Temporal and spatial variation of forest biomass in relation to stand dynamics in a mature, lowland tropical rainforest, Malaysia

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To clarify consistency in the size of carbon pool of a lowland tropical rainforest, we calculated changes in above-ground biomass in the Pasoh Forest Reserve, Peninsular Malaysia. We estimated the total above-ground biomass of a mature stand using tree census data obtained in a 6-ha plot every 2 years from 1994 to 1998. The total above-ground biomass decreased consistently from 1994 (431 Mg ha^{-1}) to 1998 (403 Mg ha^{-1}) (1 Mg = 10^3 kg). These are much lower than that in 1973 for a 0.2 ha portion of the same area, suggesting that the the total above-ground biomass reduction might have been consistent in recent decades. This trend contrasted with a major trend for neotropical forests. During 1994–1998, the forest gained 23.0 and 0.88 Mg ha^{-1} of the total above-ground biomass by tree growth and recruitment, respectively, and lost 51.9 Mg ha^{-1} by mortality. Overall, the biomass decreased by 28.4 Mg ha^{-1} (i.e. 7.10 Mg ha^{-1}·year^{-1}), which is almost equivalent to losing a 76-cm-diameter living tree per hectare per year. Analysis of positive and negative components of biomass change revealed that deaths of large trees dominated the total above-ground biomass decrease. The forest biomass also varied spatially, with the total above-ground biomass density ranging 212–655 Mg ha^{-1} on a 0.2-ha basis (n = 30 subplots, 1998) and 365–440 Mg ha^{-1} on a 1 ha basis. A large decrease of the total above-ground biomass density (> 50 Mg per ha per 2 years) in several 0.2-ha subplots contributed to the overall decrease in the 6-ha total above-ground biomass. In the present study, we discuss the association between forest dynamics and biomass fluctuation, and the implication for carbon cycling in mature forests with emphasis on forest monitoring and assessments of soil and decomposition systems.

Key words: carbon pool; forest biomass fluctuation; total above ground biomass (TAGB); tree mortality; treefall.

Introduction

Tropical forests are important carbon pools, comprising approximately 40% of terrestrial carbon storage (Dixon *et al.* 1994). They also exhibit high primary productivity among the terrestrial ecosystems in the world. During the 1970s, ecologists and foresters promoted the study of primary productivity all over the world. These studies, conducted under the International Biological Programme (IBP), contributed greatly to the field of forest productivity and carbon cycling (e.g. Kira 1978a, b). As global warming becomes apparent, the importance increases of forest biomass as the carbon pool, especially in tropical regions where forest degradation is striking (Fang *et al.* 1998; Houghton & Hackler 1999; Potter 1999).

The contribution of a forest to the carbon pool depends on its successional stage. Forest biomass generally increases with stand age, and approaches a constant level at maturity because of a decline in net primary productivity (Kira & Shidei 1967; Whitmore 1984). Mature stands, meaning those in a climax stage of succession, are acknowledged as being in an 'equilibrium with some fluctuation by disturbances' because

of gap formation and subsequent regeneration (Pickett & White 1985; Hubbell & Foster 1986; Platt & Strong 1989). In this equilibrium, organic matter flow is traditionally believed to be 'in balance', overall through the balance between growth (including a small contribution of recruitment), death, and decomposition of individual trees (Carey *et al.* 2001). However, mature forests in the Neotropics have recently been found to be increasing in biomass over the last few decades (Phillips *et al.* 1998). Carey *et al.* (2001) also claim that the net primary productivity of old-growth forests might be considerably underestimated, accounting for a substantial fraction of the missing atmospheric carbon sink. The question of whether mature forests play a significant role as a carbon sink is still open.

Biomass fluctuation with time and space involving stand dynamics can be estimated by repeated tree-census, so that changes due to growth and mortality of trees can be followed in a given area (Phillips *et al.* 1998; Chave *et al.* 2003). Phillips *et al.* (1998) compiled tree census data for 153 permanent plots in 68 sites from world-wide tropical forests, and found that biomass gain by tree growth exceeded losses by tree death in 38 of 50 Neotropical sites (Phillips *et al.* 1998). Studies of the Paleotropics included in Phillips *et al.* (1998) are sparser (33 plots in 18 sites), so that data from the Paleotropics, such as South-east Asian tropical forests, is important.

The present paper aims to (i), estimate the magnitude of the variation of forest tree biomass with time and space in a mature stand of the Pasoh Forest Reserve, Peninsular Malaysia and (ii), compare contributions of growth and death of trees to the biomass fluctuation. The association between forest dynamics and biomass fluctuation, and its implications for carbon cycling, are discussed.

Methods

Study site

The study area is located at the Pasoh Forest Reserve (2°58′N, 102°18′E; 75–150 m a.s.l.), Negeri Sembilan, Malaysia. The Forest Reserve contains Plot 1 (2 ha), a plot used extensively for studies of primary productivity of tropical rainforest during IBP (e.g. Kira 1978a, b, 1987). In 1994 we expanded Plot 1 to a 6-ha plot (200 × 300 m) in the Forest Reserve. This 6-ha plot contains Plot 1 at its center. In total, the 6-ha plot contains 574 species (> 5 cm in diameter, 1998; K. Niiyama *et al.* unpubl. data), and 814 species (≥ 1 cm in diameter, 1990) from 78 families are recorded in a 50-ha plot located near the 6-ha plot (Kochummen *et al.* 1990; Manokaran *et al.* 1992; Okuda *et al.* 1997). The topography at the 6-ha plot is a gentle plain, and

the soil condition is generally dry. The mean annual rainfall in this region is 1842 mm with two distinct peaks, in April/May and November/December Environmental characteristics and the details of stand structure of the Forest Reserve are described in other published studies (e.g. Manokaran & LaFrankie 1990; Okuda *et al.* 1997, 2003; Tang *et al.* 1999).

Tree census

We monitored the growth dynamics of tree populations in the 6-ha plot, following Niiyama *et al.* (1999). We divided the 6-ha plot into 20 × 20 m subplots (a total of 150 subplots). Every 2 years from March 1994, all the trees >5 cm in d.b.h. were tagged, identified and mapped, and their d.b.h. were measured. If a tree had large buttresses, its d.b.h. was measured just above the buttresses (Niiyama *et al.* 1999). In each census, tree mortality and its factor (standing dead, treefall and other causes of mortality) was recorded. Overall, data for three censuses, covering 4 years, are available for this study.

Biomass estimation

Estimation of forest biomass was carried out using allometric relationships obtained in this forest during IBP. This section summarizes the previous work on allometric relations in Plot 1 of the Forest Reserve (Kato *et al.* 1978). The height (H) of a given tree can be estimated from its d.b.h. (D) by the following formula:

$$\frac{1}{H} = \frac{1}{2.0D} + \frac{1}{61} \qquad [\text{m, cm}] \qquad (1)$$

From the values of D and H, the dry mass of stem, branches, and leaves of the tree are estimated as:

$$M_s = 0.0313\left(D^2H\right)^{0.9733}, \qquad [\text{kg, } 10^{-4}\,\text{m}^3] \quad (2)$$

$$M_B = 0.136\,M_s^{1.070}, \qquad [\text{kg, kg}] \qquad (3)$$

and:

$$\frac{1}{M_L} = \frac{1}{0.124\,M_S^{0.794}} + \frac{1}{125}, \qquad [\text{kg, kg}] \qquad (4)$$

where M_S, M_B and M_L, respectively, denote the dry mass of stem, branches and leaves. The constants in equations 1–4 were determined using the whole range of tree diameters from samples taking no regard of species in Plot 1 (Kato *et al.* 1978), so that these relations are applied across species. The sampling method is detailed in Kato *et al.* (1978). The total above-ground biomass (TAGB) was computed by summing the above-ground biomass of individual trees ($M_S + M_B + M_L$; Fig. 1) for >5 cm d.b.h.

We computed TAGB repeatedly in the 6-ha plot using the census data of March 1994, March 1996 and March 1998. To explore long-term trends in TAGB fluctuation, we compared TAGBs in recent years with that in 1973, measured in a part (0.2 ha) of Plot 1 (Kato *et al.* 1978). It is necessary to correct the calculated TAGBs for this comparison, since the TAGB in 1973 was estimated from samples >4.5 cm d.b.h. We assumed the same biomass for d.b.h. classes of 5.0–5.5 cm and 4.5–5.0 cm in each census. The recent

Fig. 1. Estimation of biomass of individual trees based on the d.b.h. using allometric relationships.

TAGBs for d.b.h. >4.5 cm were calculated by adding this approximation to the value computed by $M_S + M_B + M_L$.

To examine spatial variation in TAGB estimates, fine-scale variation in TAGB was examined. The calculation of TAGB density was carried out for two spatial scales; first, we divided the 6-ha plot into 20×100 m subplots ($n = 30$), with reference to the measurement during IBP. Each subplot was positioned so that longer (100 m) sides of the subplot are parallel to longer (300 m) sides of the 6-ha plot. The spatial scale of 0.2 ha and the shape of the subplot were chosen because TAGB in the IBP study (1973) was based on the result for a 20×100 m subplot (Kato *et al.* 1978). Secondly, we calculated TAGB density for every 1-ha subplot (100×100 m, $n = 6$). This is because this plot size has often been used for tree inventory samplings (e.g. Phillips *et al.* 1998). For both calculations data for 1994 and 1998 were used. The TAGB density was calculated in the same way as above.
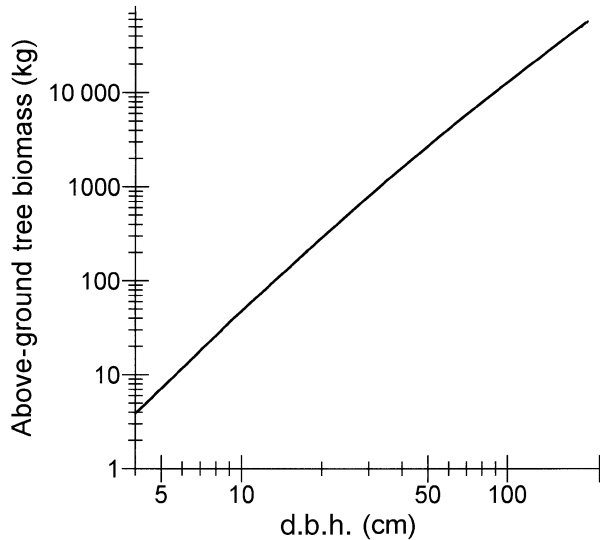
Results

Biomass change with time

The TAGB in the 6-ha plot decreased consistently during the study period (1994–1998), though the magnitude of the change was not remarkable for the basal area (Table 1). The TAGB of the forest was 431.2 Mg ha^{-1} in 1994, falling to 403.2 Mg ha^{-1} in 1998. During the period 1994–1998, the forest gained 23.0 Mg ha^{-1} of

Table 1 Recent dynamics of above-ground biomass in a mature stand (6 ha) in the Pasoh Forest Reserve

Parameter	1994	1994–1996	1996	1996–1998	1998	Overall 4 years
Above-ground biomass (Mg/ha)						
Stem, M_S	343.24		331.82		320.65	
Branch, M_B	80.43		77.56		74.70	
Leaf, M_L	6.96		6.84		7.73	
TAGB* (= $M_S + M_B + M_L$) for D >5 cm	430.63		416.22		402.07	
Net gain		−14.43		−13.74		−28.41
Corrected TAGB (D > 4.5 cm) **	431.24		417.37		403.21	
TAGB in 1973 (D > 4.5 cm) ***	475.10					
Change rate in TAGB (Mg ha^{-1} year^{-1})						
Tree growth, G_M		5.16		6.35		5.66
Recruit, R_M		0.22		0.15		0.22
Death, D_M		12.60		13.38		12.98
Net gain (= $G_M + R_M - D_M$)		−7.21		−6.87		−7.10
Basal area (BA; m^2/ha)	34.85		33.92		33.01	
Net gain		−0.94		−0.83		−1.81
BA change rate (m^2 ha^{-1} year^{-1})						
Tree growth, G_{BA}		0.44		0.57		0.49
Recruit, R_{BA}		0.04		0.04		0.05
Death, D_{BA}		0.96		1.02		0.99
Net gain (= $G_{BA} + R_{BA} - D_{BA}$)		−0.47		−0.41		−0.45

*, Total above-ground biomass (TAGB); **, Difference in minimum D and area; ***, Kato *et al.* (1978).

TAGB by tree growth and lost 51.9 Mg ha⁻¹ by mortality, resulting in a net reduction of 28.4 Mg ha⁻¹ after considering the gain by recruitment (0.88 Mg ha⁻¹, into >5 cm d.b.h.). The rates of TAGB decrease were similar between census intervals; 7.21 Mg ha⁻¹·year⁻¹ during 1994–1996 and 6.87 Mg ha⁻¹·year⁻¹ during 1996–1998, with a overall mean of 7.10 Mg ha⁻¹·year⁻¹ in this 4-year period (Table 1). In the following, we show the TAGB of 1994 and 1998 only, as the TAGB in 1996 was generally intermediate between those in 1994 and 1998. Recent TAGB values were as much as 43.9–71.9 Mg ha⁻¹ lower than those obtained in 1973 (475.1 Mg ha⁻¹; Kato *et al.* 1978).

Stand dynamics and components of biomass change

The components of the TAGB change were analysed in terms of tree growth, recruitment, and tree deaths. Biomass loss by tree death (12.6–13.4 Mg ha⁻¹ year⁻¹) was consistently more than twice higher than the biomass gain by growth (5.2–6.4 Mg ha⁻¹·year⁻¹), and recruitment accounted for only a minor fraction (Table 1). The biomass gained by growth and recruitment and that lost by mortality showed little variation among the periods between tree censuses (Table 1).

The tree mortality along a size gradient showed contrasting patterns between biomass loss and frequency (number of trees) of mortality (Figs 2 and 3). The distr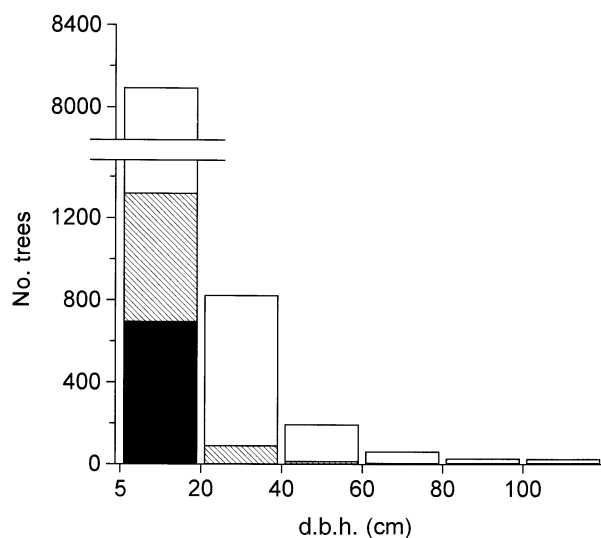ibution pattern of mortality frequency showed that most tree deaths involved small trees (Fig. 2). Deaths of larger trees (> 20 cm d.b.h.) made only a small contribution in number (19.4% during 1994–1996, 13.5% during 1996–1998, and 16.1% during overall 4 years), though multiple treefalls were caused by unusual, strong winds in 1995 and 1996 (M. Yasuda and K. Niiyama, pers. obs.). The trees recruited into and those that died within the size class 5–20 cm d.b.h. had similar frequencies during 1996–1998 (181 vs. 185 trees, respectively), although there was a small difference for 1994–1996 period (111 vs. 191). The number of trees that recruited during 1994–1996 and died during 1996–1998 was 17.

The distribution of the lost biomass among size classes showed a distinct peak in the >100 cm d.b.h. class (Fig. 3b). The tree biomass in larger size classes constituted a considerable fraction of TAGB (46.2% in 1994 census and 43.7% in 1998 census for >60 cm d.b.h.; Fig. 3a) despite the very small numbers of trees (Fig. 2). Consequently, the biomass loss in the
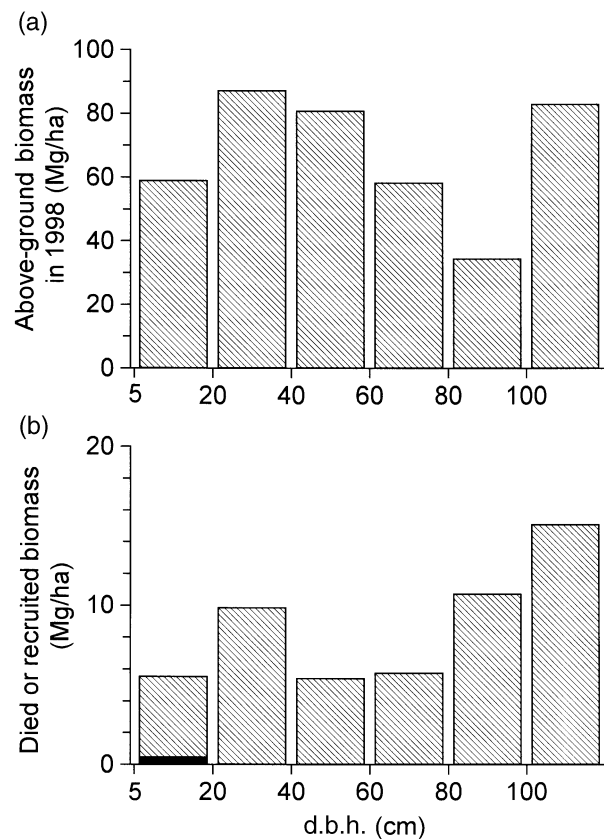

Fig. 2. The four-year dynamics of trees along tree size class in the 6-ha plot in Pasoh Forest Reserve. Data from censuses in 1994 and 1998 are shown. The trees that were recruited during 1994–1996 and died during 1996–1998 were few (17 trees), thus are not shown. (□), alive at 1994 and 1998; (▨), alive at 1994 and died during 1994-1998; (■), recruited during 1994-1998 and alive at 1998.

Fig. 3. Distribution of (a) above-ground tree biomass and (b) changes in biomass vs. tree size class. Data from censuses in 1994 and 1998 are shown. The total above-ground biomass (TAGB) fraction for trees that were recruited during 1994–1996 and died during 1996–1998 was negligible (0.029 Mg ha⁻¹, 17 trees), so that it is not shown in the figure. (b), (▨), alive at 1994 and died during 1994-1998; (■), recruited during 1994-1998 and alive at 1998.

large size class (> 60 cm d.b.h.) accounted for 59.1% of the total loss during the period 1994–1996, 62.3% during 1996–1998, and 60.8% during the overall 4 years. Of the trees whose mortality factor could be identified (*n* = 254 for 1994–1996 and 280 for 1996–1998), standing-dead trees occupied 25.2% of tree deaths (corresponding to 26.8% of biomass loss) during 1994–1996, 50.7% of those (75.8% of biomass loss) during 1996–1998, and 38.6% of total death events (51.1% of total biomass loss) during the overall 4 years.

Spatial variation of total above-ground biomass

A fine-scale analysis of the TAGB density showed that within the 6-ha plot, TAGB densities varied from 212 to 655 Mg ha^{-1} at the 0.2-ha scale in 1998 (*n* = 30 subplots; Fig. 4). The mean (± S.D). TAGB density was 431.2 (± 113.6) Mg/ha for the 1994 census and 403.2 (± 108.6) Mg/ha for 1998. Median values were

(a)

(b)

Fig. 4. Fine-scale variation of total above-ground biomass (TAGB) in the 6-ha plot (upper) and increments during a census interval (lower). Data for 1998 (upper) and for 1996–1998 (lower) are shown. The 6-ha plot was divided into 20 × 100 m subplots and the TAGB density was calculated for each subplot. The arrow in the upper panel indicates a TAGB density during International Biological Programme (IBP), at the same scale as in 1973.

412.8 Mg ha^{-1} in 1994 and 387.9 in 1998. On a 1-ha basis, the TAGB density was 431.2 ± 26.4 Mg ha^{-1} (Mean ± S.D., range 394.8–452.0) in 1994 and 403.2 ± 27.8 Mg ha^{-1} (365.7–439.6) in 1998.

The patterns of spatial variation were similar in 1994 and 1998 (data not shown, 0.2-ha basis; Kolmogorov-Smirnov test, *P* > 0.1). For both data sets, only 8 of the 30 subplots had a larger TAGB density than the IBP-study plot (475.1 Mg ha^{-1}) (Fig. 4).

During both census intervals (1994–1996 and 1996–1998), the TAGB density decreased in 15 (50%) of the 30 subplots in both periods (Fig. 4). In some plots, a large decrease of TAGB density (> 50 Mg per ha per 2 year) occurred (Fig. 4). As a result, the TAGB density totally decreased in 22 (73%) of the 30 subplots. Thus, the TAGB clearly varied with the spatial scale of observation, but the frequency of subplots in which TAGB density decreased during census interval was consistent at the 0.2-ha scale.

Discussion

Forest biomass fluctuation

Our data show that forest biomass can fluctuate significantly with time in a tropical rainforest. The TAGB showed a consistent reduction during our 4-year observation period. The stand lost 28.4 Mg ha^{-1} of biomass. The 28.4-Mg/ha of net biomass loss (i.e. a loss of 7.10 mg ha^{-1}·year^{-1}) is almost equivalent to losing a 76-cm- d.b.h. tree per hectare per year (Fig. 1). These results are in contrast with a long-term trend in neotropical forests in recent decades. In most neotropical sites, biomass gain by tree growth has exceeded losses by tree death, resulting in an increase in TAGB by an average of 1.1 Mg ha^{-1}·year^{-1} (Phillips *et al.* 1998). Chave *et al.* (2003) also documents a small TAGB increment of on average 0.2 Mg ha^{-1} for 1985–2000 in a 50-ha census plot in Barro Colorad Island (BCI), Panama. To clarify a general trend of biomass fluctuation in Southeast Asian tropical rainforests, we need to accumulate data on forest biomass fluctuation with time from a variety of locations (Okuda *et al.* in review).

Consistently, the biomass loss because of tree mortality was much larger in the 6-ha plot than the biomass gain through growth (Table 1). Although tree mortality was much rarer in the larger size classes, the biomass of a single tree in the >100-cm d.b.h. class is some 10^4 times greater than that in the small (e.g. 5–10 cm) size class (Fig. 1). The distribution of biomass loss along d.b.h. showed a peak in the largest size class (Fig. 3) despite the very rare mortality of such trees (Figs 2 and 3). This suggests that a single treefall from the larger size classes has a greater role on the biomass change in this forest than frequent deaths of small trees (see also
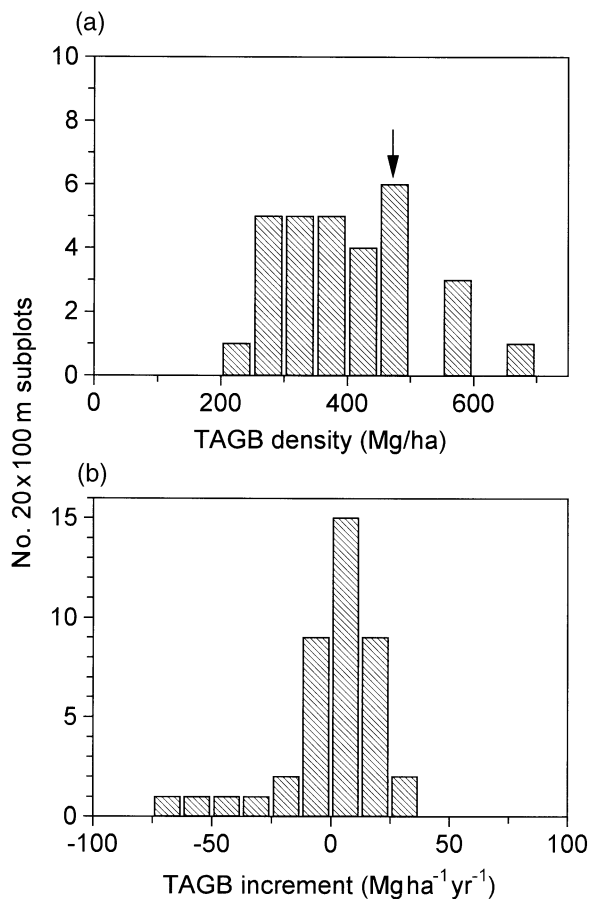
Kira 1978b). Chave *et al.* (2003) also performed similar analyses using data (for 1985–2000) for the 50-ha plot in BCI. The patterns in BCI highly contrasted with our results, however. In BCI, the mean rate of biomass loss ranges 5.2–5.6 Mg ha^{-1}·year^{-1}, approximately 40% of those in Pasoh (Table 1). Moreover, the TAGB loss in BCI was evenly distributed along d.b.h. classes with a small contribution of large-sized trees (Chave *et al.* 2003).

The larger impact of infrequent death of large trees on TAGB fluctuation in Pasoh also suggests another point concerning the association between forest structure and biomass fluctuation. Because of the relatively even distribution of biomass among size classes in mature forests (cf. Figure 3a) and because of the much larger biomass of a large-sized tree (cf. Figure 1), death of large trees can have more substantial effects on the total biomass loss in mature forests than in regrowing secondary forests, which have fewer or no large-sized trees.

The TAGB in 1998 was smaller than those in 1973 during IBP by 70 Mg ha^{-1}. Coupled with the decreasing trend during 1994–1998, the results suggest that the trend might have been consistent in recent decades. In fact, 34-year long-term data on the dynamics of a lowland rainforest near Pasoh reveals that imbalance between mortality and recruitment of trees lasted for 16 years (1947–1963, Manokaran & Kochummen 1987), probably resulted in a TAGB reduction during this period. The data compiled by Phillips *et al.* (1998) also show a decreasing trend for paleotropical sites, though statistically insignificant. Therefore, it can be possible that the TAGB in the Pasoh forest has decreased over the decades. However, caution is needed when interpreting the above comparison of TAGB, because the IBP result was based on only a 0.2-ha area. Our analysis found a large TAGB variation among 0.2-ha subplots, suggesting that this scale of estimation might have a sampling bias. No such variation was examined in the IBP study, so that we cannot make a decisive comparison. The frequency of large canopy-gap formation is of the orders 10 years (Nakashizuka & Iida 1995), so that monitoring of forest dynamics in relation to biomass change across years would be of great importance.

Implications for carbon cycling

The fluctuation of above-ground biomass with time can directly affect the forest productivity and decomposition processes (Kira 1987; Chave *et al.* 2003). The present results therefore have implications for the forest carbon cycle. The 12–13 Mg ha^{-1}·year^{-1} of tree deaths (Table 1) corresponds to the supply of decomposition substrates in the Pasoh forest. Importantly,

our data showed that relative frequency of causes of tree mortality greatly differed among the census intervals. The causes of mortality might be a significant factor which can affect the rate of carbon flows in decomposition systems. Because fallen versus standing-dead stems/branches can have differential effects on the activity of decomposers on the forest-floor, the fluctuation in the contribution of standing-dead mortality would affect the rate of subsequent decomposition of dead trees.

Besides the 12–13 Mg ha^{-1}·year^{-1} of tree death, litters that vary in size accumulates on the forest floor. In general, fine litterfall (e.g. leaf litter and fruits) ranges between 5 and 15 Mg ha^{-1}·year^{-1} in tropical forests (Proctor 1984). In Malaysian lowland dipterocarp forests it amounts to 9.6–12.8 Mg ha^{-1}·year^{-1} (Yamashita *et al.* 1995; Yamashita & Takeda 1998). Fallen branches and dead stems can be recognized as coarse litter. These suggest that a considerable amount of decomposition-substrates has been supplied to the forest floor in the Pasoh forest (a clear contrast with the Panamanian rainforest; Cheve *et al.* 2003) and that both litters and dead trees are important to understand overall carbon pathways through decomposition in a mature forest (Kira 1978a, 1987). To accurately estimate carbon cycling, further assessments are necessary on the decomposition of fine and coarse litters as well as litterfalls, and the dynamics of the below-ground system such as soil respiration.

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