Spatial variations in the net ecosystem productivity of a primeval tropical forest in a 50-ha plot in Pasoh, Peninsular Malaysia

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ABSTRACT We assessed the spatial variations in net ecosystem productivity (NEP) using a biometric method based on the dynamics of coarse woody organs in a primeval lowland tropical rain forest in Pasoh, Peninsular Malaysia. The average NEP and carbon stocks in biomass and coarse woody debris over 15 years from 1990 to 2005 were −0.75 t C ha⁻¹ y⁻¹, 205 t C ha⁻¹, and 22 t C ha⁻¹, respectively. However, there were large spatial variations among the five communities, which were correlated with edaphic and topographical features. A mature carbon cycling system with high biomass (where NEP ≈ 0) was observed in a sub-community on west-facing slopes of the hill community. Over the course of 15 years, a drought and storms were the major agents causing forest disturbances. These factors affected the spatial variations of NEP through not only spatial distribution patterns in species with different sensitivities to stress but also differences in the extent of stress depending on topography. We modeled the disturbance regime as elapsing from 1907 to 1947 basing on observed values of net primary production and biomass of five communities during the 15 years. When we extrapolated high mortalities of trees under this regime, our simulation suggested that a 50-ha plot will remain a carbon-source system for the atmosphere at an average rate of NEP = −0.95 t C ha⁻¹ y⁻¹ until 2060, with different biomass decreases among these five communities.

Key words: mortality, NEP, spatial variations, topography, tropical rain forest

INTRODUCTION

Our previous paper (Yoneda et al. 2016) dealt with inter-annual variations in the net ecosystem productivity (NEP) of a primeval tropical rain forest using a coarse-wood-based biometric method (CWBBM). The study revealed that the large variations were caused by temporal variations in the death rates of large trees. The rates of addition of coarse woody debris (CWD) from tree deaths (DR) showed large variations, not only temporally but also spatially (Yoneda et al. 1977, Clark et al. 2003). We explored the spatial variations in NEP (as largely influenced by DR) in this paper.

A forest experiencing a natural disturbance regime is composed of a mosaic of different-aged patches (White and Pickett 1985). We can categorize these patches into three phases based on their NEP: a “gap” phase with NEP < 0, a “building” phase with NEP > 0 and a “mature” phase with NEP ≈ 0. The NEP of a whole forest is determined by the balance in NEP between the gap and building phases irrespective of the mature phase. With more frequent and severe disturbance, holding NEP = 0 for the whole ecosystem, the turnover time of organic carbon in a forest is expected to be shorter with lower carbon stocks because of shorter residence time of mature phase with high biomass. Furthermore, it is expected that higher disturbance affects spatial variations in NEP because of spatial differences of impacts through diverse floristic and topographic conditions within a forest. Therefore, it is important to assess the NEP of a forest ecosystem based on spatial variations of carbon stocks and fluxes for tropical rainforest conservation.

Recent studies on large-scale research plots have shown that spatial variations in floristic and structural features were correlated with topography (Yamakura et al. 1996, Chave et al. 2003, Ito et al. 2010, Punchi-Manage et al. 2013) and soils (Palmiotto et al. 2004, Russo et al. 2005). This suggests that communities based on these spatial environmental conditions can be regarded as units for carbon cycling systems in forests. It is ecologically important to resolve whether forest dynamics are influenced mainly by unpredictable, catastrophic events such as droughts and storms or by predictable mechanisms such as...
competition (Ashton 1995). Long-term observations show that meteorological events such as droughts (Condit et al. 1995, Nakagawa et al. 2000, Yoneda et al. 2006) and storms (Zimmerman 1994, Yoneda et al. 1998) have a high impact on canopy trees. These events can affect the spatial variance in \( \text{NEP} \) among different communities because of their unique stressors and sensitivities (Comita and Engelbrecht 2009, Engelbrecht et al. 2007).

This study aimed to examine the spatial variations in the \( \text{NEP} \) of a tropical rain forest in a 50-ha plot in Pasoh, Peninsular Malaysia based on diameter at breast height (dbh) census data over the course of 18 years from 1987 to 2005. During this period, the plot suffered from a severe drought in 1997 (Noguchi et al. 2003) and from a hazardous storm in 2004 (Yoneda et al. 2005). However, seasonal droughts such as those in a 50-ha plot in Barro Colorado Island (Condit et al. 1999) were unclear in Pasoh (Noguchi et al. 2003). Davies et al. (2003) revealed correlations between three or five communities and edaphic and topographical features in a 50-ha plot in Pasoh. We first aimed to clarify the spatial variations in \( \text{NEP} \) with respect to the spatial distribution of these communities and to examine the mechanisms causing the variations in relation to the biotic and abiotic features of the communities. The second aim of this study was to evaluate the spatial variation of the carbon cycling in the 50-ha plot basing on the temporal variation of a 2-ha plot in the same forest reserve, which is in a dynamic equilibrium state (Yoneda et al. 2016), and to predict spatial variations in the 50-ha plot in the future.

**MATERIALS AND METHODS**

**Study site**

This study was conducted in a 50-ha plot in Pasoh Forest Reserve (Pasoh FR), Negeri Sembilan (2° 58’ N, 102° 18’ E), Peninsular Malaysia (Fig. 1). The Pasoh FR is 2400 ha in area, surrounded by oil palm plantations except for the eastern part, which is fringed by natural mountain vegetation. The plot is located in a primary forest at nearly the center of the reserve. The western and southern regions of Pasoh FR had been selectively logged previously under a regime of the Malayan Uniform System in the 1950s, and the biomass of the regenerating forest is still less than that of the primary forest, even 40 years after logging (Okuda et al. 2003). A carbon cycling (Kira 1987, Yoneda et al. 2016) and stand dynamics (Hoshizaki et al. 2004) of a mature forest stand have been intensively studied at a 2-ha plot (Plot 1), located 2 km southwest of the 50-ha plot, since 1969 (Fig. 1).

Pasoh FR is located in a region with a lower average annual rainfall than that in other regions of Peninsular Malaysia (Robiah et al. 1988). Annual rainfall during the study period (1987–2005) ranged from 1182 mm to 2341 mm, with the driest year being 1997 as a result of the El Nino Southern-Oscillation event (Fig. 2-A). The percentage of dry days (<60 mm of 30-days rainfall totals: Toma (2000)) was 33.4 % in 1997 (Noguchi et al. 2003). Violent winds, which occasionally occurred in Pasoh FR, killed trees, such as a series of events in 1987 (Manokaran and LaFrankie 1990), 1994 (Yoneda et al. 2005) and 2010 (Harada, personal communication). Strong winds no less than “Near gale” on the Beaufort scale, 13.9–17.1 m s\(^{-1}\), tend to come from the east-northeast in Pasoh FR basin, and meteorological data in Plot 1 reflected these trends from 2004 to 2009 (Fig. 2-B).
The 50-ha plot was located approximately 100 m above sea level on a relatively flat plain of Pleistocene alluvium, interspersed with a series of low hills comprising Triassic sediment and granite (Davies et al. 2003). Vegetation was a mixed dipterocarp forest with a predominance of *Shorea*. Floristic composition and stand structure varied across the plot in relation to edaphic and topographic variation, and Davies et al. (2003) revealed three or five unique communities using cluster analysis of species composition of 200 0.25-ha subplots (cf. Fig. 6-F).

### Calculation of similarity index

Similarity indexes of species composition between Plot 1 and five communities in a 50-ha plot were calculated based on abundance of trees above 10 cm dbh. The percentage index (PS) was assessed as the sum of the smaller relative values of abundance for common species between two sites (Whittaker 1952):

\[
PS = \sum_{i=1}^{s} \min (a_{ij}, a_{ik})
\]

where \(a_{ij}\) and \(a_{ik}\) denote the relative abundance of the \(i\)th species in the \(j\)th and \(k\)th plots, respectively, and \(s\) denotes the total number of species.

### CWBBM simulation

We simulated spatial-temporal variations in NEP in a 50-ha plot using the CWBBM (Yoneda et al. 2016) and a tree database from 1987 to 2005, with census data collected at 5-year intervals. The CWBBM is a method to estimate carbon metabolisms of a forest ecosystem caused by coarse woody organs with the assumption of the equilibrium state of fine organs and soil organic matters, and NEP is defined as a difference between a carbon fixation rate of live coarse woody organs by net primary productivity (NPP) and a carbon release rate of CWD by decomposition (HTR). We considered the year of the first census to be 1987 (Condit et al. 1999), while the plot was established between 1985 and 1988. The five censuses were conducted in 1987, 1990, 1995, 2000 and 2005. Target trees for this analysis were those larger than 10 cm dbh. Abnormal values of dbh from the time trends were corrected by interpolation using values before and after these observations. Data from 2008 (Hamada, personal communication) was used to correct for this abnormality in 2005.

Death of individual trees was determined by random occurrence during the interval between the last year of dbh measurement and the first year of confirming tree death. Ten trials were applied to obtain average annual rates of death and decay. We assumed decomposition of each dead wood to follow the logistic weight loss process (Yoneda 1975). That is

\[
w_t = \frac{w_0}{ID + (1-ID) \exp (\beta t)}
\]

in which symbols of \(t\), \(w_t\), \(w_0\), \(ID\), and \(\beta\) are duration after death, weight at \(t\), the initial weight at \(t = 0\), the index of
durability, and the coefficient of decay, respectively. A coefficient of decay is a parameter, which is affected by external environmental conditions such as temperature and moisture, to determine decay rates of CWD on the logistic process (Yoneda 1986). We adopted $\beta = 0.43$ year$^{-1}$ and $ID = 0.7 \times (dbh/2)^{0.7} \div 1.75$ for CWD, and the initial necromass of CWD = 23.6 t C ha$^{-1}$, which provided optimum results for CWBBM at Plot 1 in Pasoh FR (Yoneda et al. 2016). The initial weight of coarse woody organs including roots of a dead tree was estimated by the allometric regressions obtained in this forest reserve (Kato et al. 1978, Niyama et al. 2010). Ten trials were conducted to assess yearly changes in the following dimensional parameters for coarse woody organs with 10 dbh-database simulations from 10 trials on dead trees: biomass ($BM_c$), necromass of CWD ($CWD$), $NPP_c$, annual death rates ($DR_c$) and $HTR_c$ for total coarse woody organs, including roots. $NEP$ and an increment rate of biomass ($IR_c$) were defined as $NEP = NPP_c - HTR_c$ and $IR_c = NPP_c - DR_c$, respectively (Yoneda et al. 2016). A schematic diagram of carbon cycling with these parameters is shown in Fig. 3. Their average values during each interval of the $dbh$ census were used as the final results for this estimation.

**Evaluation of spatial variations of NEP**

We analyzed the impact of biomass ($BM_c$) and carbon-source factors ($CWD$ or $DR_c$) on $NEP$ by CAR model (Conditional Autoregressive model: Matsuura 2016) with considering spatial autocorrelation of $NEP$ variations. A response variable was normalized $NEP$ and fixed effects were combination of normalized $BM_c$ and CWD (model 1) or that of normalized $BM_c$ and $DR_c$ (model 2) with random effect of a plot (0.25 ha) in a research site (50 ha). We assumed the random effect had spatial autocorrelation in two dimensional space (Matsuura 2016). These two models could be shown by

$Norm_{NEP}(x, y) \sim \text{normal}(a_1 \times \text{Norm}_{CS}(x, y) + a_2 \times \text{Norm}_{BM}(x, y) + r(x, y), s_{NEP})$

$r(x, y) \sim \text{normal}(2 \times r(x - 1, y) - r(x - 2, y), x_r)$

$r(x, y) \sim \text{normal}(2 \times r(x, y - 1) - r(x, y - 2), y_r)$

where $Norm_{NEP}$, $Norm_{CS}$ and $Norm_{BM}$ show normalized $NEP$, normalized Carbon-source index ($CWD$ or $DR_c$) and normalized $BM_c$, respectively. Random effect for plot ($x, y$) was shown as $r(x, y), s_{NEP}$ and $s_r$ show estimated standard deviation of $NEP$ and estimated random effects. The prior distributions of $s_{NEP}$ and $s_r$ were uniform distribution above zero. The function normal ($M, S$) shows normal distribution having average as $M$ and standard deviation as $S$. The two models were compared by WAIC (Widely Applicable Information Criterion: Watatene (2010)), and the model with smaller WAIC was chosen. The CAR-model was coded with Stan and R-Stan. Monte Carlo chains were run with 10,000 iterations (1,000 warm up). The convergence in Monte Carlo simulation of the model was examined by R-hat value. We adopted models which have smaller than 1.1 of R-hat value with three chains according to Matsuura (2016).

Dimensional parameters for coarse woody organs at 200 0.25-ha subplots (50 m $\times$ 50 m) were calculated with simulated values using the data of the data of x and y coordinates of all trees above 10 cm $dbh$ in 50-ha plot. Then their spatial distribution patterns were drawn on a map of a 50-ha plot with three or four classes for visual understanding (cf. Fig. 6).

We adopted five communities by Davies et al. (2003) as a unit of a carbon cycling in a 50-ha plot. Considering the prevailing wind direction (east-northeast) of hazardous storms (Fig. 2-B), we further divided the hill community on three hills into two sub-communities on the slopes facing east-northeast and west-southwest (hereafter east-facing and west-facing slopes, respectively) by straight lines.
passing through the hill tops with a direction of north-northwest and south-southeast orthogonal to the prevailing wind direction of storms (Fig. 6-G); subplots intersected by the lines were included in east-facing slopes.

Simulation of biomass based on temporal changes of death rates

We simulated the future dynamics of these six communities, including two sub-communities instead of a Hill community, under consideration of a temporal increase in death rates over the last 18 years (1987–2005) in a 50-ha plot (cf. Fig. 5). We assumed that the potential death rate \((DR_p)\) included the intrinsic death rate \((DR_i)\) and the death rate from the present disturbance regime \((DR_d)\), that is \(DR_p = DR_i + DR_d\). The realized death rate \((RDR)\) can be defined as the weight of the current biomass \((BM(t))\) relative to the biomass under an equilibrium state \((BM_e)\) for a negative feedback involving a higher death rate with a greater biomass (Yoneda et al. 2016). That is:

\[
RDR = DR_p \times BM(t) / BM_e = (DR_i + DR_d) \times BM(t) / BM_e
\]

where \(DR_d\) is defined as \(RDR_d\) at \(BM(t) = BM_e\). \(RDR_i = NPP\), because of a biomass equilibrium state with \(DR_d = 0\). Then \(DR_d\) is given by:

\[
DR_d = RDR \times BM_e / BM(t) - DR_i = RDR / BM_e \times BM(t) - NPP
\]  
Eq. (1).

We calculated \(DR_d\) of six communities using Equation (1) and the average rates of the corresponding parameters over the 15-year period (1990–2005) to \(RDR\), \(BM(t)\) and \(NPP\), with a constant \(BM_e\) irrespective of communities. \(DR_d\) was examined within a \(BM_e\) range of 230–270 t ha\(^{-1}\), which was the maximum biomass range observed in a mature stand in Plot 1 over 43 years (Yoneda et al. 2016).

We assumed that the present disturbance regime started at \(DR_{d0} = 0\) t C ha\(^{-1}\) year\(^{-1}\) from \(T\) years before the present time, 1990–2005, in a 50-ha plot, and has been increasing linearly with the rate with time \(t\) since the start of the regime. Then, the rate at \(t\) is \(DR_{d}(t) = t \times DR_{d0}(T) / T\). \(DR_{d}(T)\) is the present \(DR_{d}\) at \(t = T\). Yearly changes in biomass were calculated using the following recurrence equation:

\[
BM(t) = BM(t-1) + NPP - RDR(t)
\]

\[
= BM(t-1) + NPP - RDR / BM_e \times BM(t) / BM_e - t \times DR_{d0}(T) / T
\]

Eq. (2).

We estimated \(BM_i(T)\) in six communities using Equation (2) and their parameters. A maximum likelihood estimate of \(T\) was determined using the root mean square error (RMSE), which assessed a relative error, as follows:

\[
RMSE = \left( \frac{1}{N} \sum \left[ \ln \left( \frac{BM_i(T)}{BM_{obs}} \right) \right] \right)^{1/2}
\]

Eq. (3),

where \(N\) and \(BM_{obs}\) are the number of communities \((N = 6)\) and the average observed biomass of each community over the last 15 years, respectively.

Field observations of aboveground CWD

Accumulation of CWD was observed in a 50-ha plot over 1.4 years from August 2004 to January 2006. All dead trees above 30 cm \(dbh\) were observed. Big fallen branches from a living tree, of which diameter at a broken end was above 30 cm, were observed additionally. We identified the history of their death using tree-number tags that were registered before the \(dbh\) census of 2000 or with tags specifically for newly dead trees after the census in 2000. A storm in September 2004 produced many dead trees in this plot, and we identified them by their states (Yoneda et al. 2005).

We observed the following characteristics of all dead trees:

1) State: standing or fallen (stem broken or root-up);
2) Decay grade: G1 indicates trees that recently died with leaves and twigs, G2 indicates dead trees still carrying some big and small branches with tissue that had decayed to the cambium tissue only, G3 indicates the loss of big branches and decay to the sap and heart wood, and G4 indicates boles of heartwood only.
3) Volume: diameter \((dbh\) or diameter at basal end) of fallen logs or \(dbh\) of standing dead trees and the length or tree height.

Newly dead trees at the last \(dbh\) census in 2005 without our registration in the CWD census were regarded as standing G1 dead trees likely produced by the storm in 2004.

We estimated the carbon amount in CWD using CWD = volume × bulk density ÷ 2. The volume of each dead tree was approximated as a cylinder for G1 and G2 dead trees based on a pipe model (Shinozaki et al. 1964a, 1964b) and as a truncated cone with an observed diameter and an estimated diameter at the top end from its \(dbh\)-tree height.
ratio, which was obtained from their allometric regression at Plot 1 (Kato et al. 1978), for those G3 and G4 dead trees without big branches. That is

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

The minimum diameter size was defined as 10 cm for this calculation. The average bulk density (\(\rho\)) of each decay grade was estimated based on the hardness of 238 samples of CWD with differing degrees of decay in the 50-ha plot.

We measured the wood hardness of the samples using a Digital Micro-Probe (Sibetec Science Co., England). The hardness was defined as the force (kg force cm\(^{-1}\)) required for the steel probe (1 mm in diameter) to penetrate the wood to a depth of 130 mm in the center. The measurement was repeated three times in the original position of the dbh. The fallen CWD was measured at both the upper and lateral sides. The average value was used to represent the wood hardness. A calibration curve between the observed bulk density (\(\rho\)) and hardness (\(DMP\)) of CWD was regressed using 44 samples of various decay grades. The relationship can be approximated using the following hyperbolic equation (\(R^2 = 0.68\); Fig. 4):

\[
\frac{1}{\rho} = 7.813/DMP + 1.403 \quad (\text{g cm}^{-3}, \text{kg f cm}^{-1}) \quad \text{Eq. (4)}
\]

The bulk density of the 238 samples was calculated using Equation (4). The average bulk density of each grade decreased with decay progression, accompanied by an increased coefficient of variation (Table 1).

### RESULTS

#### Simulated carbon accumulation and fluxes

**Temporal variations**

The biomass of the coarse woody organs (\(BM_c\)) increased slightly over the former three periods of the dbh census (1987–2000) and decreased by 4% during 2000–2005 because of the higher \(DR_c\) over \(NPP_c\). (Fig. 5). The average \(BM_c\) over the entire period was 205 t C ha\(^{-1}\) for trees above 10 cm dbh, and 73% of this value was attributed to larger trees above 30 cm dbh. The average \(BM_c\) during the latter three periods, 1990–2005, was 205 t C ha\(^{-1}\). CWD increased gradually with time after the period of 1990–1995 as a result of continuously increasing \(DR_c\). The large CWD during the period of 1987–1990 was caused by the initial conditions of CWD for this simulation. The average CWD during the latter three periods (1990–2005) was 22 t C ha\(^{-1}\), which was equivalent to 11% of \(BM_c\).

\(NPP_c\) decreased by 30% during 1995–2000, and the vegetation suffered from severe drought, although this decrease had recovered by 20% during 2000–2005. Large trees above 30 cm dbh accounted for 57% of \(NPP\), over the entire period; small trees 10–30 cm in dbh were greater contributors (43%) than those in \(BM_c\) (27% = 100% – 73% of that of big trees above 30 cm). \(DR_c\) increased linearly throughout the entire period, and large trees above 30 cm dbh increased their proportion relative to the total \(DR_c\) over time within the range 70–77%. When we assessed temporal changes in \(NEP\) (with the exception of the period of 1987–1990, which was influenced partially by the initial

| Table 1. Average bulk density (\(\rho\)) of CWD for four grades of decay categorized by visual features. The symbols M, S and CV indicate averages, standard deviations and coefficients of variation, respectively. |
|-----------------------------|----------------|----------------|----------------|----------------|
| Arbitrary grade of decay    | G1             | G2             | G3             | G4             |
| Number of samples           | 9              | 35             | 84             | 110            |
| \(\rho\) (M ± S) (g cm\(^{-3}\)) | 0.541 ± 0.0385 | 0.532 ± 0.0674 | 0.501 ± 0.120  | 0.366 ± 0.137  |
| CV (%)                      | 7              | 13             | 26             | 37             |

Fig. 4. Relationship between bulk density (\(\rho\)) and hardness (\(DMP\)) of CWD in the Pasoh FR. The hyperbolic curve in the diagram shows the regression from Equation (4).
Spatial variations in the net ecosystem productivity of a primeval tropical forest

Each period of observation is represented by Roman numerals as follows: I = 1987–1990, II = 1990–1995, III = 1995–2000 and IV = 2000–2005. BM, and CWD represent carbon accumulation including the underground parts of coarse woody organs and coarse woody debris, respectively. HTR, NPP, DR, and NEP represent the carbon fluxes for heterotrophic respiration rate, net primary productivity, death rate and net ecosystem productivity of coarse woody organs, respectively. Hatched and closed histograms show relations for trees above 10 cm and 30 cmdbh, respectively.

Table 2. Variations in average carbon stocks and fluxes estimated by CWBBM during 1990–2005 among 200 0.25-ha subplots in a 50-ha plot. Abbreviations for the dimensional features are the same as in Fig. 3. The symbols D≥10 and D≥30 indicate groups of total trees above 10 cmdbh and above 30 cmdbh, respectively. The symbols M, S and CV indicate average values, standard deviations and coefficients of variation (%), respectively.

<table>
<thead>
<tr>
<th>Carbon stocks and fluxes</th>
<th>D≥10 cm</th>
<th>D≥30 cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>BM (t C ha⁻¹)</td>
<td>M ± S</td>
<td>CV</td>
</tr>
<tr>
<td>205 ± 51.8</td>
<td>25</td>
<td>35</td>
</tr>
<tr>
<td>CWD (t C ha⁻¹)</td>
<td>22.4 ± 11.2</td>
<td>50</td>
</tr>
<tr>
<td>NPP (t C ha⁻¹ y⁻¹)</td>
<td>3.59 ± 0.76</td>
<td>21.09 ± 0.75</td>
</tr>
<tr>
<td>DR (t C ha⁻¹ y⁻¹)</td>
<td>4.74 ± 2.39</td>
<td>50</td>
</tr>
<tr>
<td>HTR (t C ha⁻¹ y⁻¹)</td>
<td>4.34 ± 1.78</td>
<td>41</td>
</tr>
<tr>
<td>NEP (t C ha⁻¹ y⁻¹)</td>
<td>-0.75 ± 1.87</td>
<td>250</td>
</tr>
</tbody>
</table>

Spatial variations

Table 2 shows the average carbon stocks and fluxes of 200 0.25-ha subplots in a 50-ha plot based on their average values over a 15-year period (1990–2005). NEP showed higher variances with respect to the coefficient of variation (250%) than did the other attributes because of the effects of multiplication of NPP, and HTR, in variances on NEP.

Two factors of CWD and DR significantly affected NEP of two hundred 0.25-ha plots under consideration of its spatial autocorrelation by CAR-model based on their average values during a 15-year period (1990–2005) (Table 3). BM, and CWD had positive and negative correlations with NEP in model 1, respectively, and absolute mean values of their coefficients showed a higher influence from CWD than from BM. A similar model (model 2) could be applicable using DR instead of CWD as an explanatory variable (Table 3); however, applicability of this model decreased with higher WAIC.

Fig. 6 (A–E) shows spatial distribution maps of the carbon stocks and fluxes for trees above 10 cm with their average values for 200 0.25-ha subplots over a 15-year period. BMt tended to be high in the area along a diagonal line extending from the northeast to southwest in a 50-ha plot (Fig. 6-A). NPP, (6-B) tended to be high on hills as well as BMt; however the range over a whole plot was smaller than that of DRt being another carbon flux from/to BMt (Table 2). CWD (6-C) and DRt also tended to have high values in hills, on east-facing slopes in particular. NEP (6-E) had a distribution pattern reverse to what were shown by CWD and DRt, of which tended to have a contiguous distribution with two areas having higher values on southwest slopes of hills and at a north-western corner of a plot including swamp area.

Carbon cycling over a 15-year period, 1990–2005, was largely different among five communities in a 50-ha plot with NEP = 0.75 t C ha⁻¹ y⁻¹ as a whole plot (Fig. 7). Swamp conditions of CWD, the positive value of 0.10 t C ha⁻¹ y⁻¹ during 1990–1995 became negative during the subsequent periods; NEP = -1.31 t C ha⁻¹ y⁻¹ during 2000–2005 for trees above 10 cmdbh. NEP for large trees above 30 cmdbh showed the similar decreasing pattern over time within a range of -1.05 t C ha⁻¹y⁻¹ to -1.52 t C ha⁻¹y⁻¹. Small trees of 10~30 cmdbh also tended to decrease over time within a range of 1.15 t C ha⁻¹y⁻¹ (1990–1995) to 0.21 t C ha⁻¹y⁻¹ (2000–2005).
accounted for 53% of the biomass, and was smaller than the sub-community on the west-facing slopes (Sub-2 W) had high NEP, $-0.25 \ t \ C \ ha^{-1} \ y^{-1}$, as much as Com-1. Another sub-community (Sub-2E) showed the lowest NEP, $-1.36 \ t \ C \ ha^{-1} \ y^{-1}$, with large biomass loss rate, $IR_r = -1.78 \ t \ C \ ha^{-1} \ y^{-1}$, caused by a high death rate. Sandy (Com-3) and Mixed (Com-4) Alluvium communities showed similar values each other in carbon stocks and fluxes except $IR_r$, showing higher decreasing rate of biomass of Com-3 over Com-4.

**DISCUSSION**

Validity of CWBBM

The simulated CWD in 2005 ($13.3 \pm 1.9 \ t \ C \ ha^{-1}$) was close to $15.6 \ t \ C \ ha^{-1}$ for CWD in a primary forest in the Bukit Timah Nature Reserve, Singapore, which had nearly the same ratio of standing to total CWD (6.61) (Ngo et al. 2013) as that of this study (0.59: Table 5). The observed CWD in 2005 ($22.1 \pm 1.7 \ t \ C \ ha^{-1}$) was also close to the observed value in Pasoh FR, $24.5 \ t \ C \ ha^{-1}$ (Yoneda et al. 1977). We examined differences between observed and simulated values for CWD. When we applied the logistic weight loss curve (Yoneda 1975) to a time trend of the remaining ratio of observed CWD (Fig. 8-A), the coefficient of decay ($\beta$) was estimated to be $0.26 \ y^{-1}$ using the nonlinear least square method under the same conditions as the other parameters of CWBBM. This lower value may result in greater CWD than an estimate using $\beta = 0.43 \ y^{-1}$ because of its longer residence time (Fig. 8-B).

Our analysis showed that the differences may have been caused by either underestimation of simulated CWD...
Spatial variations in the net ecosystem productivity of a primeval tropical forest

Due to use of an overestimated $\beta$ or overestimation of the observed CWD. The latter option, concerning the field data, may have resulted from an overestimation of the bulk density for each decay class by the hardness of CWD (Fig. 4); this may have been a result of measuring at a position near ddbh with lower decay rates due to a bias towards larger diameter sizes within each CWD sample (Yoneda 1985).

Table 4. Observed accumulation of aboveground CWD of large dead trees above 30 cm ddbh in a 50-ha plot. Dimensions are presented in t C ha$^{-1}$. The figure in parenthesis is the value for newly dead trees from the last ddbh census in 2005 without our registration in the CWD census.

<table>
<thead>
<tr>
<th>State of CWD</th>
<th>Arbitrary grade of decay</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standing</td>
<td>G1</td>
<td>6.5 (5.5)</td>
</tr>
<tr>
<td></td>
<td>G2</td>
<td>2.3</td>
</tr>
<tr>
<td>Fallen</td>
<td>G3</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>G4</td>
<td>5.7</td>
</tr>
</tbody>
</table>

Fig. 6. A–E: Average carbon stocks and fluxes during 1990–2005 in 200 quadrats, each 2500 m$^2$, in the 50-haplot.
A: $BM_c$ (3 classes: below 200, 200–225, above 225 t C ha$^{-1}$), quadrats with grey color show subplots with $BM_c < 100$ t C ha$^{-1}$ when the plot was established in 1987.
B: $NPP_c$ (3 classes: below 3, 3–4, above 4 t C ha$^{-1}$ y$^{-1}$); C: CWD (4 classes: below 10, 10–20, 20–30, above 30 t C ha$^{-1}$); D: $DR_c$ (4 classes: below 3, 3–4.5, 4.5–6, above 6 t C ha$^{-1}$ y$^{-1}$); E: NEP (4 classes: below 2, 2–4, 4–6, above 6 t C ha$^{-1}$ y$^{-1}$). Open quadrats without closed circles indicate the lowest class, and bigger circles show higher classes. The symbols for carbon stocks and fluxes are the same as in Fig. 3.


G: Units of communities for carbon cycling. Figures in the diagram indicate symbol of community from the five communities by Davies et al. (2003). A Hill community (2) was divided into two sub-communities (2 W and 2E).

H: Spatial distribution patterns of Elateriospermum tapos (closed circles) and Quercus argentina (open circles) of trees above 30 cm ddbh.

I–J: Spatial distribution patterns of $DR_c$.
I: $DR_c$ (4 classes: below 2, 2–4, 4–6, above 6 t C ha$^{-1}$ y$^{-1}$) during a dry period (1995–2000).
J: $DR_c$ (5 classes: below 1, 1–2, 2–4, 4–8, above 8 t C ha$^{-1}$ y$^{-1}$) from a storm in September 2004 for trees above 30 cm ddbh. Symbols of classes are same as one in A–E.
We examined the influence of a low value of $\beta = 0.26$ y$^{-1}$ on the results of the CWBBM, although it was not clear which $\beta$ value we should adopt for an effective simulation. The results showed a lower weight loss rate during the early stages of the decay process, and there was a delay in the time needed to reach the maximum rate by 1.75 years in comparison with $\beta = 0.43$ y$^{-1}$ (Fig. 8-B). These attributes affected NEP in each 1-ha subplot and increased NEP by approximately 0.5 t C ha$^{-1}$ y$^{-1}$ on average over the last 15 years. However, the spatial distribution pattern in the 50-ha plot was not affected because of a highly linear positive correlation between the two NEP values obtained from these two $\beta$ values ($R^2 = 0.954$). The characteristics of carbon cycling, as shown in Fig. 7, still hold in their relationships among the five communities under the conditions of $\beta = 0.26$ y$^{-1}$. Simulated NPPc, IRc, DRc and BMc were independent of $\beta$.

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Table 5. Ratios of standing to total CWD (A/B) and remaining to initial CWD (B/C) by duration after tree death based on death records. Values were obtained from a field census concerning aboveground CWD (Table 4).

<table>
<thead>
<tr>
<th>Status</th>
<th>Periods of tree death (Calendar year)</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standing CWD (t C ha$^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fallen CWD (t C ha$^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total CWD (t C ha$^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Death rate (C) (t C ha$^{-1}$ period$^{-1}$)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>A/B</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B/C</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 8. A: Time trends of CWD weight decrease during the decay process with regard to relative weight. Closed circles indicate observed values, and solid and broken curves indicate the relationships with logistic weight decreases (Yoneda 1975), with the coefficient of decay ($\beta$) being 0.43 y$^{-1}$ and 0.26 y$^{-1}$, respectively, for the two curve types. B: Time trends for the loss rates of two logistic decay curves. Solid and broken curves are the same as in the upper diagram. There is a time difference of 1.75 years between the maximum rates of the two curves.

Fig. 9. Relationships between observed aboveground accumulation and simulated aboveground CWD at 50 1-ha subplots in a 50-ha plot using logarithmic coordinates. The slope of the regressed straight line forced through origin is 0.853 ($R^2 = 0.639$).
Spatial variations in the net ecosystem productivity of a primeval tropical forest

Spatial variations in carbon cycling

Variation factors

NEP showed a spatially autocorrelated distribution in the 50-ha plot (Fig. 6-E) when we evaluated it using the average values from the last 15 years in 200 0.25-ha subplots. This was caused mainly by spatial variations in CWD and DR, (Table 3) related to plot terrain.

Dry weather and severe storms were major contributing factors to high DR, over the last 10 years in Pasoh FR (Yoneda et al.2005, Yoneda et al.2016). This area suffered from a severe drought in 1997 (Fig. 2-A). However, hills (the hill community) had low death rates during one 5-year period, 1995–2000 (Fig. 6-I), particularly for large trees above 30 cm dbh with high sensitivity to drought usually (Nagakawa et al.2000, Yoneda et al.2006). Elateriospernum tapos, for example, had a low annual mortality rate of 1.6% during this period, while Quercus argentata showed the highest mortality rate (4.5%) of all trees in a hill community. They showed allopatric distributions in a 50-ha plot (Fig. 6-H) and the major habitats of Q. argentata and E. tapos are alluvial areas and hills, respectively. Scaphium macropodum (0.6%), Ochanostachys amentacea (1.3%) and Dyera costulata (0.6%) also showed low mortality rates (as low as that of E. tapos), and these trees at their mature stage, above 30 cm dbh, were concentrated on the hill (Manokaran et al.1992).

This suggests that the spatial distribution of DR, during a drought period could be strongly affected by the topographical gradient of vegetation exhibiting different drought sensitivities (Engelbrecht et al. 2007). A low DR, during this period, 1995–2000, was also found in a swamp community (Fig. 6-I). A mortality rate of Q. argentata, having a high sensitivity against drought stress, was also lowest at this community among five communities. Hereby a low DR, of this community may be a result of low drought stress in soils due to swampy conditions even during the drought period.

An easterly storm in September 2004 produced different impacts on the east- and west-facing slopes of three hills (Fig. 6-J) (although the relative height of the highest hill from the alluvial ground was only 20 m). The storm had a maximum wind speed of 18.6 m s⁻¹ at the tower in Plot 1 and thus was categorized as a gale on the Beaufort scale, 17.2–20.7 m s⁻¹. Another gale with 18.4 m s⁻¹ winds was observed in July 2010 at the tower (Kosugi, personal communication), and this also caused a high mortality rate among canopy trees in Pasoh FR (as high as 4.7% of the 623 monitored trees above 30 cm dbh along 5.7 km of trails in this forest reserve) (Fig. 1, Harada, personal communication). These dead trees had a contiguous distribution and a high mortality rate of 5.8% along an undulating 1.7-km trail stretching in a southerly direction from the intersection of trails as much as a mortality rate, 6.6%, resulting from the storm in September 2004 in a 50-ha plot. A violent wind knocked down numerous trees in a 50-ha plot on April 15, 1987 (Manokaran and LaFrankie1990) and likely produced many of gaps in the alluvial and swamp areas at the establishment of this plot in 1987 (Fig. 6-A). The frequency of these hazardous storms (gales specifically) was once per 5.4 years (= 10.8 ÷ 2), and the direction of winds above “near-gale” force tended to be from the east-northeast (Fig. 2-B). Hence storms should be considered as factors that affect spatial variations in tree mortality through differences of impacts from strong winds in relation to topographical factors such as slope direction s in Pasoh FR. This could cause different features of a carbon cycling between two sub-communities of Sub-2 W and Sub-2E in three hills.

Ordination of the present variations

In Sub-2 W (9.25 ha), the average NEP over the last 15 years was at near equilibrium with a similar BM, and CWD in the simulated values in Plot 1 under the equilibrium regime (Fig. 7). Fig. 10-A shows the ranges of NEP and BM, variations caused by temporal changes in NPP, and DR, in Plot 1 (Yoneda et al. 2016). When we assessed the carbon-cycling system of each community using these ranges, Sub-2 W had dimensional features within a range of 1 × Standard deviation (S) under the equilibrium regime. Com-2 (17.25 ha) and Com-3 (9.25 ha) were located at 1 × S, and Sub-2E (8.00 ha) and Com-4 (7.75 ha) were nearly at 2 × S on the NEP – BM, coordinates, respectively. Com-1 (4.25 ha) and Com-5 (11.50 ha) both had a relative frequency of 0.135%, 3 × S, under the equilibrium regime. The frequency decreases more when we consider larger areas in these two communities than the area in Plot 1 (2.0 ha). Hence, these two communities had the dimensional features of a system that deviated from the regime.

Sub-2 W showed the highest similarity to Plot 1 among the six communities in terms of not only dimensional features but also species composition (Fig. 10-B). High similarity between Sub-2 W and Plot 1 suggested that their common topographical feature (a west-facing slope on a hill) must be a critical factor in ecosystem health in Pasoh FR when the region suffers from occasional droughts and storms.

The similarity of the vegetation between each community and Plot 1 tended to decrease linearly with a
decrease in biomass (Fig. 10-B). This might indicate that topographic changes in species composition are partly caused by degradation of forest stands. In turn, the potential similarity of each zone at the mature stage could be assessed by an extrapolated stage using the same biomass as Plot 1 from the linear correlation.

**Future changes in the variations**

A death rate of a 50-ha plot, $DR_c$, tended to increase linearly throughout a whole period of this observation (Fig. 5). We assumed the present death rate of each community to be a sum of a constant intrinsic death rate and an increasing death under the present regime started $T$ years before the present (1990–2005). We estimated a common $T$ values for 6 communities, including two sub-communities instead of a Hill community, by a mathematical model (see Methods). The estimated $T$ ranged from 50 to 90 years with changes in $BM_c$ (Table 6). This indicates that the present disturbance regime started during 1907–1947. During the latter half of the 1950s, selective logging was conducted in parts of Pasoh FR, approximately 1–2 km from the 50-ha plot (Fig. 1-B). Neighboring rubber plantations and secondary forests were clear-cut, and the land was converted to an oil palm plantation in the early 1970s. The deforestation rate over these 25 years (1971–1996) was estimated to be 2.2% in this area (60×60 km) (Okuda et al. 2003), and a surrounding oil palm plantation was clear-cut for replanting in the early 2000s. These continuous landscape changes in the surrounding area could be one of the factors contributing to the actualized current disturbance regime, likely via the negative impacts on tree life in the isolated reserve area, both physiologically (Kapos 1989) and physically (Yoneda et al. 1998). Manokaran and LaFrankie (1990) have also proposed effects of receding border of Pasoh FR on structural features of a 50-ha plot and large decline in basal area of a remained forest over the interval 1971 to 1984. The average mortality rate of trees above 10 cm dbh from 1947 to 1981 was not significantly different among size classes, with 2.02 y$^{-1}$ as the mean value at a lowland dipterocarp forest, 70 km west of Pasoh FR (Manokaran and Kochummen 1987). The present mortality rate in the 50-ha plot, however, tended to increase, with average values with respect to dbh from 1987 to 2005 as follows: 2.00 y$^{-1}$ (10–30 cm dbh), 2.19 y$^{-1}$ (30–50 cm dbh), 2.44 y$^{-1}$ (50–100 cm dbh) and 2.62 y$^{-1}$ (dbh≥100 cm). This size dependency of mortality rates tended to emerge more clearly during this period. This phenomenon suggests that stress caused by changes to the surrounding landscape has notable detrimental effects on larger trees. Long-term observations over 50 years in this area support

### Table 6. Estimated time ($T$) from the present time period (1990–2005) needed to satisfy $DR_{cd} = 0$ in Equation (2) under different $BM_c$ conditions. $DR_{cd}$, $BM_c$ and RMSE indicate the death rate from the present disturbance regime, the biomass under equilibrium, and the root mean square error from Equation (3), respectively.

<table>
<thead>
<tr>
<th>$BM_c$ (tC ha$^{-1}$)</th>
<th>$T$ (yr)</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>230</td>
<td>50</td>
<td>0.106</td>
</tr>
<tr>
<td>250</td>
<td>71</td>
<td>0.101</td>
</tr>
<tr>
<td>270</td>
<td>90</td>
<td>0.099</td>
</tr>
</tbody>
</table>
the assumption for death rates at a 50-ha plot to increase with time, and it would be important to examine the generality of this assumption for further analysis and application to other areas.

Fig. 11 shows the simulated time trends of biomass in the six communities including two sub-communities, Sub-2 W and Sub-2E, instead of Com-2 for the next 55 years (to 2060) using Equation (2) under the conditions of $T = 71$ years and the average biomass over a 15-year period (1990–2005), the same as the initial biomass in 1997. Closed circles with gray and black colors on the thin curve represent changes in the observed biomass in each community since 1987. Figures in the diagram represent symbols of six communities including two sub-communities, 2 W and 2E, instead of a Hill community (2).

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REFERENCE

Ashton PS. 1995. What can be learned from a 50-ha plot which cannot be learned any other way? In: Long Term Ecological Research of Tropical Rain Forest in Sarawak. Ehime University, Japan. 207–220.


Tsuyoshi Yoneda, Hiromi Mizunaga et al.

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