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Changes in biomass, productivity and decomposition along topographical gradients under different geological conditions in tropical lower montane forests on Mount Kinabalu, Borneo

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Abstract We have examined how the structure and function of a forest ecosystem change with topography (lower-slope versus ridge) and how the changes are modified by nutrient availability depending on geological substrate (Quaternary and Tertiary sedimentary rocks and ultrabasic rock) in the tropical montane rain forests of Mt. Kinabalu (Borneo) where climate is humid and aseasonal. Reflecting the difference in site age and parent rock, the pool size of soluble-P and inorganic-N in topsoils decreased from Quaternary sedimentary >Tertiary sedimentary >ultrabasic rock on the lower-slope, and they decreased from the lower-slope to the ridge on all substrates. Forest structural attributes [stature, above-ground biomass, and leaf area index (LAI)] decreased in the order of Quaternary sedimentary >Tertiary sedimentary >ultrabasic rock in association with soil nutrients on the lower-slopes, and decreased upslope consistently on each of the three substrates. Functional attributes [above-ground net primary productivity (ANPP) and decomposition rate] demonstrated similar patterns to structure. ANPP significantly correlated with LAI among the six sites, while net assimilation rate (ANPP divided by LAI assuming an even productivity between above vs below-ground system) was nearly constant. Therefore, ANPP

could be explained primarily by LAI. Topographical change in LAI could be explained by leaf mass per area (LMA) combined with stand-level leaf biomass. LMA increased upslope on all substrates in association with the decrease in individual leaf area. Stand-level leaf biomass decreased upslope on all substrates but the Tertiary sedimentary rock. Our study demonstrated that topography and geological substrates interactively affected forest structure and processes. The effect of topography on forest structure and processes was greater on nutrient-rich substrates than on poor substrates, and the effect of geological substrate was greater on lower-slopes than on ridges.

Keywords Leaf area index · Leaf morphology · Litter fall · Soil nutrients · Southeast Asia

Introduction

Biomass, productivity, and decomposition in forest ecosystems represent the stock and flows of carbon and thus are important parameters for the dynamics of carbon. Features of ecosystems are determined by the major state factors, i.e. climate, geological substrate, topography, organisms, and time (Jenny 1980). Among these factors, the effects of climate, geological substrate, and time on above-ground biomass (AGB), above-ground net primary productivity (ANPP), and decomposition rate have been relatively well studied because these factors determine large-scale patterns of forest structure and processes. For instance, in tropical rain forests, AGB, ANPP, and decomposition rate decrease with increasing altitude (decreasing temperature) (Weaver and Murphy 1990; Raich et al. 1997; Aiba and Kitayama 1999; Kitayama and Aiba 2002). Along the soil chronosequence in Hawaii, AGB and decomposition rate had a peak at 10^4 – 10^5 years and decreased at older sites (Crew et al. 1995; Kitayama et al. 1997). On the other hand, there are few studies on the

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effects of topography on ecosystem processes (Tanner 1980a, 1980b, 1981), although changes in species composition and maximum tree size with topography are well known phenomena.

A topographical gradient is a complex environmental gradient inclusive of many factors such as soil nutrients and moisture, wind, and disturbance. Ridges are generally nutrient poorer, drier, and windier with their substrata more stable than slopes. This complexity is one of the reasons why the effects of topography on forest ecosystem have not been well understood in addition to the fact that topographical effects are often localized. However, because the prediction of forest processes is required at a finer resolution in the face of global changes, the effects of topography are increasingly important.

In Jamaican montane rain forests, Tanner (1980a, 1980b, 1981) reported that AGB, ANPP, and decomposition rate decreased upslope from lower-slope to ridge corresponding to soil nutrients. However, the patterns obtained in Jamaica cannot be straightforwardly applicable to elsewhere because other factors interact with topography. As a comparable example, the pattern of altitudinal changes in forest structure [stature, AGB, and leaf area index (LAI)] and function (ANPP and decomposition) varied with geological substrate (Aiba and Kitayama 1999; Kitayama and Aiba 2002). Geological substrate as a surrogate of soil nutrients interacted with altitude. The objectives of our study are to investigate the effects of topography on forest structure and function, and the modification of topographical effects by soil nutrients (i.e. geological substrate) in order to improve the predictability of forest changes in response to resource (environmental) changes.

Mt. Kinabalu is covered with four types of geological substrates and the montane forests studied here are covered with three of them, i.e. Quaternary and Tertiary sedimentary rocks and ultrabasic (serpentine) rock (Jacobson 1978). The montane forest is humid and aseasonal during normal years; thus we can remove these effects,

which often impinge on ecosystem processes in other areas. We utilized this setting to investigate the effects of interaction of topography and geological substrate on the forest structure and function at a comparable altitude with a similar climatic condition.

Materials and methods

Study site and environment

On southern slopes of Mount Kinabalu (4,095 m above sea level, 6°5'N, 116°33'E), we established a total of six study plots, i.e. two topographical units (ridge and lower-slope) on each of the three geological substrates (Quaternary and Tertiary sedimentary rocks, and ultrabasic rock). The main massif and adjacent area are protected as the Kinabalu Park and primary forests are very well preserved. The six study plots are placed in a matrix at about 1,700 m a.s.l. in the tropical lower montane forest (Table 1). Plot area (in projected length) was 10×50 m on ridges and 50×200 m on lower-slopes except for the ultrabasic rock (40×50 m). Plot area was differently chosen among sites because of different tree size, density and species diversity, and of the limited availability of uniform topography. Lower-slopes correspond to the plots of Aiba and Kitayama (1999) and Kitayama and Aiba (2002). Myrtaceae and Fagaceae dominated throughout the six study plots. On the lower-slopes of the two sedimentary rocks, Lauraceae, Sapotaceae, Meliaceae and Myristicaceae were also abundant. Takyu et al. (2002) described the vegetation of the same sites and the details of plot settings and species composition can be found in their accounts.

The climate of Mount Kinabalu is humid tropical with little yearly fluctuation. Mean air temperature for the 2 years from 1996 to 1997 is 18.3°C at 1,560 m a.s.l. (Kitayama et al. 1999). Mean yearly rainfall is 2,380 mm and mean saturation deficit of the air is 0.23 kPa at this elevation.

Below 3,000 m a.s.l., Tertiary sedimentary rock predominantly covers this mountain with mosaic distributions of Quaternary sedimentary and ultrabasic rocks (Jacobson 1978). According to Jacobson (1978), the Quaternary sedimentary rock originated from the re-deposition of tilloid 30,000–40,000 years ago. The deposits consist of two distinct types of material. The lower unit contains unconsolidated, poorly sorted gravel mainly derived from sedimentary rocks. The upper unit contains partly consolidated, poorly sorted boulder gravel, whose lithology is varied including glacially striated adamellite boulders derived from the summit area. The

Table 1 Outline of the six study plots that are arranged in a matrix of two topographical units and three substrate types on Mount Kinabalu. Inclination of the ridge is shown in parentheses for ridge plots. The inorganic-N content (NH₄-N and NO₃-N) and soluble-P

and net mineralization rate of N in topsoil are cited from Takyu et al. (2002) and SD is in parenthesis. In soil nutrients, plots not sharing the same letters differ significantly from each other within each column at $P < 0.05$ by LSD test after one way ANOVA

Site	Altitude (m)	Plot area (m ²)	Aspect	Inclination	Content of soil nutrients (g/m ²)			Net mineralization rate of N (μg/g/10 days)
					Inorganic-N		Soluble-P	
					NH ₄ -N	NO ₃ -N		
Quaternary sedimentary rock								
Ridge	1,860	500	W	38 (8)	0.11 (0.03) a	0.01 (0.00) a	0.02 (0.01) a	1.48 (0.84) a
Lower-slope		10,000	W	15	0.66 (0.19) b	1.11 (0.24) b	0.19 (0.09) b	7.79 (1.11) b
Tertiary sedimentary rock								
Ridge	1,560	500	S85 W	40 (16)	0.54 (0.12) ab	0.01 (0.01) a	0.01 (0.00) a	-1.34 (2.51) a
Lower-slope		10,000	S55 W	17	1.54 (0.37) c	0.01 (0.02) a	0.12 (0.03) b	1.05 (2.28) a
Ultrabasic rock								
Ridge	1,860	500	N10E	12 (9)	0.75 (0.37) b	0.01 (0.01) a	0.02 (0.02) a	-1.87 (2.15) a
Lower-slope		2,000	S30E	24	1.27 (0.34) c	0.02 (0.01) a	0.02 (0.16) a	-1.49 (2.95) a

Tertiary sedimentary rock consists of sandstone and shale formed about 40 million years ago. The ultrabasic rock consists largely of serpentinized peridotite and it has similar age as the Tertiary sedimentary rock.

The topography on the two sedimentary rocks is characterized by narrow ridgecrests comprised of steep side slopes exceeding 30° (Table 1). Below the side slopes, slopes become gentler (footslope) and have some steplike terraces, which connect to valley floor. A roundish ridge with gentle and straight sideslopes, which are dissected by narrow gullies, characterizes the topography of the ultrabasic rock.

Soil nutrients and water condition have been studied by Takyu et al. (2002) and the detailed descriptions can be found in their accounts. Here we summarize the nutrient and water status of the soils based on their accounts. In each plot, Takyu et al. (2002) set three line transects, and sampled ten 15-cm-deep soil cores (3.7 cm in diameter) at 5 m intervals on each line transect 1 day after rain in February 1997. Five cores were additionally collected at 10-m intervals after three sunny days in January 1999. Soil cores of each transect were combined and three composite samples were made for each plot. The 1997 samples were used for the analysis of nitrogen (N) and the 1999 samples for phosphorus (P). Soluble-P was extracted with hydrochloric-ammonium fluoride solution, and determined colorimetrically according to the Murphy-Riley method (1962). Net soil N mineralization rate was determined using the polyethylene bag methods (Kitayama et al.1998). Each composite soil sample was incubated for 10 days without the amendment of soil moisture at 20.5±0.4°C in a laboratory at 1,560 m a.s.l. Subsamples before and after the incubation were extracted with 1.5 N KCl solution for initial and final NO₃ and NH₄, respectively. NO₃- and NH₄-N concentrations were determined colorimetrically. The net mineralization rate was determined as final minus initial NO₃-N+NH₄-N. On the ridge and the lower-slope of the Tertiary sedimentary rock, Takyu et al. (2002) measured soil water potential using tensiometers with an air pool system (DIK-3100, Daiki Rika Kogyo, Tokyo, Japan). During the severe drought triggered by El Niño in 1998, soil water potential was measured using soil moisture blocks (257 Watermark Soil Moisture Block, Campbell Scientific, Utah, USA), since soil water potential exceeded the capacity of the tensiometer. Finally, to supplement the continuous measurement at the fixed-points, we set a 50-m line transect in each of the six plots and measured instantaneous soil water potential at ten points at 5-m intervals on the line transect 1 day after rain in November 1999 using a tensiometer (2900FL Soilmoisture probe, Soilmoisture Equipment, Santa Barbara, USA).

Soil nutrient condition varied among the geological substrates, reflecting the difference in site age and parent rock. The contents of major nutrients (inorganic-N and soluble-P) and the net mineralization rates of N in topsoils on the lower-slopes, where soils most developed, decreased in the order of Quaternary sedimentary >Tertiary sedimentary >ultrabasic rock (Table 1) (Takyu et al.2002). The contents of inorganic-N and soluble-P and net mineralization rates of N decreased upslope from lower-slope to ridge on each substrate. The contents of inorganic-N and soluble-P and net mineralization rates of N were not distinctively different among the three substrates on the ridges. The magnitude of changes in soil nutrient availability along topographical gradients was greater on nutrient rich substrate than on poor substrate. Soil water potential was not different among the topographical units and substrates, and it was above -10 kPa (field capacity in general case, Rowell,1994) at all six plots 1 day after rain in November 1999 (Takyu et al.2002). The wet condition was kept irrespective of topography in normal periods for about 2 years except for a severe drought from the end of December 1997 to early May 1998 caused by El Niño. If soil moisture is different between topographical units, this difference will be exacerbated during El Niño drought. However, we did not find such a difference. During the El Niño drought, soil water potential was not different between topographical units on the Tertiary sedimentary rock where we set tensiometers and soil moisture blocks. Soil water potential fell below -1,500 kPa (permanent wilting point) at both the ridge and

the lower-slope on the Tertiary sedimentary rock and the duration below -1,500 kPa was similar at the two sites (1-6 days).

Above-ground biomass

The first tree census was carried out in February and June 1997 on the ridges and October to December 1997 on the lower-slopes. In each plot, all trees ≥5 cm in trunk diameter were measured for trunk diameter at breast height (DBH, about 1.3 m above ground). Buttressed trees were measured at well above (ca. 50 cm) the protrusions. The measuring point was marked with aluminum tag and spray paint. On the ridges, tree height was measured for all trees ≥5 cm in DBH. On the lower-slopes, a 10-m-wide transect was laid within each plot (100 m long for the Quaternary sedimentary rock, 60 m for Tertiary sedimentary rock, and 50 m for ultrabasic rock) and tree height for trees ≥5 cm in DBH within the transect was measured. We repeated tree censuses in October to November in 1998 and in the same season in 1999. The second census was not carried out on the lower-slope of the Quaternary sedimentary rock.

The relationship between DBH, D (cm), and tree height, H (m), was regressed by a hyperbolic allometric equation (Ogawa and Kira1977):

$$1/H = 1/AD + 1/H^* \quad (1)$$

where A (m cm⁻¹) and H^* (m) are regression constants. AGB (kg m⁻²) was estimated from an empirical allometric relationship reported for a tropical lowland dipterocarp forest in East Kalimantan, Indonesia (Yamakura et al.1986):

$$\begin{aligned} W_s &= 0.02903(D^2H)^{0.9813}, \\ W_b &= 0.1192W_s^{1.059}, \end{aligned} \quad (2)$$

and

$$W_l = 0.09146(W_s + W_b)^{0.7266},$$

where W_s , W_b and W_l (kg) are the dry mass of the trunk stem, branches and leaves of the tree, respectively, and $W = W_s + W_b + W_l$. In the calculation, estimated H from Eq. 1 was used instead of measured H . AGB at stand level was calculated for living trees in 1997.

Leaf area, leaf mass per area and leaf area index

For measuring leaf area and leaf mass per area (LMA), we sampled at least six leaves from each of multiple trees per species. LMA was determined for more than 90% of the species appeared in each plot. Sun-leaves were collected from the crown tops for canopy species using a slingshot, while shade-leaves were collected for sub-canopy and shrub species. Collected leaves were wiped, measured for area using a portable area meter (CID, Vancouver, Wash., USA), oven-dried at 70°C for 3 days, and measured for oven-dried mass. LMA was calculated as oven-dried mass divided by area. See Takyu et al. (2002) about the details of sampling procedure.

We optically measured LAI for each plot using a LAI-2000 plant canopy analyzer (LI-COR, Lincoln, Neb.). We set three to five line transects (50-m for the ridges and 100-m line transects for the lower-slopes) at each plot except for the lower-slope of the ultrabasic rock (only one transect). Line transects in each plots were at least 2.5 m apart from each other. We took 10 LAI-2000 readings at 5 m intervals (10 m intervals on the lower-slopes) along each line transect, and recorded an arithmetic mean of the ten readings. Measurements were carried out in September 1997 and March 1999 on the ridges of the Tertiary sedimentary and ultrabasic rock, in February 1998 on the lower-slopes of the Tertiary sedimentary and ultrabasic rock, and in March 1999 on the ridge and lower-slope of the Quaternary sedimentary rock. We got more than four replicates (totally 40 LAI-2000 readings) at each plot, but we could not get replicates on the lower-slope of the ultrabasic rock. Optically

measured LAI (LAI_{opt}) values were compared with those (LAI_{est}) estimated from stand-level leaf biomass (calculated from Eq. 2) divided by the mean LMA.

Litterfall and ANPP

To collect fine litterfall, we set litter traps that were made of 1 mm mesh and were cone-shaped with 0.5 m² opening. Twenty traps were placed 1 m above the ground at 10-m intervals along two line transects at each plot on lower-slopes. Similarly, ten traps were placed at each ridge plot. We collected fine litter from litter traps every 2 weeks on the same day from all plots, and immediately oven-dried at 70°C for at least 3 days. For each trap, litter was sorted into the following fractions: leaves (including petiole), reproductive organs (fruits and flowers), branches (≥ 2 cm girth, including bark), epiphytes (all parts combined), palms and bamboos (all parts combined), and dust (unidentifiable particles that pass through 2 mm mesh).

ANPP was calculated as annual increment in AGB of surviving trees between the first and third tree censuses plus mean annual fine litterfall for 2 years from July 1997 to June 1999. However, because the period from the first and second tree censuses included the drought period, litterfall increased and increment of AGB decreased during the drought compared to those after the drought. Therefore, we separately calculated ANPP in the year including El Niño drought and the year after the drought; ANPP in the year including El Niño drought was calculated as the annual increment in the AGB between the first and second tree censuses plus annual fine litterfall from July 1997 to June 1998, ANPP after the drought was calculated as the annual increment in the AGB between the second and third tree censuses plus annual fine litterfall from July 1998 to June 1999. Fallen stems and branches >2 cm girth were not included in the calculation of ANPP.

Decomposition rate

We estimated the in situ decomposition rate of litter by the mass balance method. Standing fine litter was collected within a circular frame (44 cm diameter) at ten points at 10-m intervals along one or two line transects at each plot. The collection was repeated five times on the lower-slopes (July and November 1996, and February, June, and September 1997) and six times on the ridges (March, May, July, September, November 1998, and January 1999). We collected from the different points at each time. Standing litter was oven-dried at 70°C for 3 days and weighted for each fraction, i.e. branches ≤ 2 cm girth, leaf and other fractions ≥ 1 cm². We

calculated arithmetic mean of five (six) collections to represent a mean standing litter crop at each plot. Decay constant (k) was approximated as mean annual litterfall from July 1997 to June 1999 divided by mean standing litter crop.

Data analysis

Variables of soil nutrients and LAI_{opt} were compared among the six study plots by one way ANOVA and multiple comparison among the plots were done by LSD test after the ANOVA. Mean annual litterfall and percentage of leaf litter in litterfall for 20 (10) litter traps was compared among the six plots in each year (from July 1997 to June 1998 and from July 1998 to June 1999) and the mean of 2 years by the LSD test after one way ANOVA. To detect the effect of El Niño drought on litterfall, mean annual litterfall in the year from July 1997 to 1998 including El Niño drought was compared with that in the year after the El Niño drought for each plot by one way ANOVA using within-subject design. Differences in mean leaf area and LMA between plots were tested by sequential Bonferroni test after Mann-Whitney's U test. Correlation among LAI_{opt} , ANPP, decay constant, and the content of soluble-P in topsoil was examined by Pearson correlation coefficient and the significance of correlation was tested by sequential Bonferroni test.

Results

Forest structure

Stature and AGB in 1997 decreased upslope from lower-slope to ridge on all substrates (Table 2). On the lower-slopes, stature and AGB decreased from Quaternary sedimentary >Tertiary sedimentary >ultrabasic rock in association with soil nutrients, especially with the contents of soluble-P and NO₃-N (Table 1). However, stature and AGB on the ridges did not follow the same order. Stature and AGB on the ridges of the Quaternary sedimentary and ultrabasic rock converged to a narrow range, in accordance that soil nutrient pool also converged. The stature and AGB of the Tertiary sedimentary rock, however, demonstrated a greater value. The magnitude of the reduction in stature and AGB from lower-

Table 2 Forest structural attributes at six plots. Maximum tree height, Above-ground biomass (AGB), mean individual leaf area and LMA, and optically measured LAI (LAI_{opt}) and estimated LAI (LAI_{est}) based on stand-level leaf biomass and mean LMA are shown in this table. SD is in parenthesis. Differences in mean leaf

area and LMA between plots were tested by sequential Bonferroni test after Mann-Whitney's U test and those in LAI_{opt} were tested by LSD test after one way ANOVA. In leaf area, LMA, and LAI, plots not sharing the same letters differ significantly at $P < 0.05$

Site	Max. tree height (m)	AGB (kg/m ²)	Leaf biomass (kg/m ²)	Leaf area (cm ²)	LMA (g / m ²)	LAI_{opt}	LAI_{est}
Quaternary sedimentary rock							
Ridge	13.0	16.18	0.44	18.7 (14.7) a	203.6 (45.8) a	1.75 (0.22) a	2.05
Lower-slope	32.1	35.47	0.57	40.1 (31.4) b	130.4 (49.6) b	4.76 (0.78) d	4.45
Tertiary sedimentary rock							
Ridge	16.5	26.45	0.60	22.5 (19.9) a	174.4 (65.9) c	3.46 (0.30) c	3.44
Lower-slope	30.0	30.86	0.52	44.7 (43.0) b	134.7 (48.0) b	3.84 (0.23) c	3.94
Ultrabasic rock							
Ridge	12.5	10.23	0.33	15.7 (29.3) ab	247.9 (44.9) d	2.89 (0.26) b	1.35
Lower-slope	22.6	24.57	0.57	39.3 (56.2) b	214.7 (53.4) ad	3.65 () ^a	2.65

^a There are no replicates

slope to ridge decreased from Quaternary sedimentary >ultrabasic >Tertiary sedimentary rock.

LAI showed the similar trends as seen in stature and AGB (Table 2). Optically measured LAI_{opt} and estimated LAI_{est} showed similar values on the two sedimentary rocks. However, LAI_{opt} was greater than LAI_{est} at the two plots on the ultrabasic rock. In both types of LAI, LAI decreased upslope on all substrates. On the lower-slopes, LAI decreased with decreasing pool size of soil nutrients along the geological gradient (Quaternary sedimentary >Tertiary sedimentary >ultrabasic rock). On the ridges, LAI on the Tertiary sedimentary rock was greater than the other two ridges. The topographical change in LAI was explained by LMA and leaf area of individual leaves combined with stand-level leaf biomass. Mean LMA increased and mean individual leaf area decreased upslope on all substrates. Mean LMA was greater on the ultrabasic rock than on the two sedimentary rocks at a comparable topographical unit, while mean leaf area showed the reverse pattern. Stand-level leaf biomass decreased upslope on all substrates but the Tertiary sedimentary rock.

Productivity

Mean ANPP for 2 years (1997–1999) changed with topography and geological substrates consistently with forest structure (Table 3), and ANPP significantly correlated with LAI among the six plots ($r=0.87$, $P<0.05$,

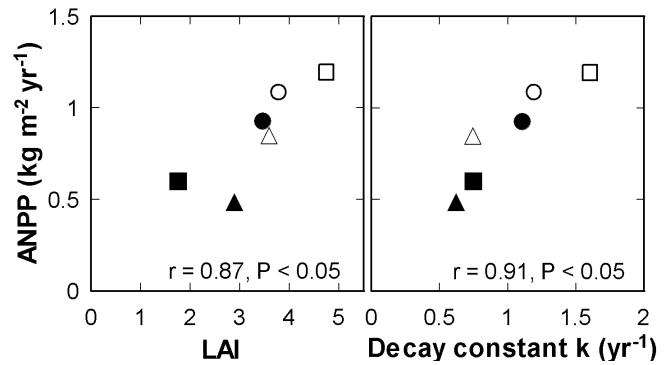


Fig. 1 Relationships between LAI and ANPP, and decomposition rate and ANPP among the six plots. *Square* The Quaternary sedimentary rock; *circle* the Tertiary sedimentary rock; *triangle* the ultrabasic rock. *Open and filled symbols* show lower-slope and ridge plots, respectively. Pearson correlation coefficient r and significance level by sequential Bonferroni test after ANOVA are shown in each relationship

Fig. 1). When ANPP was divided into two components, i.e. wood increment and litterfall, differences in litterfall between the ridges and the lower-slopes were small, but wood increments on the ridges were 2–4 times lower than those on the lower-slopes on all three substrates. Consequently, litterfall per wood increment ratio was greater on the ridges than the lower-slopes. Percentage of leaf litter in total litterfall was also greater on the ridges than the lower-slopes. Accordingly, trees on the ridges allocated more assimilated products to produce leaves rather than

Table 3 Above-ground net primary productivity (ANPP) by component (wood increment and litterfall with percentage of leaf litter) and ratio of litterfall to wood increment (Litter/ Δ Wood) at six study plots. Values for the year from 1997 to 1998 include the El Niño drought, and for the year from 1998 to 1999 the year after El Niño drought; means of 2 years from 1997 to 1999 are separately shown. In litterfall and percentage of leaf litter, SD among 20 (10) litter traps is shown in parentheses. Within each year and means of

2 years, mean annual litterfall and percentage of leaf litter were compared by LSD test after one way ANOVA, and plots not sharing the same letters differ significantly at $P<0.05$. Mean annual litterfall in the year from July 1997 to 1998 including El Niño drought was compared with that in the year after the drought for each plot by ANOVA using within-subject design. * indicates plots with significant difference in litterfall between the 2 years

	Quaternary sedimentary		Tertiary sedimentary		Ultrabasic	
	Ridge	Lower-slope	Ridge	Lower-slope	Ridge	Lower-slope
From 1997 to 1998 including El Niño drought						
Δ Wood (kg/m ² /year)	0.05		0.09	0.23	0.07	0.23
Litterfall (kg/m ² /year)	0.64 (0.17) ab*	0.96 (0.18) c	0.85 (0.23) c*	0.86 (0.22) c*	0.50 (0.14) a*	0.70 (0.15) b*
Leaf litter in litterfall (%)	81.6 (4.9) ab	72.7 (5.5) c	76.6 (9.9) bc	74.0 (7.7) c	83.9 (5.3) a	73.0 (7.8) c
Litterfall / Δ Wood	13.4		9.1	3.7	7.4	3.1
ANPP (kg/m ² /year)	0.69		0.96	1.09	0.57	0.93
From 1998 to 1999 after El Niño drought						
Δ Wood (kg/m ² /year)	0.14		0.30	0.34	0.09	0.17
Litterfall (kg/m ² /year)	0.45 (0.17) a	0.91 (0.30) d	0.71 (0.16) bc	0.77 (0.18) c	0.34 (0.03) a	0.61 (0.09) b
Leaf litter in litterfall (%)	58.2 (9.8) a	50.5 (11.4) b	53.1 (7.4) ab	54.7 (9.7) ab	57.1 (4.9) ab	51.7 (5.2) b
Litterfall / Δ Wood	3.2		2.4	2.3	3.8	3.6
ANPP (kg/m ² /year)	0.59		1.01	1.11	0.43	0.78
Mean of two years from 1997 to 1999						
Δ Wood (kg/m ² /year)	0.06	0.26	0.14	0.27	0.07	0.19
Litterfall (kg/m ² /yr)	0.54 (0.15) ab	0.93 (0.20) d	0.79 (0.18) c	0.81 (0.17) c	0.42 (0.08) a	0.66 (0.10) b
Leaf litter in litterfall (%)	71.9 (6.5) a	61.7 (8.3) b	66.0 (7.8) b	64.5 (7.7) b	72.8 (5.7) a	62.8 (5.1) b
Litterfall / Δ Wood	9.6	3.6	5.5	3.0	6.4	3.4
ANPP (kg/m ² /year)	0.60	1.19	0.93	1.08	0.49	0.85

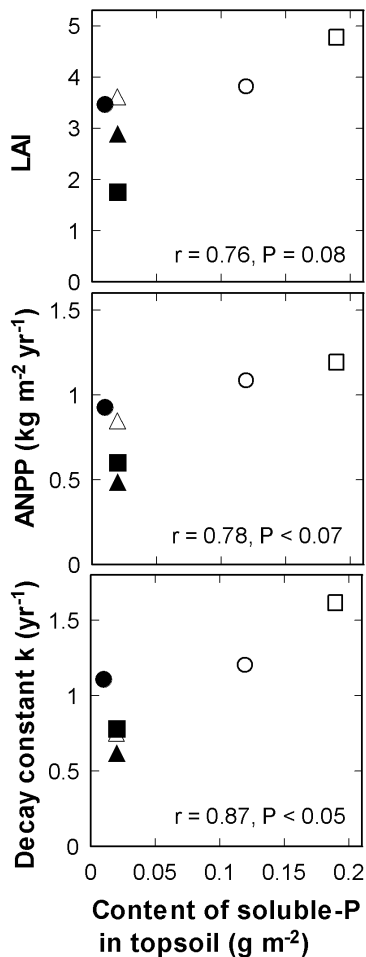


Fig. 2 Effect of available P in topsoils on LAI, ANPP, and decomposition rate for the six plots. Symbols are the same as in Fig. 1. Pearson correlation coefficient r and significance level by sequential Bonferroni test after ANOVA are shown in each relationship

stems. These patterns were consistent irrespective of drought. However, the El Niño drought increased litterfall and percentage of leaf litter in total litterfall, and decreased wood increment and ANPP (except for the ridge of the Quaternary sedimentary rock). These effects were much greater on the ridges than on the lower-slopes. Especially on the ridges of the Quaternary sedimentary and the ultrabasic rock, litterfall in the year including the drought period was 1.5 times greater than that after the drought.

Decomposition rate

Decay constant k also demonstrated similar patterns as forest structure and productivity (Fig. 1), and it significantly correlated with AGB ($r=0.90$, $P<0.05$) and ANPP ($r=0.91$, $P<0.05$, Fig. 1). Sites with greater biomass and productivity had greater decomposition rates.

Discussion

The magnitude of the reduction in forest structure (stature, AGB, and LAI) and functional attributes (ANPP and decomposition) from slopes to ridges along topography varied among the geological substrates. Geological substrate is a source of sedimentary-type minerals and thus the initial condition of ecosystem development reflects geological substrate. It is known that available P decreases with time due to leaching and geochemical immobilization (Walker and Syers 1976; Crew et al. 1995). Ultrabasic rock is generally poor in primary-mineral P (Proctor 1971). In our case, the content of soluble-P in topsoils decreased from Quaternary sedimentary > Tertiary sedimentary > ultrabasic rock on the lower-slopes where soils most developed. But the content of soluble-P in topsoils converged to a narrow range among the three geological substrates on the ridges. The magnitude of topographical change in pool size of available P was greater on the P richer substrate. Odeh et al. (1991) suggested a slower weathering rate of bedrock on ridges than on lower-slopes as a consequence of a less optimal moisture condition on ridges. The catena model suggests that redistribution of soil particles by runoff water results in upslope decrease in silt, clay, organic matter, and nutrients (Schimel et al. 1985; Burke et al. 1995; Hook and Burke 2000). Possibly, the slower weathering rate of bedrock and redistribution of soil particles may mask the effects of geology (bedrock) on soil nutrient pools on the ridges. Since stature, AGB, and LAI became greater with increasing content of soluble-P (Fig. 2), the magnitude of topographical changes in these forest structural attributes was greater on P richer substrate. ANPP showed a consistent pattern as the structural attributes (Fig. 2), since ANPP was determined by LAI as explained below (Fig. 1). Decomposition rate also showed a consistent pattern as the structural attributes and productivity, and it became greater with increasing content of soluble-P (Fig. 2). On the lower-slopes of P richer substrates, both litterfall and litter decomposition were relatively faster. Faster fluxes (i.e. litterfall and decomposition) combined with greater pool of soluble-P and inorganic-N suggest that the competition for these nutrients between plants and soil microbes is more moderate on the lower-slopes of P richer substrates. Accordingly, our present results suggest that differentiation of forest ecosystem (vegetation and soil system) along topography is strongly influenced by the initial condition determined by geological substrates, and the magnitude of topographical changes in forest structure and functions was greater on nutrient rich substrate than on poor substrate in the tropical lower montane forest on Mt. Kinabalu.

It is known that not only soil nutrients but also microclimatic conditions limit productivity and decomposition on ridges, i.e. dry conditions (Katagiri and Tsutsumi 1974; Fogel and Cromack 1977; Butler et al. 1986; Ishizuka et al. 1998; Yanagisawa and Fujita 1999; Enoki and Kawaguchi 2000) and strong winds (Lawton 1982; Bellingham 1991; Jones 1992). Severe microclimatic conditions

may also hide the effects of geological substrates (difference in initial condition) on the development of vegetation on the ridges.

Variance in ANPP was primarily explained by LAI for the six plots. Although trees on the ridges allocated more assimilated products to leaves rather than stems, LAI on the ridges was lower than that on the lower-slopes. The lower LAI on the ridges was brought about by the greater LMA, which is associated with the smaller area of individual leaves, combined with the lower stand-level leaf biomass. It is well-known that trees with small and thick leaves dominate at stressful habitats (Ohsawa and Ozaki 1992). Small and thick leaves are thought of as an adaptation to water stress (Jones 1992) or to nutrient shortage (Buckley et al. 1980; Medina et al. 1990), because their small surface areas can decrease transpiration and/or nutrient leaching. When we defined net assimilation rate (NAR) as ANPP divided by LAI assuming similar allocation of above- and below-ground parts, there were no distinct differences in NAR among the six plots. Nutrient (N and P) concentration in leaf litter on a weight basis was lower on the ridges than the lower-slopes on each substrate (Takyu and Kitayama, unpublished data). But, the nutrient content of intact leaves on an area basis was similar between topographical units, when we estimated it from nutrient concentration of leaf litter multiplied by mean LMA of intact leaves because we had no data for nutrient concentration in intact leaves. For example, content of N was 1.29 g m^{-2} on the ridge and 1.27 g m^{-2} on the lower-slope of the Quaternary sedimentary rock, 1.33 g m^{-2} on the ridge and 0.92 g m^{-2} on the lower-slope of the Tertiary sedimentary rock, and 1.37 g m^{-2} on the ridge and 1.29 g m^{-2} on the lower-slope of the ultrabasic rock. Nutrient concentration in intact leaves may be different from that in leaf litter, because plants withdraw nutrients before abscising leaves. However, if we take the effects of withdrawal into consideration, the pattern of greater foliar nutrients (area basis) will be reinforced, because the amount of withdrawal is generally greater on ridges (Enoki and Kawaguchi 1999). Accordingly, small and thick leaves contributed to increase nutrient content of leaves on an area basis and to maintain NAR, but it reduced LAI. The changes in LAI due to the changes in leaf morphology primarily explained ANPP along topographical gradients. Small and thick leaves might also result in the low decomposition rate on the ridges. Leaf toughness due to the high LMA and the low nutrient concentration of litter on a weight basis may lower decomposition (Gillon et al. 1994). Our study demonstrated that topography and geological substrates interactively affected forest structure and processes. The effect of topography on forest structure and processes was greater on nutrient rich substrates than on poor substrates, and the effect of geological substrates was greater on lower-slopes than on ridges.

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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
- Bellingham PJ (1991) Landforms influence patterns of hurricane damage: evidence from Jamaican montane forests. *Biotropica* 23:427–433
- Buckley RC, Corlett RT, Grubb PJ (1980) Are the xeromorphic trees of tropical upper montane rain forests drought-resistant? *Biotropica* 12:124–136
- Burke IC, Elliott ET, Cole CV (1995) Influence of microclimate, landscape position, and management on soil organic matter in agroecosystems. *Ecol Appl* 5:124–131
- Butler J, Goetz H, Richardson JL (1986) Vegetation and soil Landscape relationships in the North Dakota Badlands. *Am Midl Nat* 116:378–386
- Crew TE, Kitayama K, Fownes JH, Riley RH, Herbert DA, Mueller-Dombois D, Vitousek PM (1995) Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* 76:1407–1424
- Enoki T, Kawaguchi H (1999) Nitrogen resorption from needles of *Pinus thunbergii* Parl. growing along a topographic gradient of soil nutrient availability. *Ecol Res* 15:425–434
- Enoki T, Kawaguchi H (2000) Initial nitrogen content and topographic moisture effects on the decomposition of pine needles. *Ecol Res* 15:425–434
- Fogel R, Cromack K Jr (1977) Effect of habitat and substrate quality on Douglas fir litter decomposition in western Oregon. *Can J Bot* 55:1632–1640
- Gillon D, Joffre R, Ibrahima A (1994) Initial litter properties and decay rate: a microcosm experiment on Mediterranean species. *Can J Bot* 72:946–954
- Hook PB, Burke IC (2000) Biogeochemistry in a shortgrass landscape: control by topography, soil texture, and microclimate. *Ecology* 81:2686–2703
- Ishizuka S, Tanaka S, Sakurai K, Hirai H, Hirotsu H, Ogino K, Lee HS, Kendawang JJ (1998) Characterization and distribution of soils at Lambir Hills National Park in Sarawak, Malaysia, with special reference to soil hardness and soil texture. *Tropics* 8:31–44
- Jacobson G (1978) The geology. In: Kinabalu, summit of Borneo. The Sabah Society, Kota Kinabalu, pp 101–110
- Jenny H (1980) The soil resource. Springer, Berlin Heidelberg New York
- Jones HG (1992) Plants and microclimate: a quantitative approach to environmental plant physiology. Cambridge University Press, Cambridge
- Katagiri S, Tsutsumi T (1974) The relation between site condition and circulation of nutrients in forest ecosystem. II. Moisture index as a means of evaluation of site condition (in Japanese with English summary). *J Jpn For Soc* 56:434–440
- Kitayama K, Aiba S (2002) Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil P pools on Mount Kinabalu, Borneo. *J Ecol* 90:37–51
- Kitayama K, Schuur EAG, Drake DR, Mueller-Dombois D (1997) Fate of a wet montane forest during soil ageing in Hawaii. *J Ecol* 85:669–679

- Kitayama K, Aiba S, Majalap-Lee N, Ohsawa M (1998) Soil N mineralization rates of rain forests in a matrix of elevations and geological substrates on Mount Kinabalu, Borneo. *Ecol Res* 13:301–312
- Kitayama K, Lakim M, Wahab MZ (1999) Climate profile of Mount Kinabalu during late 1995–early 1998 with special reference to the 1998 drought. *Sabah Parks Nature J* 2:85–100
- Lawton RO (1982) Wind stress and elfin stature in a montane rain forest tree: an adaptive explanation. *Am J Bot* 69:1224–1230
- Medina E, Garcia V, Cuevas E (1990) Sclerophylly and oligotrophic environments: Relationships between leaf structure, mineral nutrient content, and drought resistance in tropical rain forests of the Upper Río Negro Region. *Biotropica* 22:51–64
- Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. *Anal Chim Acta* 27:31–36
- Odeh IOA, Chittleborough DJ, McBratney AB (1991) Elucidation of soil-landform interrelationships by canonical ordination analysis. *Geoderma* 49:1–32
- Ogawa H, Kira T (1977) Methods of estimating forest biomass. In: Shidei T, Kira T (eds) *Primary productivity of Japanese forests*. JIBP Synthesis 16. University of Tokyo Press, Tokyo, pp 15–25
- Ohsawa M, Ozaki K (1992) Hierarchical analysis of vegetation / environment pattern for east Asian extra-tropical evergreen broad-leaved forests (in Japanese with English summary). *Jpn J Biometeorol* 29:93–103
- Proctor J (1971) The plant ecology of serpentine. II. Plant response to serpentine soils. *J Ecol* 59:397–410
- Raich JW, Russel AE, Vitousek PM (1997) Primary productivity and ecosystem development along an elevational gradient on Mauna Loa, Hawai'i. *Ecology* 78:707–721
- Rowell DL (1994) *Soil science: methods and applications*. Longman, UK
- Schmel DS, Stillwell MA, Woodmansee RG (1985) Biogeochemistry of C, N, and P in a soil catena of the shortgrass steppe. *Ecology* 66:276–282
- 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
- Tanner EVJ (1980a) Studies on the biomass and productivity in a series of montane rain forests in Jamaica. *J Ecol* 68:573–588
- Tanner EVJ (1980b) Litterfall in montane rain forests of Jamaica and its relation to climate. *J Ecol* 68:833–848
- Tanner EVJ (1981) The decomposition of leaf litter in Jamaican montane rain forests. *J Ecol* 69:263–275
- Walker TW, Syers JK (1976) The fate of phosphorus during pedogenesis. *Geoderma* 15:1–19
- Weaver PL, Murphy PG (1990) Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* 22:69–82
- Yamakura T, Hagiwara A, Sukardjo S, Ogawa H (1986) Above-ground biomass of tropical rain forest stands in Indonesian Borneo. *Vegetatio* 68:71–82
- Yanagisawa N, Fujita N (1999) Different distribution patterns of woody species on a slope in relation to vertical root distribution and dynamics of soil moisture profiles. *Ecol Res* 14:165–177