.8
I03	Middle slope	662.5 (62)	921.8 (83)	2.4	16.4
I04	Middle slope	766.2 (87)	950.6 (87)	0.1	4.8
K06	Middle slope	44.8 (0)	83.1 (0)	0.9	6.0
K09	Middle slope	237.7 (44)	161.8 (0)	3.9	17.5
K10	Middle slope	1168.4 (61)	119.2 (0)	67.5	379.7
K07	Lower slope	211.9 (0)	156.0 (0)	4.9	39.3
M06	Lower slope	235.9 (0)	321.7 (0)	0.8	5.0
M07	Lower slope	151.5 (0)	81.0 (0)	4.0	64.4
M08	Lower slope	200.4 (0)	88.6 (0)	5.2	43.7
M09	Lower slope	364.5 (46)	224.3 (0)	12.4	54.5
M10	Lower slope	413.3 (0)	291.5 (58)	11.5	150.6
O06	Lower slope	620.3 (65)	1000.5 (69)	2.6	22.5
O07	Lower slope	68.7 (0)	21.0 (0)	3.1	0.3
O08	Lower slope	78.9 (0)	102.0 (0)	0.1	0.1
O09	Lower slope	393.7 (41)	528.6 (63)	0.2	4.6
O10	Lower slope	448.2 (0)	213.4 (0)	13.5	125.1

Aboveground biomass (1993 and 2011) was calculated from all living trees above 10 cm in dbh using an equation developed by Chave et al. (2014); percentages of AGB > 70 cm dbh are shown in parentheses