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Dynamics, productivity and species richness of tropical rainforests along elevational and edaphic gradients on Mount Kinabalu, Borneo

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Abstract We studied the dynamics of nine tropical rainforests on Mount Kinabalu, Borneo, at four elevations (700, 1,700, 2,700 and 3,100 m) on various edaphic conditions for four 2-year periods over 8 years (1995–2003), and examined the relationships with above-ground productivity. Mean growth rate of stem diameter, basal area turnover rate and estimated recruitment rate (using growth rate and size distribution) correlated with productivity among the nine forests in all periods. These rates based on growth rates of surviving stems appeared to be good measures of stand turnover. However, observed recruitment rate and mortality (and turnover rate as mean of these rates) based on direct observation of recruits and deaths did not correlate with productivity in some periods. These rates may not be useful as measures of stand turnover given small sample size and short census interval because they were highly influenced by stochastic fluctuation. A severe drought associated with the 1997–1998 El Niño event inflated mortality and depressed mean growth rate, recruitment rate and basal area turnover rate, but had little effect on the correlations between these rates (except mortality) and productivity. Across broad elevational and edaphic gradients on Mount Kinabalu, forest turnover, productivity and species richness correlated with each other, but the

causal interpretation is difficult given the different histories and species pools among forests at different elevations.

Keywords Growth · Mortality · Productivity · Recruitment · Turnover

Introduction

Based on a worldwide analysis of humid tropical forests, Phillips et al. (1994) showed that tree species richness correlated with stem turnover rate (mean of recruitment and mortality rates) and with basal area turnover rate, and argued that these rates were measures of productivity. Because turnover rate is far easier to measure than productivity, research on interesting questions involving productivity, such as diversity-productivity relationship, will be greatly facilitated if turnover rate can be used as a surrogate of productivity. However, the linkage between turnover and productivity was questioned (Sheil 1996; Condit 1997), and to our knowledge there has been no study that directly examined the relationship between turnover and productivity for tropical forests. Weaver and Murphy (1990) showed that both above-ground productivity and turnover rate diminished with increasing elevation on a subtropical mountain in Puerto Rico, but this could not be tested statistically because there were only three plots.

On Mount Kinabalu, Borneo, the highest mountain in southeast Asia between the Himalayas and New Guinea, we have been conducting tree censuses at nine permanent plots every 2 years since 1995. These plots are established at four elevations and on different edaphic conditions that reflect diverse geological substrates. A direct estimate of above-ground net primary productivity is available in these plots because litterfall was also monitored, and it has been shown that elevation (as a surrogate of temperature) and edaphic

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conditions (as a surrogate of soil nutrient conditions) synergistically determine productivity (Kitayama and Aiba 2002; Takyu et al. 2003; Kitayama et al. 2004). Stand dynamics during 1995–1999 were analysed by Aiba and Kitayama (2002). In this paper, we study variation in stand dynamics (turnover rates as well as growth rates) among the nine plots over 8 years (1995–2003), and examine the relationship with productivity.

On Mount Kinabalu, a severe drought occurred in 1997–1998 in association with the El Niño–Southern Oscillation event, and growth rates and mortality were significantly affected by the drought (Aiba and Kitayama 2002). It is necessary to consider the impact of the drought in order to study stand dynamics (Sheil 1995; Phillips 1995). We therefore calculated growth and turnover rates for each of four 2-year census intervals, of which one (1997–1999) included the drought (drought period) and the other three (1995–1997, 1999–2001 and 2001–2003) did not (non-drought periods). This is also because long census intervals underestimate turnover (recruitment and mortality) rates due to population heterogeneity within a stand and unrecorded mortality of recruits (Sheil 1995; Sheil and May 1996; Kohyama and Takada 1998). We also calculated recruitment rate and mortality over the entire study period (1995–2003) because short census intervals, when combined with small sample sizes, may lead to stochastic fluctuation in these rates. Finally, we will demonstrate the correlation between productivity and species richness for our plots, and discuss the relationships among forest turnover, productivity and species richness.

Methods

Study sites

The geological substrates of Mount Kinabalu (4,095 m, 6°05'N, 116°33'E) are dominated by Tertiary sedimentary

rock below c. 3,000 m and by granite above that. Ultrabasic (or serpentine) rock and unconsolidated Quaternary sediment are distributed as patches at some elevations. We selected a total of nine study sites of primary forests on gentle sideslopes ($\leq 27^\circ$) at four common elevations (700, 1,700, 2,700 and 3,100 m) on these substrates (Table 1). At each elevation, we have a pair of sites on ultrabasic versus non-ultrabasic substrate (Tertiary sedimentary rock at 700, 1,700 and 2,700 m and granite at 3,100 m), and at 1,700 m we have an additional site on Quaternary sediment. Selecting the two (or three) sites on different substrates at exactly the same elevation was not always possible due to heterogeneous distribution of the substrate and precipitous topography. Reflecting diverse geology, edaphic conditions differ greatly between two (or three) forests at the same elevation. In short, soil fertility (in terms of biologically available nitrogen and phosphorus) is the lowest on ultrabasic rock, intermediate on Tertiary sedimentary rock (or granite), and the highest on Quaternary sediment at each elevation (Kitayama and Aiba 2002; Takyu et al. 2002; Kitayama et al. 2004). Annual mean temperature (24.3°C at 550 m) decreases with increasing elevation following a lapse rate of 0.55°C per 100 m (Kitayama and Aiba 2002). Mean annual rainfall varies little with elevation, and was ample (>2,000 mm) everywhere except during the drought. The El Niño drought occurred from late 1997 to early 1998, and the climatic departure from normal conditions seemed to become greater with increasing elevation (Aiba and Kitayama 2002). According to our measurements using climatic stations at the four elevations, the drought culminated in March to April 1998: the lowest 30-day running totals (the sum of rainfall of a particular day and the preceding 29 days) were 14.4 mm at 550 m, 0.9 mm at 1,560 m, 1.0 mm at 2,650 m and 0.6 mm at 3,270 m. Forest structure and floristic composition of these sites were analysed by Aiba and Kitayama (1999), Aiba et al. (2002) and Takyu et al. (2002).

Table 1 Characteristics of the nine study plots, established at four common elevations on different geological substrate of Mount Kinabalu, Borneo

Common elevation (m)	Geological substrate	Abbreviation	Exact elevation (m)	Plot area (ha)	Basal area ($\text{m}^2 \text{ha}^{-1}$) ^a	Stem density (ha^{-1}) ^a	Above-ground net primary productivity ($\text{kg m}^{-2} \text{year}^{-1}$)	Litterfall rate ($\text{kg m}^{-2} \text{year}^{-1}$)
700	T	07S	650	1.00 ^b	36.2	1,064	1.91	1.11
700	U	07U	700	1.00	40.7	1,175	1.72	1.11
1,700	T	17S	1,560	0.50	40.0	1,730	1.22	0.80
1,700	Q	17Q	1,860	1.00	49.3	2,045	1.35	0.94
1,700	U	17U	1,860	0.20	49.9	3,535	0.81	0.63
2,700	T	27S	2,590	0.25	53.5	2,116	0.78	0.53
2,700	U	27U	2,700	0.20	41.5	3,775	0.73	0.59
3,100	G	31S	3,080	0.20	64.0	3,665	0.82	0.63
3,100	U	31U	3,050	0.06	25.1	4,383	0.20	0.16

T Tertiary sedimentary; U ultrabasic; Q Quaternary sedimentary; G granitic rocks

^aFor stems ≥ 4.8 cm dbh

^bTrees in a large gap (0.14 ha area) were excluded from analysis

Permanent plot censuses

At each of the nine study sites we have established a permanent plot (Table 1, 0.06–1.00 ha area) and conducted the first tree census from October 1995 to August 1996 (1995 census). The subsequent censuses were conducted biennially (in 1997, 1999, 2001 and 2003) from September to December. In each tree census, care was taken to enable correct remeasurement. A point without any stem irregularities was selected at around breast height (1.3 m above ground), the girth measured to the nearest millimetre, and the tree marked with spray paint. Stem diameter at breast height (dbh cm) was calculated as the girth divided by π . Multiple stems were measured separately. Buttressed stems were measured well above the protrusion. Death of stems, and new recruits, were recorded in the second and later censuses. In the two lowland plots (07S and 07U, see Table 1 for the abbreviations of the plots), all stems ≥ 10 cm dbh (31.4 cm girth) were measured in 1-ha plots; stems $10 \text{ cm} > \text{dbh} \geq 4.8 \text{ cm}$ (15 cm girth) were measured in two $10 \times 100\text{-m}$ (0.1-ha) transects laid within the plots. In the seven plots at $\geq 1,700$ m, all stems ≥ 4.8 cm dbh were measured. In the 07S plot, a large canopy gap (0.14 ha area) was formed by tree falls between the 1995 and 1997 censuses. Trees in this part of the plot were excluded from the analysis.

Calculating growth and turnover rates

Growth rate (cm year^{-1}) was calculated as absolute difference in dbh between two censuses divided by census interval (days between census midpoints divided by 365). Mean growth rates were computed for two dbh classes (4.8–10 and ≥ 10 cm) separately because stems < 10 cm dbh were measured in subsamples in the two lowland plots. Mortality ($\% \text{ year}^{-1}$) was calculated as percentage of fatalities per year (Sheil et al. 1995). Recruitment rate ($\% \text{ year}^{-1}$) was calculated in the symmetrical form to mortality (Sheil et al. 2000). These formulations yielded virtually identical values to those obtained from logarithmic models used by Phillips et al. (1994). We used both observed and estimated number of recruits outgrowing the minimum dbhs that were defined arbitrarily. Estimation of number of recruits was done by Gf estimation (Kohyama and Takada 1998). The Gf estimate of the number of recruits per area at the midpoint (6 and 11 cm) of the minimum size classes (5–7 and 10–12 cm) is the stem density f in the minimum size class multiplied by average growth rate G of survivors within the size class divided by the class width (2 cm). Stem turnover rate ($\% \text{ year}^{-1}$) was calculated as mean of mortality and observed recruitment rates (Phillips et al. 1994). Basal area turnover rate ($\text{cm}^2 \text{ m}^{-2} \text{ year}^{-1}$) was calculated as the increase by the growth of surviving stems divided by the census interval. These rates were computed for two minimum dbhs (≥ 4.8 and ≥ 10 cm, except Gf estimate of recruitment rate where minimum

dbhs were ≥ 6 and ≥ 11 cm) to take into account the small sample sizes for stems < 10 cm dbh in the two lowland plots (07S and 07U) and for stems ≥ 10 cm dbh in the 31U plot. For the two lowland plots, the number of stems (survivors, fatalities and recruits) for < 10 cm dbh were multiplied by the sample area for ≥ 10 cm dbh divided by one for < 10 cm dbh, and these area-corrected values were added to values for ≥ 10 cm dbh to calculate mortality and recruitment rate for stems ≥ 4.8 cm (or ≥ 6 cm for Gf estimate of recruitment rate).

Checking the error

In the second and later censuses, some stems far larger than the minimum dbh were recorded as recruits. These stems might have been overlooked in the previous censuses. We determined the valid record of dbh of the recruit that showed maximal growth rates in each plot (usually stems of the fast-growing species that showed high growth rates in successive censuses). We assumed that a recruit was present (but overlooked) in the previous censuses if dbh of that recruit was greater than dbh of the valid recruit, and predicted the dbh in the previous censuses using mean growth rate of that stem (or assigned the same dbh if that stem was recorded only once). Some stems that had been considered as dead in one or more censuses were found alive in subsequent censuses. Dbh of such stems was interpolated using growth rate between the preceding and subsequent censuses. Stems with dbh predicted by the above-mentioned methods, as well as stems that showed negative growth of $> 5\%$, were omitted from the calculation of mean growth rate (Condit et al. 1993), but were included in the calculation of observed recruitment rate and basal area turnover rate.

Productivity and species richness

Litterfall monitoring started in February 1996 in all plots (April 1996 in the 17Q plot), and ended in July 1999 in the 07U plot (but continued in the other plots). Above-ground net primary productivity (ANPP) was estimated by above-ground biomass increment for surviving stems (1995–1997) plus fine litterfall (excluding branches > 2 cm girth) for the period before the culmination of the drought (before February 1998) (Clark et al. 2001). Temporal change in productivity was not considered due to the lack of litterfall data after July 1999 in the 07U plot. The productivity values with litterfall from February 1996 to February 1998 for all plots except the 17Q plot were cited from Kitayama and Aiba (2002). Kitayama et al. (2004) reported the productivity values with litterfall from November 1996 to November 1997 for the 17T and 17Q plots. From the ratio of the 17Q to 17T plots during this period, we estimated the productivity value of the 17Q plot with litterfall from February 1996 to February 1998. Small contribution of

biomass increment by recruits was neglected in these estimates, and this might produce slight underestimates.

The relationship between productivity and various rates of forest dynamism (log-transformed when appropriate) was examined using Pearson correlations for each of the four census intervals and also for the entire study period in the case of observed recruitment and mortality rates. The ANPP may correlate with mean growth rate, Gf estimate of recruitment rate or basal area turnover rate simply because all of these rates were calculated from the same data, i.e. growth rates of surviving stems. Therefore, we used litterfall rate as a surrogate of productivity when examining the correlations involving these rates. It is noted that similar results were obtained if we used ANPP, because ANPP correlated highly with litterfall rates among the nine plots ($r=0.98$, $P<0.001$). Differences in regression lines for forest dynamics against productivity among periods were examined by analysis of covariance (ANCOVA). Differences in intercepts were tested after homogeneity of slopes was confirmed. We used both arcsine-transformed and non-transformed values for recruitment and mortality rates, and obtained similar results. Only the results using non-transformed values were reported. Finally, we evaluated species richness of each plot using Fisher's α , a diversity index that is relatively independent of sample size (Rosenzweig 1995; Condit et al. 1996; Aiba et al. 2002), citing the data from Aiba et al. (2002).

Results

Among various rates of forest dynamism, mean growth rates for both dbh classes (4.8–10 and ≥ 10 cm) and basal

area turnover rates for both minimum dbhs (≥ 4.8 and ≥ 10 cm) significantly correlated with productivity among the nine plots in all of the four census intervals (Table 2, $r \geq 0.75$, all $P < 0.05$, examples for ≥ 10 cm dbh in Fig. 1a and b). The Gf estimates of recruitment rate for both minimum dbhs (≥ 6 and ≥ 11 cm) also correlated with productivity in all intervals ($r \geq 0.59$, examples for ≥ 11 cm dbh in Fig. 1c) although the correlations were marginally insignificant in one period for each minimum dbh (1999–2001 for ≥ 6 cm dbh and 1995–1997 for ≥ 11 cm dbh). It is noted that all of these rates are based on growth rates of surviving stems. However, observed recruitment rates (both ≥ 4.8 cm and ≥ 10 cm dbh) only correlated significantly with productivity in some intervals, and mortalities (both ≥ 4.8 cm and ≥ 10 cm dbh) did not in any of the four intervals ($r \leq 0.66$, all $P > 0.05$) (examples for ≥ 10 cm dbh in Fig. 1d, e). Reflecting this, turnover rates (mean of observed recruitment and mortality rates) did not necessarily significantly correlate with productivity in some intervals for both minimum dbhs.

Periods when observed recruitment rate significantly correlated with productivity were not consistent between the two minimum dbhs (1995–1997 for ≥ 4.8 cm dbh, and 1997–1999 and 2001–2003 for ≥ 10 cm dbh). In the case of observed recruitment rate ≥ 10 cm dbh, the insignificant correlations with productivity were partly because of outlying values from the 31U plot (Fig. 1d). In this plot, the sample size for ≥ 10 cm dbh was small (54–58 stems in each census), and the few recruits observed (two and three stems) resulted in exceptionally large recruitment rates during 1995–1997 and 1999–2001. Exclusion of the 31U plot improved the correlation between observed recruitment (and also turnover) rate (≥ 10 cm dbh) and productivity among the other

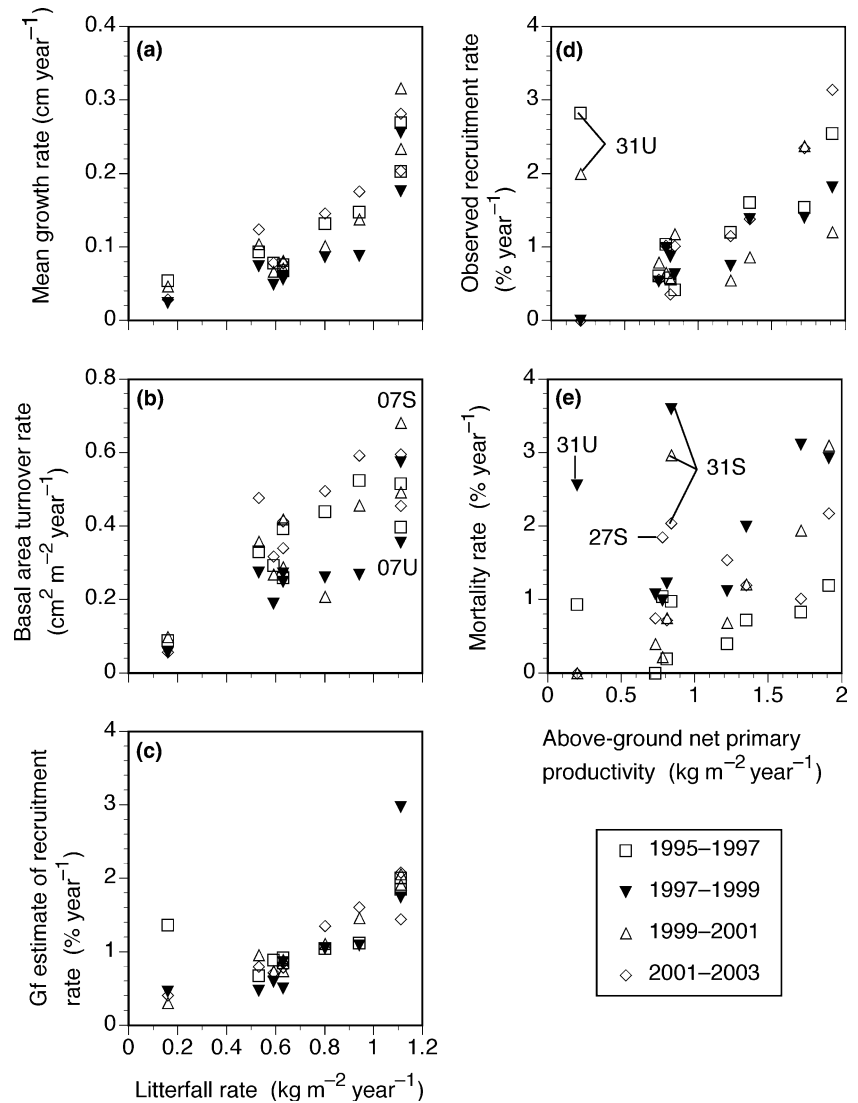
Table 2 Pearson correlation coefficients between productivity (litterfall rate or above-ground net primary productivity) and various rates of forest dynamism for each of four census intervals (ns $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$), and the results of ANCOVA for the difference in the regression lines for forest dynamism against productivity among intervals

Productivity and dynamism	Dbh (cm)	Census intervals				P (ANCOVA)	
		1995–1997	1997–1999	1999–2001	2001–2003	Slope	Intercept
Litterfall rate ($\text{kg m}^{-2} \text{ year}^{-1}$)							
Mean growth rate (cm year^{-1}) ^a	4.8–10	0.87**	0.89**	0.82**	0.94***	0.63	0.16
Mean growth rate (cm year^{-1}) ^a	≥ 10	0.93***	0.94***	0.92***	0.94***	0.55	0.009
Basal area turnover rate ($\text{cm}^2 \text{ m}^{-2} \text{ year}^{-1}$)	≥ 4.8	0.83**	0.81**	0.75*	0.85**	0.89	0.005
Basal area turnover rate ($\text{cm}^2 \text{ m}^{-2} \text{ year}^{-1}$)	≥ 10	0.87**	0.84**	0.82**	0.84**	0.90	0.01
Gf estimate of recruitment rate ($\% \text{ year}^{-1}$)	≥ 6	0.75*	0.68*	0.59ns	0.71*	0.90	0.84
Gf estimate of recruitment rate ($\% \text{ year}^{-1}$)	≥ 11	0.63ns	0.80**	0.96***	0.93***	0.18	0.98
Above-ground net primary productivity ($\text{kg m}^{-2} \text{ year}^{-1}$)							
Observed recruitment rate ($\% \text{ year}^{-1}$)	≥ 4.8	0.69*	0.56ns	0.21ns	0.65ns	0.21	0.002
Observed recruitment rate ($\% \text{ year}^{-1}$)	≥ 10	0.20ns	0.93***	0.15ns	0.94***	0.04	0.61
Observed recruitment rate ($\% \text{ year}^{-1}$) ^b	≥ 10	0.92**	0.89**	0.62ns	0.94***	0.07	0.32
Mortality rate ($\% \text{ year}^{-1}$)	≥ 4.8	0.35ns	–0.03ns	0.53ns	0.20ns	0.68	0.02
Mortality rate ($\% \text{ year}^{-1}$)	≥ 10	0.26ns	0.30ns	0.66ns	0.55ns	0.43	0.01
Mortality rate ($\% \text{ year}^{-1}$) ^b	≥ 10	0.50ns	0.52ns	0.57ns	0.25ns	0.58	0.02
Turnover rate ($\% \text{ year}^{-1}$)	≥ 4.8	0.68*	0.29ns	0.64ns	0.58ns	0.69	0.23
Turnover rate ($\% \text{ year}^{-1}$)	≥ 10	0.24ns	0.65ns	0.59ns	0.85**	0.32	0.33
Turnover rate ($\% \text{ year}^{-1}$) ^b	≥ 10	0.85**	0.72*	0.65ns	0.77*	0.99	0.07

^aLog-transformed because this yielded a better fit for the regression

^bExcluding the 31U plot that had a small sample size

Fig. 1 The relationships between above-ground productivity (litterfall rate or above-ground net primary productivity, $\text{kg m}^{-2} \text{year}^{-1}$) and various rates of tree growth and stand turnover for stems ≥ 10 cm dbh during four 2-year periods among nine plots on Mount Kinabalu, Borneo. The 1997–1999 period included the El Niño drought. Outliers explained in the text were indicated by plot abbreviations (Table 1). **a** Mean growth rates of dbh (cm year^{-1}); **b** basal area turnover rate ($\text{cm}^2 \text{m}^{-2} \text{year}^{-1}$); **c** Gf estimates of recruitment rates ($\% \text{year}^{-1}$); **d** observed recruitment rates ($\% \text{year}^{-1}$); **e** mortality ($\% \text{year}^{-1}$)



eight plots, but the correlations were still insignificant for 1999–2001 for both recruitment and turnover rates. It might be that small sample sizes are problematic only when census intervals are short. We therefore calculated the observed recruitment rate over all 8 years (1995–2003). We used cumulative number of recruits by including stems that had been recruited and died during this period in order not to underestimate recruitment rate (and counting only once when a stem was recruited twice by shrinkage and subsequent growth). Observed recruitment rates over 8 years significantly correlated with productivity for both minimum sizes, even when the 31U plot was included (Fig. 2a, $r=0.68$ for ≥ 4.8 cm dbh and $r=0.84$ for ≥ 10 cm dbh, both $P < 0.05$).

The small sample size for ≥ 10 cm dbh in the 31U plot also resulted in fluctuation in short-term (2-year) mortality (Fig. 1e). However, exclusion of the 31U plot did not improve the correlation between mortality (≥ 10 cm dbh) and productivity, reflecting unexpectedly high mortalities in two other plots (27S and 31S). We

calculated mortality over 8 years (1995–2003) to remove the effects of short census intervals. As for recruitment rate, we used the cumulative number of fatalities by including the death of recruits. Mortalities over 8 years correlated with productivity, but the correlations were insignificant (Fig. 2b, $r=0.32$ for ≥ 4.8 cm dbh and $r=0.58$ for ≥ 10 cm dbh, both $P > 0.05$). We identified two factors that collapsed the correlations between mortality over 8 years and productivity. One is unexpectedly low mortality in the 07U plot for ≥ 4.8 cm dbh. This reflected the small sample size for 4.8–10 cm dbh (133–152 stems in each census) and few fatalities (only three stems over 8 years) recorded in this size class. The other is that mortalities (both ≥ 4.8 cm and ≥ 10 cm dbh) in two plots (27S and 31S) were unexpectedly high. Close inspection of data (Figs. 1e, 2b) indicated that mortality became elevated especially at smaller dbh (< 10 cm dbh) during and after the drought period (1997–1999) in these plots. When these outliers were excluded, the correlations between mortality over 8 years (1995–2003) and productivity became significant

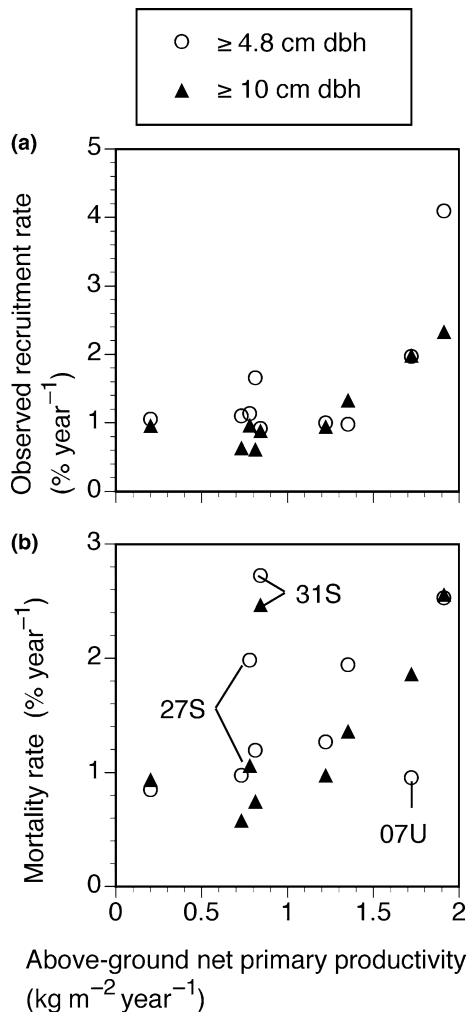


Fig. 2 The relationships between above-ground net primary productivity ($\text{kg m}^{-2} \text{ year}^{-1}$) and observed recruitment or mortality rates over 8 years (1995–2003) for stems ≥ 4.8 cm and ≥ 10 cm dbh. Outliers explained in the text were indicated by plot abbreviations (Table 1). **a** Observed recruitment rates ($\% \text{ year}^{-1}$); **b** mortality ($\% \text{ year}^{-1}$)

($r = 0.93$, $P < 0.01$, for ≥ 4.8 cm dbh, excluding 07U, 27S and 31S plots; $r = 0.83$, $P < 0.05$, for ≥ 10 cm dbh, excluding 27S and 31S plots).

Mean growth rates (≥ 10 cm dbh), basal area turnover rates (both ≥ 4.8 and ≥ 10 cm dbh), observed recruitment rates (≥ 4.8 cm dbh) and mortality (both ≥ 4.8 and ≥ 10 cm dbh) differed among four census intervals when intercepts of the regression lines against productivity were compared (Table 2, ANCOVA, $P < 0.05$). During the drought interval (1997–1999), mean growth rates, basal area turnover rates and observed recruitment rates were depressed, and mortality was inflated (examples in Fig. 1). As was pointed out earlier, the drought elevated mortality in the 27S and 31S plots in particular, and the effects could be recognized even after the drought. If we examined temporal patterns in the correlations between various rates of forest dynamism and productivity (Table 2), there was no consistent pattern in comparison

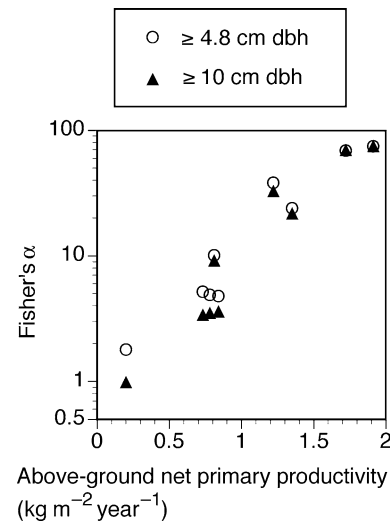


Fig. 3 The relationship between productivity ($\text{kg m}^{-2} \text{ year}^{-1}$) and Fisher's α for stems ≥ 4.8 cm and ≥ 10 cm dbh

between drought period versus non-drought periods. Therefore, the drought had little effect on the correlations between these rates (except mortality) and productivity.

Sample-size adjusted index of species richness (Fisher's α) showed a highly significant correlation with productivity for both minimum dbhs (Fig. 3, $r = 0.96$, $P < 0.001$ for both ≥ 4.8 cm and ≥ 10 cm dbh, using log-transformed Fisher's α). Therefore, forest turnover, productivity and species richness correlated with each other across broad elevational and edaphic gradients on Mount Kinabalu.

Discussion

The present results demonstrated that some measures of stand dynamics correlated with productivity among forests across broad elevational and edaphic gradients on a single tropical humid mountain. Among various measures tested, mean growth rate and turnover rates based on growth rates of surviving stems (Gf estimate of recruitment rate and basal area turnover rate) highly correlated with productivity. However, turnover rates based on direct observations of recruits and fatalities did not necessarily correlate with productivity. So, our results generally support the argument of Phillips et al. (1994) on turnover-productivity relationship, but the stem turnover rate they used (mean of observed recruitment and mortality rates) may not be universally useful as a measure of stand dynamics.

Among three measures highly correlated with productivity, mean growth rate showed the strongest correlations, and the other two rates (Gf estimate of recruitment rate and basal area turnover rate) showed similar magnitudes of correlation with one another. Mean growth rate may be the best measure of stand productivity, although it has not been used previously.

Phillips et al. (1994) stated that basal area turnover rate was a direct measure of productivity. However, this rate was unexpectedly small in the two lowland plots (07S and 07U) during non-drought periods in the present results (Fig. 1b), reflecting the relatively small basal areas in these plots (Table 1). Generally, tropical lowland forests exhibit smaller basal areas than montane forests (Edwards and Grubb 1977; Tanner 1980; Weaver and Murphy 1990; Lieberman et al. 1996; Aiba and Kitayama 1999). So, basal area turnover rate may not be a good measure of forest productivity when comparing montane and lowland forests.

Why did mean growth rate and turnover rates based on growth rates of surviving stems correlate highly with productivity, while observed rates of recruitment and mortality did not? The former measures are based on average values of relatively large samples of observations, and therefore are likely to yield relatively unbiased estimates for the populations. By contrast, the latter ones rest upon relatively rare events that are highly unpredictable in both space and time, and these rates, observed in small samples during short time intervals, fluctuate greatly in a stochastic manner. This was exemplified by recruitment and mortality rates for ≥ 10 cm dbh in the 31U plot and by mortality for ≥ 4.8 cm dbh in the 07U plot in the present results (Figs. 1d, e, 2b). Phillips et al. (1994) used turnover rates as the mean of recruitment and mortality rates to dampen the effects of such fluctuation. However, in our case, turnover rate as well as observed recruitment and mortality rates did not always correlate with productivity. Lengthening the time interval could diminish the short-term fluctuation for recruitment rate, but did not make the correlation for mortality significant (Fig. 2). We noted that the correlations between these rates and productivity were usually positive, although they were insignificant. So, increasing the number of plots may yield significant positive correlations.

Observed recruitment is also affected by an incomplete census that results in recruits being overlooked in one or more censuses and a sudden recruitment of large stems in subsequent censuses. Although we have tried to correct for this, errors might still remain especially for ≥ 4.8 cm dbh. We suggest that direct counts of recruits and fatalities may not be useful as measures of turnover rate because they are highly influenced by stochastic fluctuation and methodological errors, especially when the sample size is small and the census interval is short. The Gf estimation of recruitment rate developed by Kohyama and Takada (1998) is a powerful tool to resolve such problems, but there is no appropriate method for mortality estimation.

Phillips and Gentry (1994), Phillips (1996) and Phillips et al. (2004) suggested that tropical tree populations experienced increased rates of mortality and recruitment in the latter part of the 20th century. In our short-term data set, there was no clear temporal increase in turnover rates, the impact of the drought was overriding. As was pointed out by the present results, as well as our

earlier analysis (Aiba and Kitayama 2002), the severe 1997–1998 El Niño drought inflated mortality, and reduced growth rate, recruitment rate and basal area turnover rate. Long-term mortalities (1995–2003) were greater than expected in the two high-altitude plots (27S and 31S) on non-ultrabasic substrates (Fig. 2b), and this appeared to be partly due to the long-term impact of the drought. Similar long-term effects could be detected when temporal correlations in individual stem growth rates were examined for all nine plots (S. Aiba, unpublished data). However, the present results also indicated that the drought had little effect on the correlation between turnover rates (except mortality) and productivity. The correlation between stand turnover and productivity appeared to be so strong that even the impact of a severe drought could not confound it.

The present results also indicated that forest turnover, productivity and species richness correlated with each other. This seems to support a general pattern at regional to global scales for forest ecosystems (Phillips et al. 1994; Bellingham et al. 1999; Burslem and Whitmore 1999; Waide et al. 1999), but the causal interpretation of this pattern is difficult. We could not assume that forests at different elevations have the same species pools, because these forests have experienced different histories (Sheil 1996). Forest zonation has shifted along the mountain slope during past climatic changes (Morley 2000), and each forest still might not have reached equilibrium conditions. Forests at higher elevations may be less species-rich, simply because they have smaller species pools reflecting more severe past climatic disturbance. Also, there are circular relationships among forest turnover, productivity and species richness: for example, high species richness can be both a cause and a result of high productivity (Waide et al. 1999). Alternatively, apparent correlations among these attributes may be the product of an unidentified common cause: for example, both high turnover and species richness could be ascribed to the early successional status of the forest (Sheil 1996). Comparing sites with the same species pool (at the same elevation on a mountain) at the same successional stage would be the first step towards untangling the cause and effect behind these correlations.

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References

- Aiba S, Kitayama K (1999) Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecol* 140:139–157
- Aiba S, Kitayama K (2002) Effects of the 1997–1998 El Niño drought on rain forests of Mount Kinabalu, Borneo. *J Trop Ecol* 18:215–230

- Aiba S, Kitayama K, Repin R (2002) Species composition and species-area relationships of trees in nine permanent plots in altitudinal sequence on different geological substrates of Mount Kinabalu. *Sabah Parks Nature J* 5:7–69
- Bellingham PJ, Stewart GH, Allen RB (1999) Tree species richness and turnover throughout New Zealand forests. *J Veg Sci* 10:825–832
- Burslem DFRP, Whitmore TC (1999) Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forest. *J Veg Sci* 10:767–776
- Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J (2001) Measuring net primary production in forests: concepts and field methods. *Ecol Appl* 11:356–370
- Condit R (1997) Forest turnover, diversity, and CO₂. *Trends Ecol Evol* 12:249–250
- Condit R, Hubbell SP, Foster RB (1993) Identifying fast-growing native trees from the Neotropics using data from a large, permanent plot census plot. *For Ecol Manag* 62:123–143
- Condit R, Hubbell SP, LaFrankie JV, Sukumar R, Manokaran N, Foster RB, Ashton PS (1996) Species-area and species-individual relationships for tropical trees: a comparison of three 50-ha plots. *J Ecol* 84:549–562
- Edwards PJ, Grubb PJ (1977) Studies of mineral cycling in a montane rain forest in New Guinea. I. The distribution of organic matter in the vegetation and soil. *J Ecol* 65:943–969
- Kitayama K, Aiba S (2002) Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *J Ecol* 90:37–51
- Kitayama K, Aiba S, Takyu M, Majalap N, Wagai R (2004) Soil phosphorus fractionation and phosphorus-use efficiency of a Bornean tropical montane rain forest during soil aging with podzolization. *Ecosystems* 7:259–274
- Kohyama T, Takada T (1998) Recruitment rates in forest plots: Gf estimates using growth rates and size distribution. *J Ecol* 86:633–639
- Lieberman D, Lieberman M, Peralta R, Hartshorn GS (1996) Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *J Ecol* 84:137–152
- Morley RJ (2000) *Origin and evolution of tropical rain forests*. John Wiley and Sons Ltd, Chichester
- Phillips OL (1995) Evaluating turnover in tropical forests: response. *Science* 268:894–895
- Phillips OL (1996) Long-term environmental change in tropical forests: increasing tree turnover. *Environ Conserv* 23:235–248
- Phillips OL, Baker TR, Arroyo L, Higuchi N, Killeen TJ, Laurance WF, Lewis SL, Lloyd J, Malhi Y, Monteagudo A, Neill DA, Núñez Vargas P, Silva JNM, Terborgh J, Vásquez Martínez R, Alexiades M, Almeida S, Brown S, Chave J, Comiskey JA, Czimczik CI, Di Fiore A, Erwin T, Kuebler C, Laurance SG, Nascimento HEM, Olivier J, Palacios W, Patiño S, Pitman NCA, Quesada CA, Salidas M, Torres Lezama A, Vinceti B (2004) Pattern and process in Amazon tree turnover, 1976–2001. *Phil Trans R Soc Lond B* 359:381–407
- Phillips OL, Gentry AH (1994) Increasing turnover through time in tropical forests. *Science* 263:954–958
- Phillips OL, Hall P, Gentry AH, Sawyer SA, Vázquez R (1994) Dynamics and species richness of tropical rain forests. *Proc Natl Acad Sci USA* 91:2805–2809
- Rosenzweig ML (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge
- Sheil D (1995) Evaluating turnover in tropical forests. *Science* 268:894
- Sheil D (1996) Species richness, tropical forest dynamics and sampling: questioning cause and effect. *Oikos* 76:587–590
- Sheil D, Burslem DFRP, Alder D (1995) The interpretation and misinterpretation of mortality rate measures. *J Ecol* 83:331–333
- Sheil D, Jennings S, Savill P (2000) Long-term permanent plot observations of vegetation dynamics in Budongo, a Ugandan rain forest. *J Trop Ecol* 16:765–800
- Sheil D, May RM (1996) Mortality and recruitment rate evaluations in heterogeneous tropical forests. *J Ecol* 84:91–100
- Takyu M, Aiba S, Kitayama K (2002) Effects of topography on tropical lower montane forests under different geological conditions on Mount Kinabalu, Borneo. *Plant Ecol* 159:35–49
- Takyu M, Aiba S, Kitayama K (2003) Changes in biomass, productivity and decomposition along topographical gradients under different geological conditions in tropical lower montane forests on Mount Kinabalu, Borneo. *Oecologia* 134:397–404
- Tanner EVJ (1980) Studies on the biomass and productivity in a series of montane rain forests in Jamaica. *J Ecol* 68:573–588
- Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R (1999) The relationship between productivity and species richness. *Annu Rev Ecol Syst* 30:257–300
- Weaver PL, Murphy PG (1990) Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* 22:69–82