ORIGINAL ARTICLE

Inter-annual variations of net ecosystem productivity of a primeval tropical forest basing on a biometric method with a long-term data in Pasoh, Peninsular Malaysia

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ABSTRACT Inter-annual variability of net ecosystem productivity (*NEP*) was assessed by a biometric method observing dynamics of coarse woody organs in a primeval lowland tropical rain forest in Pasoh, Peninsular Malaysia. Yearly changes of *NEP* estimated by biometric method well agreed with those measured by Eddy Covariance Method (ECM), when we observed a stand within a distance of 125–150 m from the tower for ECM. Annual *NEP* at a 2-ha stand ranged from $-5.0 \text{ t Carbon ha}^{-1} \text{ y}^{-1}$ to $2.1 \text{ t Carbon ha}^{-1} \text{ y}^{-1}$ during the last 43 years (1969–2012) with two times depressions. They were caused by man-made and natural disturbances that affected as much as 10% of the 2-ha stand area, and negative *NEP* was maintained during around 10 years after disturbances. Inter-annual variances of *NEP*, biomass and necromass of coarse woody debris were evaluated by a mathematical simulation with observed properties of net primary productivity and a death rate of coarse woody organs. Simulated *NEP* was $0.00 \pm 1.52 \text{ t C ha}^{-1} \text{ y}^{-1}$ under equilibrium regimes, and the variance increased under the conditions of a higher mean death rate leading to decrease of biomass. Basing on variances of *NEP*, we estimated a turnover time of an equilibrium system at 400 years for a 2-ha stand, which is equivalent to 800 ha in area.

Key words: carbon cycling, coarse woody debris, inter-annual variations, *NEP*, tropical rain forest

INTRODUCTION

Net ecosystem productivity (*NEP*) is an important ecosystem characteristic because it integrates activities of all organisms living in an ecosystem. It summarizes the entire carbon/energy flux of an ecosystem in a single number, and is an important determinant of the world carbon cycle (Sprugel 1985). Death of a big tree changes the distribution of carbon stock in a forest ecosystem, and induces a negative value of *NEP* locally because of increased carbon release rates through decomposition of fresh mass litter (Vitousek & Reiners 1975, Yoneda 1997, 2003). A forest under stable natural disturbance regimes is composed of a mosaic of patches of different ages (White & Pickett 1985), and hence spatial variances of *NEP* would be substantial. How much the minimum area or time is it necessary for the equilibrium state under such regimes? Understanding of these intrinsic variances of *NEP* of a primeval tropical rain

forest is important as a scientific basis not only for the conservation and management under degradation of tropical forests but also for evaluating impacts on global climate changes because of large contributions of mature tropical rain forests in global carbon cycle (Brown & Lugo 1982).

NEP is defined as differences between net primary productivity (*NPP*) and heterotrophic respiration rates (*HTR*) in an ecosystem (Whittaker 1975). There have been few studies (Miller et al. 2004) that biometrically examined spatial-temporal variances of *NEP* for forest ecosystems because of the lack of data about these two rates of *NPP* and *HTR*. This study aims to clear the topics by using the data from a long-term field observation in a primeval lowland tropical rain forest.

Thanks to long-term ecological studies in the tropics, spatial-temporal variances of biotic dimensions such as biomass, productivity, and mortality have been observed (Baker et al. 2004, DAAC 2015, Phillips et al. 2010,

List of principal abbreviations and acronyms:

<i>BM</i>	Total biomass (t Carbon ha ⁻¹)
<i>BM_c</i>	Biomass of coarse woody organs (t Carbon ha ⁻¹)
<i>BM_{ce}</i>	Theoretical <i>BM_c</i> under the equilibrium conditions (t Carbon ha ⁻¹)
CWBBM	Coarse-wood-based biometric method
<i>CWD</i>	Necromass of coarse woody debris (t Carbon ha ⁻¹)
<i>CWD_e</i>	Theoretical <i>CWD</i> under the equilibrium conditions (t Carbon ha ⁻¹)
<i>dbh</i>	Stem diameter at breast height of a tree (cm)
<i>DR_c</i>	Annual death rates of coarse woody organs (t Carbon ha ⁻¹ y ⁻¹)
ECM	Eddy covariance method
<i>HTR</i>	Heterotrophic respiration rates (t Carbon ha ⁻¹ y ⁻¹)
<i>HTR_c</i>	Heterotrophic respiration rates of coarse woody debris (t Carbon ha ⁻¹ y ⁻¹)
<i>HTR_f</i>	Heterotrophic respiration rates of fine litter (t Carbon ha ⁻¹ y ⁻¹)
<i>HTR_s</i>	Heterotrophic respiration rates of soil organic matter (t Carbon ha ⁻¹ y ⁻¹)
<i>ID</i>	Index of durability of coarse woody debris against decomposition (g cm ^{-2.8})
<i>IR_c</i>	Annual increment rates of coarse woody organs (t Carbon ha ⁻¹ y ⁻¹)
<i>NEP</i>	Net ecosystem productivity (t Carbon ha ⁻¹ y ⁻¹)
<i>NPP</i>	Net primary productivity (t Carbon ha ⁻¹ y ⁻¹)
<i>NPP_c</i>	<i>NPP</i> allocated to coarse woody organs (t Carbon ha ⁻¹ y ⁻¹)
<i>NPP_f</i>	<i>NPP</i> allocated to fine organs (t Carbon ha ⁻¹ y ⁻¹)
<i>RDR_c</i>	Realized annual death rates of coarse woody organs (t Carbon ha ⁻¹ y ⁻¹)
<i>β</i>	Coefficient of decay of coarse woody debris (y ⁻¹)

Yamakura et al. 1996, Yoneda et al. 1994, Yoneda et al. 2000). Spatial-temporal variations of *NEP* have, however, not been clear because of a less tractable parameter of *HTR* particularly for coarse woody debris (*CWD*) and soil organic matter.

Eddy covariance method (*ECM*) for *NEP* has been adopted to evaluate CO₂ flux from various vegetation to the

atmosphere at global scale (FLUXNET 2015), and seasonal and inter-annual changes of *NEP* have been observed in tropical rain forests (Kim et al. 2012, Kosugi et al. 2012). To assess a stand dynamics basing on these *ECM* data, it is necessary to clear a relation between *ECM* and a biometric method (Miller et al. 2004, Goulden et al. 2011).

Carbon cycling in a primeval tropical lowland rain forest was revealed through a comprehensive study in Pasoh, Peninsular Malaysia under the International Biological Program (IBP) (Kira 1987), and it was suggested that *NEP* of a forest ecosystem was largely influenced by large variances of supply rates of *CWD* ranging from 1.6 t Carbon ha⁻¹ y⁻¹ to 10.3 t C ha⁻¹ y⁻¹, coefficient variance (CV) of which was 77% among five 2-ha plots against CV = 19% of necromass of *CWD* (*CWD*) (Yoneda et al. 1977).

Stand dynamics at a 2-ha permanent plot for IBP in Pasoh has been successively monitored, and observation by *ECM* has been continued in this stand since 2003. This study aims to clear the following three subjects with these data in this plot. They are 1) to evaluate yearly changes of *NEP* during the last 43 years by a biometric method that relies on dynamics of coarse woody organs (Yoneda 2003), 2) to examine correlation between biometric method and *ECM* with a horizontal distance from the tower for *ECM* as a major parameter, and 3) to evaluate intrinsic variances of *NEP*, biomass and *CWD* under equilibrium regimes by a mathematical simulation, and to consider the minimum spatial-temporal extent for the equilibrium state.

MATERIALS AND METHODS

Study site and field data

This study was conducted with filed data about stand dynamics and carbon cycling of a primeval tropical rain forest, which had been obtained at a permanent research plot P1 in the Pasoh Forest Reserve of Peninsular Malaysia under several scientific projects during 1969–2012 (Kira 1987, Yoneda et al. 2002, Hoshizaki et al. 2004, Kosugi et al. 2012,).

Pasoh forest, situated about 70 km to the southeast of Kuala Lumpur in the state of Negeri Sembilan, is a lowland mixed dipterocarp forest dominated by two genera of *Shorea* and *Dipterocarpus* (Davies et al. 2003), and the average annual rainfall (1500–2000 mm in 1983–1995 at P1) is less than that in other regions of Peninsular Malaysia (Noguchi et al. 2003). Plot 1 was first established as a 2-ha plot in the primary forest in 1969 (Fig. 1A). Studies on primary productivity and carbon cycling had been inten-

Fig. 1. **A:** Maps of forest stands for this study. A outer rectangle: 6-ha P1, an inner rectangle: 2-ha P1, a black rectangle: 0.2-ha destructive sampling stand, and grey-colored fun-shaped area: six stands for comparative analysis of relationships between CWBBM and ECM. **B:** A laser diagram of wind direction at the top of a 52 m-tower in P1. Wind direction is an average one at 30 minutes intervals during 7.3 years from 2003. Open and closed circles show directions at day and night times, respectively.

Table 1. A list of coefficient (β) of decay of CWD for this study. These values were obtained from field observation at Plot 1.

β (y^{-1})	State and diameter of CWD	Method (measure of decay rates)	Reference
0.81	fallen, 3–4 cm	CO ₂ evolution	Yoneda et al. (1977)
0.76	newly fallen, 1.5–6.5 cm	weight loss	Yoneda et al. (1977)
0.72	fallen, 5 cm	CO ₂ evolution	Yoneda et al. (2004)
3.27	fallen, 5 cm	weight loss	Yoneda et al. (2004)
0.223	snag, $\text{dbh} \geq 20$ cm	bulk density loss	Yoneda et al. (2006)
0.332	fallen, $\text{dbh} \geq 20$ cm	bulk density loss	Yoneda et al. (2006)
0.430	root-up, $\text{dbh} \geq 20$ cm	bulk density loss	Yoneda et al. (2006)

sively conducted in this P1 under IBP during 1970–1974 (Kira 1978, 1987).

Tree census for diameter at breast height (dbh) was conducted five times at a 2-ha P1 during 1969–1991 by Forest Research Institute of Malaysia (FRIM) and a Japanese team of IBP, and has been repeated every other year at an expanded 6-ha plot by Forestry and Forest Products Research Institute of Japan since 1994. This study used available data of fifteen censuses during 1969–2012. The average interval of tree census was 3.1 years. The x and y coordinates of all trees in the plot were measured. Target trees of this study were bigger trees ≥ 10 cm in dbh .

Biomass was estimated by allometric relations obtained in this forest reserve. Regressions for aboveground and root biomass were observed by destructive samplings at a 0.2-ha stand in P1 in 1973 (Kira 1987) and at a forest compartment 47 in this reserve (Niiyama et al. 2010), respectively. All trees in the 0.2-ha stand were clear-cut and these logs were

remained on the forest ground after measurement. Necromass of CWD observed in 1971 (Yoneda et al. 1977) was adopted as the initial value of this study in 1969. We have examined decay rates of CWD with an observed coefficient of decay (β) at this plot (Yoneda et al. 1977, Yoneda et al. 2004, Yoneda et al. 2006) and physical parameters of diameter and initial bulk density of each dead wood (Yoneda 1985, 1986). The coefficient of β is affected by state (fallen or standing, aboveground or belowground) of CWD and measures of decay rates (Yoneda 1975), and observed β values ranged from 0.223 to 3.27 y^{-1} (Table 1). In this study, we did not consider the variation of β depending on the state of CWD because of no information available for the status of CWD in the plot and of uncertainty of the appropriate measure of decay rate. We therefore calculated seven different estimates of NEP using the seven observed values of β (Table 1).

CO₂ exchange at the canopy has been observed at a

52 m tower in the expanded (6-ha) P1 since 1995 by ECM (Tani et al. 2003). Yearly changes of *NEP* during 2003–2011 by ECM (Kosugi et al. 2012) were compared with results by a biometric method at a fan-shaped area expanded from the tower with a radius of 170 m. This fan-shaped area was divided into six stands by varied distances from the tower (50, 75, 100, 125 and 150 m). All trees in the fan-shaped area were sorted to the six stands by their coordinates in the 6-ha plot. The prevailing wind at the tower has been coming from the original (2-ha) P1 during both day and night (Fig. 1B).

Definition of net ecosystem productivity, (*NEP*)

When we examine yearly changes of *NEP*, it would be a reasonable way to evaluate two fluxes through coarse woody organs such as stems, branches and big roots and fine organs such as leaves, twigs and fine roots separately because of their different dynamics under live and dead conditions in a forest (Kira 1987). Spatial-temporal variances of yearly litter-fall rates of fine organs were small (Yoneda et al. 2002) compared to coarse woody organs (Yoneda et al. 1977, Yoneda et al. 2005), and fast decomposition of fine litter (Ogawa 1978, Tashiro et al. 2013) released carbon to atmosphere almost within one year in contrary to long-decay process of CWD over several years (Yoneda 1997). Basing on these different attributes of these two fluxes, we considered that yearly changes of *NEP* are mainly caused by coarse woody organs accompanied with the equilibrium state of fine organs. Carbon budget of soil organic matter (SOM) may also affect *NEP* because SOM is one of the major carbon pools (Kira 1987). There was, however, no significant differences ($P = 0.250$) in accumu-

lated carbon amount in soils between undisturbed forest stands and regenerating stands in the Pasoh forest Reserve, which were $69.6 \pm 7.9 \text{ t Carbon ha}^{-1}$ and $78.5 \pm 9.2 \text{ t C ha}^{-1}$, respectively (Yoda & Kira 1982). Hence we assumed that soil carbon held the equilibrium state under stable natural disturbance regimes, although humus from dead woods including roots was considered in this study as a refractory component of CWD at the late stage of the logistic decay process (Yoneda 1975). Consequently, this paper defined *NEP* by the following equations.

$$\begin{aligned} NEP &= NPP - HTR \\ &= (NPP_c + NPP_f) - (HTR_c + HTR_f + HTR_s) \end{aligned}$$

When we assume that $NPP_f = HTR_f + HTR_s$,

$$NEP = NPP_c - HTR_c$$

in which symbols of NPP_c , NPP_f , HTR_c , HTR_f and HTR_s are *NPP* of coarse woody organs and fine organs, and *HTR* of CWD, fine litter and soil organic matter, respectively.

We assume a conversion rate of organic matter to carbon weight to be 0.5.

Estimation of *NEP* basing on dynamic of coarse woody organs

We estimate *NEP* as a difference between a carbon fixation rate of live coarse woody organs by net primary productivity (NPP_c) and a carbon release rate of CWD by decomposition (HTR_c) (Fig. 2A). We call this biometric method considering only the dynamics of coarse woody organs as CWBBM (coarse-wood-based biometric method) against ECM.

Non-yearly data of *dbh* for surviving trees were trans-

Fig. 2. **A:** A schematic diagram of carbon cycling in a forest through a dynamics of coarse woody organs. Symbols of *NEP*, NPP_c , HTR_c , IR_c , and DR_c are carbon fluxes of net ecosystem productivity, net primary productivity, a heterotrophic respiration rate, an increment rate of biomass, and a death rate, respectively. BMc and *CWD* are carbon accumulation including underground parts in biomass of coarse woody organs and coarse woody debris, respectively. **B:** Observed carbon cycling through a dynamics of coarse woody organs at 2-ha P1 under IBP (redrawn from Kira (1987)). Biomass and CWD are aboveground one only in this diagram. Dimensions of carbon accumulation and fluxes are [t C ha^{-1}] and [$\text{t C ha}^{-1} \text{ y}^{-1}$], respectively. **C:** Simulated average carbon cycling by CWBBM under the conditions with an observed mean death rate.

formed to yearly one by linear interpolation between two censuses. For trees that died between the two censuses, time of each death is an important parameter to estimate the following decay rate of a dead tree because of different decomposition proceeds depending on tree sizes. Individual-tree death was determined by random occurrence during the period between the last year for *dbh* measurement and the first year for confirming the death. Ten trials were applied to get average annual rates of death and decay.

We define coarse woody organs to be a stem, branches, and roots of a tree ≥ 10 cm in *dbh*, though it includes fine woody organs as minor components in mass. Weights of these components were calculated by the following allometric regressions obtained in this forest reserve (Kato et al. 1978, Niiyama et al. 2010).

$$1/H = 1/(2.0 \text{ } dbh) + 1/61 \quad [\text{m, cm}] \quad \text{Eq. (1)}$$

$$w_s = 0.313 (dbh^2 H)^{0.973} \quad [\text{kg, dm}^3] \quad \text{Eq. (2)}$$

$$w_b = 0.136 w_s^{1.070} \quad [\text{kg, kg}] \quad \text{Eq. (3)}$$

$$w_r = 0.023 dbh^{2.59} \quad [\text{kg, cm}] \quad \text{Eq. (4)}$$

in which symbols of H , w_s , w_b , and w_r are tree height and weights of a stem, branches and roots of a tree, respectively. Then weight of coarse woody organs (w_c) of a tree was defined to be $w_c = w_s + w_b + w_r$, and biomass (BM_c) of coarse woody organs in a plot was total amount of w_c of trees ≥ 10 cm in *dbh*. We assumed regenerations of BM_c to be caused only by death of a tree, then NPP_c at a given year was the sum total of growth rates of surviving trees during the last one year. Recruited trees were incorporated in the calculation of NPP_c only after the census when they were first recorded as exceeding the minimum *dbh* (10 cm). A death rate at a given year (DR_c) was calculated with total w_c of dead trees during the last one year.

HTR_c at a given year was defined as annual weight loss rate of total big dead woody debris during the last one year. We assumed decomposition of each dead wood to follow the logistic weight loss process (Yoneda 1975, 1986). That is

$$w_{ct} = \frac{w_{c0}}{ID + (1 - ID)\exp(\beta t)} \quad \text{Eq. (5)}$$

in which symbols of t , w_{ct} , w_{c0} , ID , and β are duration after death, weight at t , the initial weight at $t=0$, the index of durability, and the coefficient of decay, respectively. Index

of durability (ID) of each CWD could be approximated by the product of the initial bulk density and the 0.2th power of diameter of CWD (Yoneda 1985, 1986). We assumed the initial bulk density to be constant irrespective of species as 0.70 g cm^{-3} being the maximum value of CWD in this forest (Yoneda et al. 1977), and diameter of CWD to be half of *dbh* of each dead tree regardless of diameter distribution of woody organs within a tree (Shinozaki et al. 1964). ID should be a positive value less than 1 from definition of Eq. (5), and then we corrected ID as a value of calculated ID divided by $1.75 \text{ g cm}^{-2.8} (0.70 \times (194.4/2)^{0.2})$ under consideration of the maximum *dbh*, 194.4 cm, of dead trees in this plot. Weight loss processes of every dead wood including roots were calculated by Eq.(5) with their *dbh* and ID . We applied the ID value from an average diameter of all dead trees in 6-ha plot, $ID = 0.64 \text{ g cm}^{-2.8}$, for the accumulated CWD in 1969 because of no information of their *dbh*. HTR_c at a given time was defined as a total loss rate of all CWD during the last one year.

Ten trials were conducted for yearly changes of NEP with ten *dbh*-database resulting from ten trials about dead trees. Their average values were used as the final results of this estimation.

Fig. 3. Frequency distributions of net primary productivity (A) and an annual death rate (B) of coarse woody organs during the last 43 years in P1. Two bell-shaped curves are their regressed log-normal distributions. X axis is a logarithmic coordinate. Open circles in diagram B show a frequency distribution of observed mean death rates between 14 censuses during 39 years after 1973.

Table 2. Simulated mean values of BM_c , CWD , and NEP during 17000 years (1700 years $\times$ 10 trials) under equilibrium regimes at eight different classes of mean death rates (DR_c). Classes are shown as a relative ratio (%) of a geometric mean DR_c (G. mean) to a geometric mean NPP_c in $\log_{10}$ value. A symbol of "A. mean" is an arithmetical mean value. RDR_c is a realized death rate. Figures in parenthesis are theoretical values from Eq.(6) for BM_c and Eq.(8) for CWD . Values of BM_c and NEP are arithmetical mean values, and one of CWD is a geometric mean value. Turnover time is defined as the minimum duration for the equilibrium state in NEP at a 2-ha forest stand. Figures with same superscript (a) for CWD are not significantly different ($P > 0.05$), and NEP with b is significantly different from the others ($P < 0.05$).

Class(%)	Mean death rate (DR_c)		RDR_c	BM_c (t C ha ⁻¹)	CWD (t C ha ⁻¹)	NEP (t C ha ⁻¹ y ⁻¹)	Turnover time (year)
	G. mean (t C ha ⁻¹ y ⁻¹)	A. mean (t C ha ⁻¹ y ⁻¹)	A. mean (t C ha ⁻¹ y ⁻¹)				
50	1.96	2.14	4.02 $\pm$ 1.78	511 $\pm$ 15 (506)	19.4 $\pm$ 1.2 (17.6)	0.02 $\pm$ 1.12	500
80	3.00	3.78	4.03 $\pm$ 3.07	290 $\pm$ 18 (286)	19.1 $\pm$ 1.3 (17.7)	0.00 $\pm$ 1.37	400
90	3.50	4.68	4.03 $\pm$ 3.49	234 $\pm$ 19 (231)	18.9 $\pm$ 1.3 (17.7)	0.00 $\pm$ 1.48	400
91.2	3.60	4.87	4.05 $\pm$ 3.62	226 $\pm$ 18 (222)	18.8 $\pm$ 1.4 ^a (17.7)	0.00 $\pm$ 1.52	400
100	4.00	5.71	4.04 $\pm$ 4.09	192 $\pm$ 19 (189)	18.6 $\pm$ 1.4 ^a (17.7)	0.00 $\pm$ 1.60	400
110	4.74	7.21	4.04 $\pm$ 4.49	152 $\pm$ 20 (150)	18.5 $\pm$ 1.4 (17.7)	0.00 $\pm$ 1.66	300
120	5.46	9.13	4.04 $\pm$ 5.56	124 $\pm$ 19 (119)	18.3 $\pm$ 1.5 (17.7)	0.00 $\pm$ 1.80	300
150	8.57	17.7	4.09 $\pm$ 7.49	63 $\pm$ 19 (61)	17.6 $\pm$ 1.6 (17.9)	0.05 $\pm$ 2.32 ^b	200

Simulation of yearly changes of NEP

We simulated yearly changes of NEP by CWBBM with frequency distributions of NPP_c and DR_c during 43 years (1969–2012) at P1. These two rates could be approximated by log-normal distribution functions with mean values of 3.86 ± 1.28 t C ha⁻¹ y⁻¹ for NPP_c and 3.44 ± 2.12 t C ha⁻¹ y⁻¹ for DR_c (0.587 ± 0.106 and 0.536 ± 0.327 , respectively, when $\log_{10}$ -transformed) (Fig. 3). This mean death rate was not significantly different from an observed mean value obtained from fourteen censuses after the logging in 1973 ($P = 0.165$, Fig. 3B). We estimated yearly changes of NPP_c by random occurrence with this function in order to avoid unlimited increase of NPP_c , though observed NPP_c tended to increase monotonically throughout the study period ($R^2 = 0.882$). DR_c at a given time was also estimated by random occurrence with the log-normal function.

Yearly changes of biomass were calculated by the following recurrence equation.

$$BM_{c_t} = BM_{c_{t-1}} + NPP_{c_t} - DR_{c_t} \times BM_{c_{t-1}} \div BM_{c_0}$$

Eq. (6)

where BM_{c_t} , $BM_{c_{t-1}}$, NPP_{c_t} , DR_{c_t} , and BM_{c_0} are BM_c at a given time (t), BM_c at the previous year ($t-1$), NPP_c and DR_c at t from randomization of their log-normal distribution functions, and the initial BM_c of a 2-ha P1 in 1969. BM_{c_0} is constant. A term of $DR_{c_t} \times BM_{c_{t-1}} \div BM_{c_0}$ in Eq. (6) is a realized death rate (RDR_c) weighed by current biomass

($BM_{c_{t-1}}$) relative to the initial biomass (BM_{c_0}). This weighing of DR_c means a negative feedback for biomass with a higher death rate at higher biomass against no-regulation for NPP_c by biomass.

Yearly changes of a decay rate were estimated by the same procedure as CWBBM with an average ID at P1 and $\beta = 0.43$ y⁻¹ producing high correlation with ECM (Cf. Fig. 4D in Result).

Yearly changes of NEP , BM_c and CWD were simulated along dynamics of a primeval forest stand during 2000 years under conditions of eight different mean DR_c within the range from 50 to 150% of a mean value of NPP_c (Table 2). The initial BM_c and CWD were values at P1 in 1969. Ten trials were conducted for each death rate.

RESULTS

Correlation between NEP estimated by CWBBM and ECM

Fig. 4 shows yearly changes of NEP estimated by CWBBM with the monitoring data of dbh at six stands in a fan-shaped area during the last 17 years from 1995. Two parameters of a coefficient of decay (β) and a distance from the tower both largely affected variances of NEP estimated by CWBBM, which generally increase with increase of β and with decrease of a distance. ECM-based NEP waved during the last 9 years in yearly changes, and nearly agreed with NEP estimated by CWBBM under the conditions of $\beta = 0.43$ y⁻¹ and a distance = 125–150 m (Fig. 4D).

Fig. 4. Yearly changes of NEP at six fun-shaped stands in 6-ha plot, P1 (Fig. 1). Thin solid and broken curves are yearly changes of NEP estimated by CWBBM with a parameter of distances from a tower. Thick curves are one of ECM-based NEP (Kosugi et al. 2012). A, B, and C show results at different β conditions. D shows a part of B. Figures in each diagram show distances from a tower.

Fig. 5. **A:** Yearly change of biomass (BM_c), death rates (DR_c), and carbon fluxes at a 0.2-ha stand after clear logging in 1973. Thick and thin solid, and broken curves in the bottom diagram show NEP estimated by CWBBM, net primary production (NPP_c) and a decay rate (HTR_c), respectively. **B:** Yearly changes at 2-ha plot including a logged 0.2-ha stand. Thin broken curves in these diagrams show the relations at 6-ha plot, and a thick solid curve in the bottom diagram is yearly changes of ECM-based NEP . Death rates, DR_c , in both diagrams are moving averages during three years.

Yearly changes of NEP during the last 43 years

NEP of the clearly logged 0.2-ha stand rapidly decreased after the logging in 1973 because of higher decay

rates (HTR_c) of mass woody debris than NPP_c of regenerated vegetation, and had the minimum value at $-39 \text{ t C ha}^{-1} \text{ y}^{-1}$ within a few years after logging (Fig. 5A). NEP gradually increased with time, and changed to a positive value in 1990,

17 years after the logging. *NEP* in 2011, 38 years after logging, was still increasing at a rate of $5.1 \text{ t C ha}^{-1} \text{ y}^{-1}$ with 127 t C ha^{-1} in biomass of coarse woody organs (BM_c) being restored to 46% of one before logging. However, secondary forest species were still dominant such that two species of *Melicope glabra* (Rutaceae) and *Endospermum diadenum* (Euphorbiaceae) accounted for 43% of the biomass.

When we evaluated yearly changes of *NEP* estimated by CWBBM at a 2-ha plot (P1) including a logged 0.2-ha stand, *NEP* ranged from $-5.0 \text{ t C ha}^{-1} \text{ y}^{-1}$ to $2.1 \text{ t C ha}^{-1} \text{ y}^{-1}$ during the last 43 years (Fig. 5B). Two depressions existed regardless of monotonous increase of NPP_c throughout the period. The first depression was resulted from the logging, but the magnitude of carbon flush decreased in comparison with that at a 0.2-ha logged stand alone because of compensation by a remaining 1.8-ha intact forest stand. The second one was caused by high death rates during 1991–1994. A total death rate during this period was nearly equivalent to one due to logging in 1973. This caused a longer but lower depression at the minimum value of *NEP* than the first one.

Yearly changes of *NEP* estimated by CWBBM at a 2-ha plot were nearly equivalent to one of ECM-based *NEP* during the last 9 years from 2003. The 6-ha plot had lower *NEP* estimated by CWBBM than one by ECM during the period of 2003–2008 in particular, though the yearly changes tended to show similar patterns.

Inter-annual variability of BM_c , *CWD* and *NEP* under dynamic equilibrium conditions

Simulated BM_c , *CWD* and *NEP* showed some monotonic changes during the initial 300 years, and then showed dynamic equilibrium features. Hence their yearly variability was examined basing on results during the following 1700 years.

BM_c showed a normal distribution pattern in frequency regardless of death rates (Fig. 6). A mean value of BM_c clearly decreased with increase of the death rate ($P < 0.001$), and the standard deviation tended to be constant (Table 2). Hence a coefficient of variance increased with increase of the death rate. A mean value of simulated biomass was $226 \pm 18 \text{ t C ha}^{-1}$ at an observed death rate (91.2%), while the range of observed one was 231–272 t C ha^{-1} at a 2-ha plot during 43 years.

CWD showed a log-normal distribution pattern. A mean value tended to decrease with increase of a mean death rate accompanying with lower kurtosis ($P < 0.05$), while a range of mean values was limited.

NEP was approximated by a normal distribution with a

Fig. 6. Frequency distributions of BM_c (A), *CWD* (B), and *NEP* (C) during their 17000 years (1700 years $\times$ 10 trials) under equilibrium regimes at different death rates (a–e). Mean death rates of a, b, c, d, and e are 150%, 120%, 100%, 91.2% (observed mean value), and 80% as much as a geometric mean value of observed NPP_c , respectively. X axis of diagram B is a logarithmic coordinate.

mean value of $NEP = 0.0 \text{ t C ha}^{-1} \text{ y}^{-1}$ irrespective of death rates (Table 2), and the standard deviation tended to increase with increase of death rates. A mean value of NEP at an observed death rate (91.2%) was $0.00 \pm 1.52 \text{ t C ha}^{-1} \text{ y}^{-1}$ (Table 2).

NEP at a given time was regressed by the following multiple linear regression model with current BM_c and *CWD* as explanatory variables (all significant at $P < 0.001$).

$$NEP = a \times BM_c + b \times CWD + c \quad \text{Eq. (7)}$$

Coefficient of determination of this model increased with increase of death rates (Table 3). BM_c and *CWD* had positive and negative correlation with *NEP* respectively, and their partial correlation coefficients showed a higher influence of *CWD* than BM_c . These two variables had significant negative correlations ($P < 0.01$).

Table 3. Regressed three coefficients (a , b , c) of Eq.(7) and a correlation coefficient (R) between current BM_c and CWD for simulated results during 17000 years (1700 years $\times$ 10 trials). A symbol of R^2 is a coefficient of determination, and figures in parenthesis are partial correlation coefficients of a multiple linear regression model. **: $P < 0.01$, ***: $P < 0.0001$.

Mean death rate (relative value: %)	$NEP = a \times BM_c + b \times CWD + c$				$BM_c - CWD$ R
	R^2	a	b	c	
50	0.128	0.00181** (0.026)	-0.133*** (-0.356)	1.70	-0.039**
80	0.284	0.00698*** (0.110)	-0.131*** (-0.516)	0.570***	-0.120**
90	0.332	0.00942*** (0.142)	-0.133*** (-0.553)	0.420***	-0.137**
91.2	0.366	0.0110*** (0.160)	-0.137*** (-0.578)	0.214	-0.153**
100	0.355	0.0127*** (0.184)	-0.126*** (-0.577)	0.060	-0.142**
110	0.380	0.0138*** (0.199)	-0.126*** (-0.581)	0.400***	-0.159**
120	0.404	0.0192*** (0.247)	-0.121*** (-0.585)	0.008	-0.185**
150	0.517	0.0392*** (0.397)	-0.110*** (-0.613)	-0.300***	-0.273**

DISCUSSION

Evaluation of CWBBM and yearly changes of NEP during the last 43 years

A time trend of ECM-based NEP well agreed with one estimated by CWBBM at a fan-shaped stand within a distance of 125–150 m from the tower under the conditions of $\beta = 0.43 \text{ y}^{-1}$. Fetch length (horizontal distance) for which $> 80\%$ of the flux measurements are expected to come from was around 2000 m from the tower to the windward direction, and the contribution was higher at closer sites (Takanashi et al. 2010). ECM-based NEP was calibrated by the relation between soil respiration and soil water content for nighttime ecosystem respiration at a neighboring site to the tower (Kosugi et al. 2012). These high influences from closer sites suggest that high correlation between two kinds of NEP has been derived from the same phenomenon of a forest ecosystem. This shows that CWBBM is a useful method to assess annual changes of NEP corresponding to ECM-based NEP .

Let's examine validity of CWBBM through different dynamics between coarse woody organs and fine organs consisting leaves and fine woody organs in a forest. Total NPP of this 2-ha plot was estimated at $12.6 \text{ t C ha}^{-1} \text{ y}^{-1}$ based on field observation, and a share of coarse woody organs (NPP_c) was $4.5 \text{ t C ha}^{-1} \text{ y}^{-1}$ (36%) (Fig. 2B: Kira

1987). Fine organs got remained 64% of NPP , and used almost every production for their regeneration through the fall of leaves and twigs without tree death because of their short lives (Kira 1987; Yoneda 1982). Annual rates of fine litter-fall (Ogawa 1978; Yoneda et al. 2002) were fairly uniform in time and space compared to CWD (Yoneda et al. 1977). The 95% disappearance time of fine litter through decay process was 1.2 years against 15.8 years of CWD (Kira 1978). These features of fine organs would have few influences on yearly changes of NEP , though a rate of flux was about twice larger than CWD . This is one of reasons for validity of CWBBM. Dynamics of soil organic matter should be affected by disturbance, but various local environmental conditions in soils and various physicochemical structures of refractory humus would decrease their responsiveness to disturbance (Yoda & Kira 1982). To incorporate dynamics of soil carbon into CWBBM, it would be necessary to clear their responses under consideration with changes of environmental conditions in soils basing on a long-term observation.

A large amount of CWD caused by the 1973 logging as much as 9.8% of biomass before the logging at 2-ha plot produced a long-term negative NEP during successive 10 years with the minimum rate of $-5.0 \text{ t C ha}^{-1} \text{ y}^{-1}$ (Fig. 5B). The second depression during the 43 years was caused by a high natural-death rate of big trees in the early 90's (Hoshizaki et al. 2004). A storm (Whitmore 1984, Yoneda

et al. 1998) and dry weather (Nakagawa et al. 2000, Yoneda et al. 2000, Phillips et al. 2010) are hazardous factors for big trees in a tropical rain forest. A storm attack in September 2004 caused 9.5% loss in basal area at a 15-ha stand of the 50-ha plot in the Pasoh Forest Reserve (Yoneda et al. 2005). This study suggests that a similar magnitude of carbon flush as the depressions at a 2-ha stand in P1 (11.3% loss in basal area by logging) has been caused by the storm at a 15 ha stand.

Dynamics of stand structure and *NEP* under stable natural disturbance regimes

Fig. 2C showed the simulated carbon cycling with average values of *BMc*, *CWD* and *NEP* under an observed mean death rate, $DR_c = 4.56 \text{ t C ha}^{-1} \text{ y}^{-1}$. Fluxes of *HTR_c*, *RDR_c* and *IR_c* could be determined by the following procedure from definition, respectively.

$$\begin{aligned} HTR_c &= NEP - NPP_c, \\ RDR_c &= DR_c \times BMc \div BMc_0, \text{ and} \\ IR_c &= NPP_c - RDR_c. \end{aligned}$$

Carbon stocks and fluxes nearly agreed with observed values except *RDR_c* and *IR_c* under IBP (Fig. 2B). These two observed rates under IBP were obtained from field observation at 2-ha plot during three years. When we adopt the *RDR_c* from five 2-ha plots during the same three years to be $4.7 \text{ ha}^{-1} \text{ y}^{-1}$ (Yoneda et al. 1977), differences between observed and simulated values was slight. Hereby this modified CWBBM with *NPP_c* and *DR_c* from their frequency distribution functions could well simulate observed values for carbon cycling of a mature stand in Pasoh.

A negative feedback system of biomass by a realized death rate (*RDR_c*) produced a dynamic equilibrium state with $RDR_c = NPP_c$ irrespective of a mean death rate (Table 2), and mean *BMc* clearly decreased with increase of a mean death rate. We examine this result basing on the definition of Eq.(6).

A biomass under stationary state (*BM_{ce}*) should satisfy the condition of $BM_{ce} = BMc_t = BMc_{t-1}$. Then *BM_{ce}* could be given by $BM_{ce} = BMc_0 \times NPP_c \div DR_c$ from Eq.(6). When we adopt arithmetic means of *NPP_c* and *DR_c* for this calculation, a calculated *BM_{ce}* nearly agrees with a simulated mean biomass (Table 2). Hence a mean biomass of coarse woody organs under the dynamic equilibrium state was able to be determined by a ratio of net primary productivity (*NPP_c*) to a death rate (*DR_c*).

CWD tended to decrease slightly with increase of a

mean death rate. Yoneda (1985) showed that *CWD* at the stationary state (*CWD_e*) was determined by the following equation, when decay process of *CWD* could be approximated by a logistic curve, Eq.(5).

$$CWD_e = RDR_c \times \ln \left\{ \frac{1}{(1-ID)} \right\} \div (\beta \times ID) \quad \text{Eq. (8)}$$

Eq. (8) shows that *CWD_e* is in proportion to a realized death rate (*RDR_c*) because of two parameters of β and *ID* being constant in this simulation. A calculated *CWD_e* was approximately proportional to a mean *CWD* (Table 2), though a calculated one was about 5% lower than a mean value.

Another trait of simulated results was larger inter-annual variations of carbon stocks and *NEP* in coefficient of variance at higher *DR_c*. This is caused by larger variations of *RDR_c* in standard deviation at higher *DR_c* (Table 2). High variances of these dimensional features under the conditions of high death rates largely affect not only global carbon cycling but also many organisms, especially late-successional species, in a forest ecosystem, though these systems still preserve the conditions of *NEP* = 0 as a total system in time.

We define the minimum period as a turnover time of a system to maintain the equilibrium regime with an average value of *NEP* being not significantly different ($P > 0.05$) from one of *NEP* for 17000 years-sequence (1700 years $\times$ 10 trials) under the equilibrium conditions. A turnover time ranges from 200 years to 500 years with some tendency being shorter at higher death rates (Table 2). When we translate this duration at an observed death rate (400 years) for the 2-ha plot into space, the minimum area for the equilibrium system would be 800 hectare (2 ha $\times$ 400 plots). This evaluation might be one criterion of the minimum area for conservation, though it is necessary to examine validity of a 2-ha stand as a unit of mosaic structure of a primeval tropical forest and independency of death rates among units.

This study revealed that *NEP* and carbon stock (biomass and *CWD*) of tropical forest are largely affected by three parameters of dynamic attributes of forest stand, i.e. net primary productivity, death rate and decay rates of coarse woody organs. All these three parameters are susceptible to climate change such as global warming. Therefore, clarifying how these parameters respond to climate change and anthropogenic disturbance would be important to predict the *NEP* and carbon stock of tropical rain forests in the future.

ACKNOWLEDGEMENTS This study was conducted under NIES-FRIM-UPM Joint Research Project on Tropical Forest Ecology and Biodiversity. We sincerely thank Dr. Abdul Rahim Nik and Dr. Saw Leng Guan for their cooperation as the former and present leaders of the organizing committee in FRIM, and Dr. Christine Fletcher for her understanding as a site manager of the Pasoh Forest Reserve in FRIM. We also acknowledge all members to joint field observations for their cooperation in field and understanding for this study. We express our thanks to anonymous referees for their valuable comments to this manuscript. This study was partially supported by the Ministry of the Environment, Japan through Global Environment Research Fund.

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Received: February 17, 2015

Accepted: July 17, 2015