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Soil nutrients and size-dependent tree dynamics of tropical lowland forests on volcanic and sedimentary substrates in Sabah, Malaysian Borneo

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ABSTRACT Soil nutrient concentrations and tree dynamics were examined in two Bornean tropical forests on contrasting geological substrates, one on volcanic and the other on sedimentary rocks. Concentrations of P extracted by the Hadley fractionation method and inorganic N of topsoils were much greater in the volcanic site than in the sedimentary site. Dipterocarps showed greater relative growth rates in the volcanic site than in the sedimentary site at the smallest size class (10 cm ≤ diameter at breast height < 20 cm), but not at larger size classes. Dipterocarps in the two sites demonstrated the same values of crown position index (a surrogate of light conditions), implying that the greater tree growth in the volcanic site was associated with the greater soil nutrient availability, but not with light availability. On the other hand, relative growth rates of non-dipterocarps did not differ between the sites at all size classes despite the considerable differences in the soil nutrient concentrations, suggesting that factors other than N and P availabilities limit the growth of these trees. Contrary to growth rate, annual mortality rate was greater in the volcanic site at all size classes for all phylogenetic groups. Our results suggest that the volcanic site is characterized as high soil nutrient availability and a greater tree turnover, and that tree size is an important factor that differentiates tree growth between the two tropical forests with contrasting nutrient availabilities.

Key words: Phosphorus, Nitrogen, Growth, Mortality, Permanent plots

INTRODUCTION

Soil nutrient is an important factor that underlies the spatial variation in the dynamics and structure of tropical rain forests (Phillips et al. 1994, Kitayama and Aiba 2002, Stephenson and Mantgem 2005, Paoli et al. 2006, Slik et al. 2009, Condit et al. 2013). Soils derived from aged geological substrates in the tropics are highly weathered due to the hot and humid climate, and often contain very low concentrations of total phosphorus (P) (e.g. 49-340 μg g⁻¹ total P for topsoils in the Bornean rain forests; Proctor et al. 1983, Kitayama et al. 2004, Baltzer et al. 2005, Russo et al. 2012). The decrease in total P is associated with a reduction of plant-available P (Johnson et al. 2003), which is known to be the factor that frequently limits productivity and structure among tropical lowland forests (Elser et al. 2007, Vitousek et al. 2010). On the other hand, soils derived from young volcanic substrates can be rich in minerals (e.g. P) because of rich primary minerals contained in the parental rocks. For instance, young tropical soils derived from volcanic substrates showed extremely high concentrations of P in Hawaii and Costa Rica (over 1000 μg g⁻¹ total P) (Crews et

al. 1995, Johnson et al. 2003, Tully et al. 2013). This implies that the tree dynamics of the tropical forests on young volcanic substrates may considerably differ from that on highly weathered soils. However, few studies compared the dynamics of the tropical forests on young volcanic substrates with that on nutrient-impooverished weathered soils in S.E. Asia. We will merit from such a comparative study to elucidate the effects of soil fertility on the forest dynamics.

Although it is known that fertile tropical forests show a greater tree turnover (greater growth and mortality rates) than infertile forests (Phillips et al. 1994, Aiba et al. 2005, Stephenson and Mantgem 2005, Russo et al. 2005), few studies have investigated how soil nutrient availability influences tree dynamics in relation to tree size. Previous studies have demonstrated that growth rates of tropical trees change with trunk diameter (Héroult et al. 2011, Rüger et al. 2012). In addition, Ashton and Hall (1992) and Nilus (2004) compared tree growth rates among Bornean tropical forests with different soil nutrient concentrations, and found that trees at the smaller size class (e.g. diameter at breast height < 30 cm) increased growth rates with increasing soil nutrient concentrations whereas trees at a larger size class

did not. On the other hand, some previous studies reported that annual mortality rate did not change with tree size for trees with ≥ 10 cm in trunk diameter at breast height among tropical forests (Lieberman and Lieberman 1987, Swaine et al. 1987, Condit et al. 1993, Milton et al. 1994, Nilus 2004). Furthermore, Russo et al. (2005) compared tree mortality among tropical forests on the soils with different nutrient availabilities, and demonstrated that tree mortality was consistently lower in the site with the low nutrient availability at all size classes. These studies suggest that nutrient availability differently affects tree growth across tree size classes, and affects tree mortality irrespective of the size. However, it is still unknown if the same pattern is observed among tropical forests on various soil types.

In this study, we compared soil nutrient concentrations and the size-dependent tree dynamics between two forests; one on soils derived from young volcanic substrates in the Tawau Hills Park (volcanic site) and the other on infertile soils derived from sedimentary rocks in the Deramakot Forest Reserve (sedimentary site). We used tree inventory data of a 2-ha plot in each site. The dynamics of Dipterocarps and non-dipterocarps were analyzed separately because dipterocarp trees dominate the canopy layer in Bornean lowland forests with a wide range of soil nutrient availabilities and they may show different responses to changes of soil nutrient availability from the other tree species. Furthermore, because light is an important factor to affect the tree dynamics (Chazdon and Pearcy 1986, King 1994, Davis 2001, Graham et al. 2003), we also investigated the crown position index (CPI), which can be a surrogate of the light condition of individual trees (Aiba et al. 2004). Specifically, we asked the following three questions. (1) Are soils richer in minerals (especially for P) in the volcanic site than in the sedimentary site? (2) Are tree growth and mortality rates greater in the volcanic site than in the sedimentary site? (3) How does tree size influence the tree dynamics in the volcanic and sedimentary sites?

MATERIALS AND METHODS

Study sites

This study was conducted in a 2-ha plot of the Tawau Hills Park ($4^{\circ} 24' N$, $117^{\circ} 53' E$), and the Deramakot Forest Reserve ($5^{\circ} 22' N$, $117^{\circ} 25' E$). Both sites are located in the northeast part of Sabah, Malaysian Borneo. The forests in the Tawau Hills Park lie on the andesitic volcanic ash derived from the past eruptions ca. 27000 years ago by Mt. Magdalena, Mt. Lucia, and Mt. Maria (Seino et al. 2007). On the

other hand, soils in the Deramakot Forest Reserve are derived from tertiary sedimentary rocks (Imai et al. 2010). The mean annual temperature and precipitation are $27^{\circ}C$ and 2200 mm for the Tawau Hills Park (Meteorological data provided by the Sabah government, http://www.sabah.gov.my/htan_caims/Level%201%20frame%20pgs/index_main_fr.htm), and $27^{\circ}C$ and 3500 mm for the Deramakot Forest Reserve (Kleine and Heuveldop 1993). The three most dominant species in Dipterocarpaceae (number of individuals with ≥ 10 cm in diameter at breast height in the 2-ha plots) are *Shorea johorensis* Foxw. (92), *S. macrophylla* (de Vr.) Ashton (37) and *Parashorea tomentella* (Symington) Meijer (15) in the volcanic site, and *S. multiflora* (Burck) Symington (91), *S. macroptera* (28) and *S. gibbosa* Brandis (23) in the sedimentary site. The three most dominant species of non-Dipterocarpaceae are *Xanthophyllum affine* Korth. Ex Miq. (66), *Mallotus caudatus* Merr. (55) and *Litsea caulocarpa* Merr. (32) in the volcanic site, and *Gluta wallichii* (Hook.f.) Ding Hou (104), *Lophopetalum glabrum* Ding Hou (28), and *Croton argyratus* Blume (19) in the sedimentary site. *S. johorensis* comprised 40 % of basal area in a 2-ha plot of the Tawau Hills Park, whereas *S. multiflora* comprised 7 % of basal area in the Deramakot Forest Reserve (Table 1). The tallest individual of *S. johorensis* in the plot of the Tawau Hills Park is 78.1 m in height and 163 cm in trunk diameter at breast height (DBH); this value is one of the highest records in Borneo (Seino et al. 2007). On the other hand, basal area (≥ 10 cm DBH) in the Tawau Hills Park and the Deramakot Forest Reserve is 27.3 and 34.7 $m^2 ha^{-1}$, which is comparable with other lowland forests in Sabah (e.g. Danum Valley, 26.6 $m^2 ha^{-1}$, Newbery et al. 1996; two plots in Kinabalu, 34.0 and 38.3 $m^2 ha^{-1}$, Aiba and Kitayama 1999).

Field survey

A 2-ha (100 m \times 200 m) vegetation plot was established in pristine forests without any evidence of logging disturbances in November 2001 for the Tawau Hills Park by Seino et al. (2007), and in September 2006 for the Deramakot Forest Reserve by Imai et al. (2010). Each plot was divided into contiguous two hundred 10 \times 10-m subplots. All living trees larger than 10 cm in DBH were measured, and their locations were mapped in the plots. Trees were re-censused in February 2013 for the Tawau Hills Park and in July 2014 for the Deramakot Forest Reserve (11.25- and 8-year interval, respectively). Voucher specimens were collected to identify species at the first census. To indirectly evaluate the light conditions of individual trees, we classified canopy

Table 1. Stand characteristics in the two study sites in the Tawau Hills Park (volcanic site) and the Deramakot Forest Reserve (sedimentary site). Basal area was calculated for trees with ≥ 10 cm DBH.

	Volcanic	Sedimentary
Basal area ($\text{m}^2 \text{ha}^{-1}$)	27.3	34.7
Max. DBH (cm)	163	129
Max. Height (m)	78.2	63.5
Dominant species	<i>Shorea johorensis</i>	<i>Shorea multiflora</i>
RBA of the dominant species (%)	40.6	9.7

conditions based on the crown position index (CPI) of Aiba et al. (2004) into three categories: lower understory trees whose crowns are below a forest canopy (index 1); lower canopy trees whose crowns are exposed vertically, and are partly shaded by the neighbor trees (index 2); upper-canopy trees whose crowns are almost fully exposed (index 3).

For studying soil nutrients, we established one 40 m transect in the center of the 2-ha plot in the Tawau Hills Park, and collected soil cores at three layers (0–5, 5–15, 15–30 cm depth beneath the litter layer) at 10-m intervals along the transect. Five soil cores collected at each layer were combined to one composite sample. The composite samples ($N=3$) were manually homogenized with stones and root removed, and immediately stored in a refrigerator at 4°C.

The soil nutrient concentrations of the Deramakot Forest Reserve were cited from Imai et al. (2010) for P and Imai (*unpublished data*) for inorganic N. The detail of the soil sampling method is described in Imai et al. (2010). In the 2-ha plot, they excavated three soil pits down to 1 m deep at each of the three topographic positions defined by the inclination: flat ridge (2.1–10°), and gentle (10°–30°) and steep slope (30°–43.7°). Three cores of soil samples (0–5 cm deep) were collected at each pit vertically with a core sampler (diameter 37 mm). Three samples per pit were combined to one composite sample (i.e. 3 composites \times 3 topographic positions = 9 composites in total). Soil samples below 5 cm (a horizon at 5–16 cm and a horizon at 16–41 cm in depth) were collected horizontally from the wall of the soil pit using the same core sampler. For each of soil samples at 5–16 cm and 16–41 cm depth, one sample was collected per pit. Soils from three pits per horizon were combined to one composite sample per topographic position (i.e. 1 composite \times 3 topographic positions = 3 composites in total for the soil sample at each depth).

Soil analysis

We analyzed the soil chemical properties using the

same methods as Imai et al. (2010). Soil pH was determined on slurry of 1:2 fresh soil to deionized water. To determine the concentration of inorganic N, 3 g (fresh weight) soil samples were extracted with 30 ml 1.5N KCl. The suspension was shaken for 0.5 h, equilibrated for 12 h, and filtered through Whatman No. 2 filter paper (Whatman International Maidstone, Kent, UK). Concentrations of $\text{NH}_4^+ - \text{N}$ and $\text{NO}_3^- - \text{N}$ were determined colorimetrically using a Furura Autoanalyzer (Alliance).

The concentrations of inorganic P (Pi) and organic P (Po) were sequentially extracted with 0.5 M NaHCO_3 (adjusted to pH 8.5 with NaOH), 0.1 M NaOH, 1.0 M HCl, concentrated hot HCl and concentrated H_2SO_4 (cf. Tiessen and Moir 1993, Kitayama et al. 2000). A subsample of 4 g (fresh weight) from each composite sample was used for the extraction. The bicarbonate-extractable P ($\text{CO}_3\text{-Pi}$ and $\text{CO}_3\text{-Po}$) is considered as the most labile fraction of P in this study. The hydroxide-extractable P is assumed to represent the iron and aluminum surface-bound inorganic P (OH-Pi) and the partially stabilized organic P in soil organic matter (OH-Po). The 1.0 M HCl-extractable P is assumed to be the Ca-associated primary mineral P (Ca-Pi). The hot-HCl extracted Pi and the residual P were summed and considered as the highly recalcitrant occluded Pi. Pi in the bicarbonate-, hydroxide- and hot-HCl extracts was determined after precipitating organic matter by acidifying subsample solutions to pH 1.5 with 0.9 M H_2SO_4 . The Pi concentrations in the solutions except for the fraction extracted by concentrated H_2SO_4 was determined colorimetrically on a spectrophotometer at 712 nm by the molybdate-ascorbic acid procedure of Murphy and Riley (1962). The total P in the bicarbonate-, hydroxide-, hot-HCl and concentrated- H_2SO_4 extracts was determined by the inductively coupled plasma emission spectrometry (ICPS-7510, Shimadzu, Kyoto). The concentration of organic P of each fraction (bicarbonate, hydroxide, and hot HCl) was determined as the total P minus Pi.

Data analysis

To compare the percentages of trees with shaded crown in the two study sites, the ratios of trees with each CPI (1-3) were calculated at different DBH classes (5-cm intervals, $10 \text{ cm} \leq \text{DBH} < 40 \text{ cm}$) for three phylogenetic groups (all species, dipterocarps and non-dipterocarps). We analyzed the differences in the ratio of trees with CPI = 1 (shaded crown) between the sites by performing the analysis of generalized linear models (GLMs) with a binomial error distribution. Full models were as follows:

$$\text{logit (the ratios of the trees with CPI = 1)} \sim \text{DBH} + \text{Site (Volcanic or Sedimentary)} + \text{DBH : Site} \quad (1)$$

Akaike's information criterion (AIC) was used to compare the models, and the models with the minimum AIC were considered as the best-fit models. Because the ratio of trees with CPI = 1 should decrease with increasing DBH, the coefficient of DBH must be negative (< 0). On the other hand, the negative (and positive) coefficient of Site (volcanic) indicates the lower (and higher) ratios of trees with shaded crowns in the volcanic site than in the sedimentary site. We did not include the trees with $\geq 40 \text{ cm}$ DBH in the analysis because most trees $\geq 40 \text{ cm}$ DBH had exposed crowns (CPI = 2 or 3).

Relative growth rates of stem diameters (RGR) were calculated for each tree in the 2-ha plots using the equation;

$$\text{RGR (cm cm}^{-1} \text{ year}^{-1}) = \frac{\ln(\text{DBH}_t) - \ln(\text{DBH}_0)}{t} \quad (2)$$

where DBH_t and DBH_0 are the DBH at the second and first census respectively, and t is the census interval (in years). Differences in RGR between the study sites were tested with Mann-Whitney U-statistics for three phylogenetic groups (all species, dipterocarps and non-dipterocarps) at three size classes ($10 \text{ cm} \leq \text{DBH} < 20 \text{ cm}$, $20 \text{ cm} \leq \text{DBH} < 40 \text{ cm}$, $40 \text{ cm} \leq \text{DBH}$). We divided the trees of each phylogenetic group into three size classes because these groups significantly differ in CPI (i.e. light condition), which may strongly affect the tree dynamics. In addition to the mean values of RGR, we compared the variation in RGR between the sites.

Mean annual mortality rate (m) was also estimated for the three phylogenetic groups (all species, dipterocarps and non-dipterocarps) at three size classes ($10 \text{ cm} \leq \text{DBH} < 20 \text{ cm}$, $20 \text{ cm} \leq \text{DBH} < 40 \text{ cm}$, $40 \text{ cm} \leq \text{DBH}$) using the equations provided in Sheil et al. (1995):

$$m = 1 - \left(\frac{N_t}{N_0} \right)^{\frac{1}{t}} \quad (3)$$

where N_0 is the number of trees at the first census, and N_t is the number of trees survived at the second census. To com-

pare annual mortality rates between the sites, the 95% confidence intervals of annual mortality rates were estimated using F ratios from a binomial distribution (as performed in Davis 2001). All statistics were performed by the R software, version 3.1.0 (R Core Team, 2014).

RESULTS

Soil conditions

Soil pH at 0-5 cm depth was 4.8 in the volcanic site (Tawau), and 3.4 in the sedimentary site (Deramakot) (Table 2, Imai et al. 2010). The soil N and P concentrations at 0-5 cm depth were consistently greater in the volcanic site than in the sedimentary site. The sum of labile P concentrations ($\text{HCO}_3\text{-Pi} + \text{OH-Pi}$) at 0-5 cm depth was about five-fold greater in the volcanic site ($46.9 \mu\text{g g}^{-1}$ in the volcanic site; $8.8 \mu\text{g g}^{-1}$ in the sedimentary site) (Table 2, Imai et al. 2010). The concentrations of Ca-Pi and Po at 0-5 cm depth were respectively about five-fold and three-fold greater in the volcanic site (10.4 and $158 \mu\text{g g}^{-1}$ in the volcanic site; 2.0 and $50.3 \mu\text{g g}^{-1}$ in the sedimentary site) (Table 2, Imai et al. 2010). In addition, the sum of inorganic N concentrations ($\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$) at 0-5 cm depth was about four-fold greater in the volcanic site ($143.4 \mu\text{g g}^{-1}$ in the volcanic site; $36.7 \mu\text{g g}^{-1}$ in the sedimentary site) (Table 2, Imai unpublished data). We found almost the same patterns for the deeper soils (i.e. greater nutrient concentrations in the volcanic site).

Forest structure and tree dynamics

The ratios of trees with CPI = 1 (shaded canopy) decreased with increasing DBH in each study site (Fig. 1). In the GLM analysis, only DBH was selected as an explanatory variable in all phylogenetic groups (Table 3), indicating that there is no difference in the ratios of trees with shaded crown between the two sites.

The tree density was lower in the volcanic site than in the sedimentary site at all size classes for all phylogenetic groups (Table 4). Frequency distribution of RGR for the two phylogenetic groups (all size included) demonstrated the unimodal distribution (Fig. 2). The range of RGR was similar in the two study sites for dipterocarps, whereas the mode of RGR was greater in the volcanic site (Fig. 2a). On the other hand, the range and mode of RGR were similar between the two study sites for non-dipterocarp trees (Fig. 2b); this suggests that the overall pattern of RGR distribu-

Table 2. Concentrations of P ($\text{CO}_3\text{-Pi}$, bicarbonate-extractable inorganic P; OH-Pi , hydroxide-extractable inorganic P; Ca-Pi , diluted HCl extractable Pi; Occl-Pi , occluded P; Po , organic P) and inorganic N in topsoils in the Tawau Hills Park (volcanic site) and the Deramakot Forest Reserve (sedimentary site). The references are as follows: Volcanic site, this study; Sedimentary site, Imai et al. (2010) and Imai (*unpublished data*). Soil pH was determined on a slurry of 1:2 fresh soil to deionized water. The concentrations of inorganic N of deeper soils (5–16 cm and 16–41 depth) in the Sedimentary site were not available (indicated as N.A.).

Site	Depth (cm)	pH (H_2O)	P ($\mu\text{g g}^{-1}$)						Inorganic N ($\mu\text{g g}^{-1}$)	
			$\text{HCO}_3\text{-Pi}$	OH-Pi	Ca-Pi	Occl-P	Po	Total P	$\text{NH}_4\text{-N}$	$\text{NO}_3\text{-N}$
Volcanic	0–5	4.8	5.2	41.7	10.4	297	158	512	73.6	69.8
	5–15	4.3	1.5	17.3	2.9	190	98	309	20	17.7
	15–30	4.6	0.6	17.9	2.3	173	60	254	13.7	5
Sedimentary	0–5	3.4	3.2	5.6	2	208	50.3	268	16.8	19.9
	5–16	3.7	2.8	5.2	1.4	234	18.9	262	N.A.	N.A.
	16–41	3.8	2.7	4.5	1.1	223	24.3	246	N.A.	N.A.

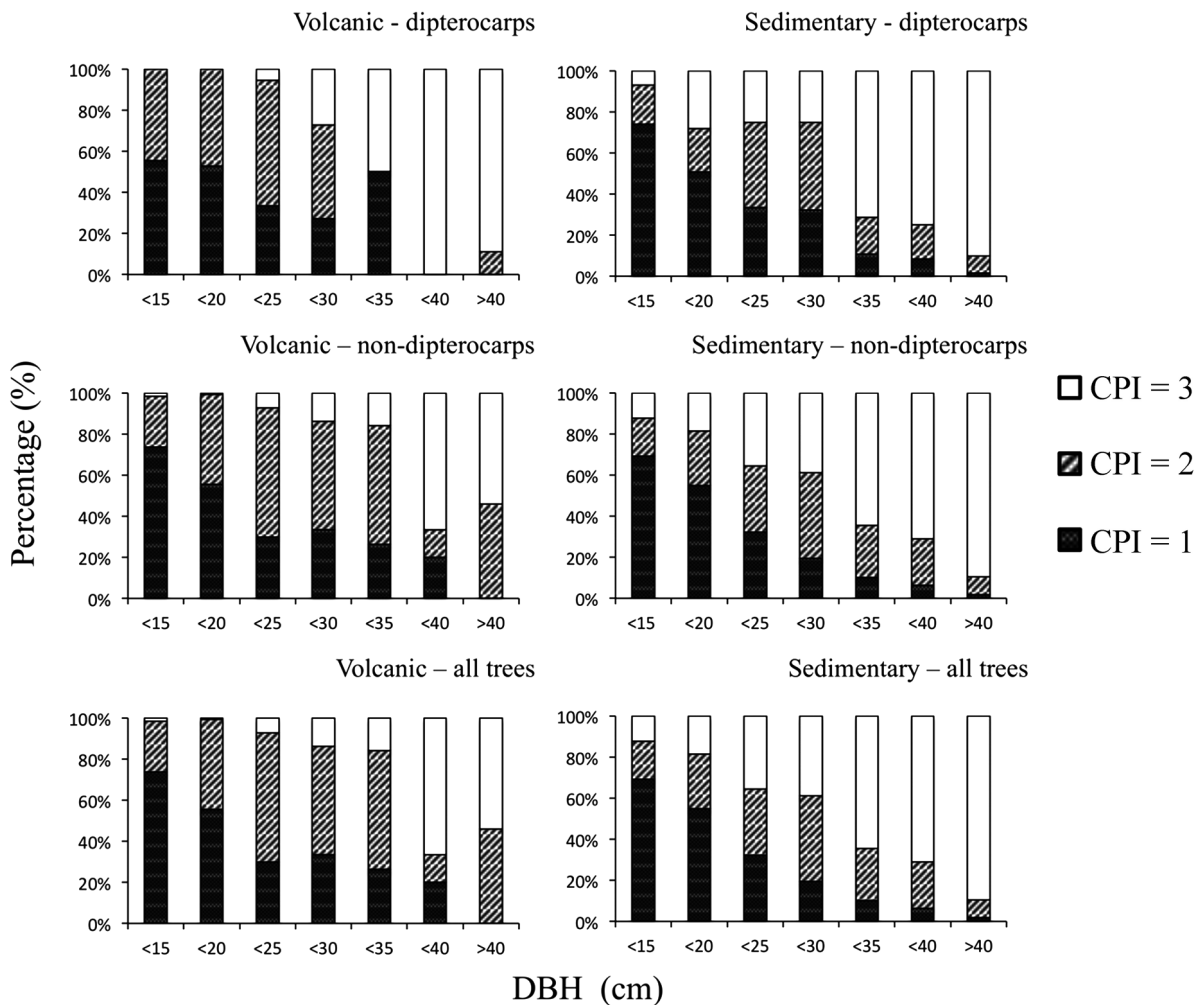


Fig. 1. The ratios of trees with each crown position index (CPI) at different DBH classes ($10 \text{ cm} \leq \text{DBH} < 40 \text{ cm}$, 5-cm intervals) for all species, dipterocarps and non-dipterocarps in the Tawau Hills Park (volcanic site) and the Deramakot Forest Reserve (sedimentary site). Each value of the CPI indicates as follows: 1, shaded in the understory; 2, partly exposed vertically; 3, completely exposed vertically.

tions is not different between substrate types against our expectation. Mean value of RGR of dipterocarps was significantly greater in the volcanic site than in the sedimentary

site at the smallest size class ($P < 0.005$, t-test, Table 5), whereas RGR of all species and non-dipterocarps did not differ at all size classes between the sites ($P > 0.05$, t-test,

Table 3. Results of the generalized linear model (GLM) analysis for the ratios of trees with CPI = 1 for all species, dipterocarps and non-dipterocarps in the Tawau Hills Park (volcanic site) and the Deramakot Forest Reserve (sedimentary site). Full model was as followed: $\text{logit}(\text{Percentage of trees with CPI} = 1) \sim \text{DBH} + \text{Site (volcanic and sedimentary)} + \text{DBH}:\text{Site}$. Akaike's information criterion (AIC) was used to compare the models, and the models with the minimum AIC were considered as the best-fit models. In all cases, the best-fit models include only DBH as an explanatory variable.

	Model AIC		Coefficients	
	Full	Min.	Intercepts	DBH
All species	2144	2140	2.46 (0.15)	-0.13 (0.01)
Dipterocarps	418	414	2.65 (0.33)	-0.14 (0.02)
Non-dipterocarps	1732	1730	2.42 (0.17)	-0.13 (0.01)

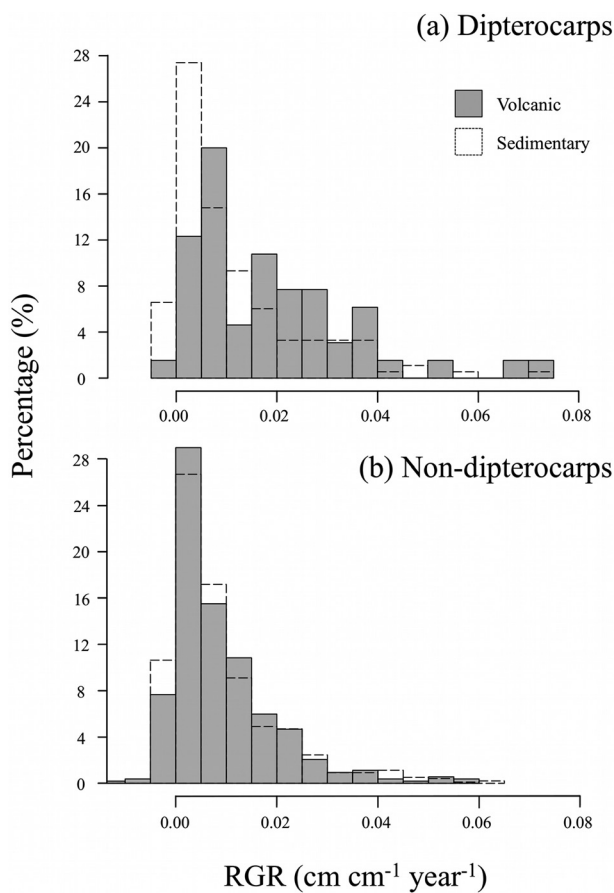


Fig. 2. The histograms of relative growth rates of trees with all size classes in the Tawau Hills Park (volcanic site) and the Deramakot Forest Reserve (sedimentary site) for dipterocarps (a) and non-dipterocarps (b). Shaded bars with solid lines indicate trees in the volcanic site, and open bars with dashed lines indicate trees in the sedimentary site.

Table 5). Mean annual mortality rate tended to be greater in the volcanic site than in the sedimentary site at all size classes for all phylogenetic groups (Table 6). Mean annual mortality rate varied with DBH class, but there are no consistent trends among the phylogenetic groups; annual mortality

Table 4. Tree density at the first census for all species, dipterocarps and non-dipterocarps at three size classes in the Tawau Hills Park (volcanic site) and the Deramakot Forest Reserve (sedimentary site).

Density (2 ha^{-1})	Volcanic	Sedimentary
All species		
10 cm \leq DBH < 20 cm	537	786
20 cm \leq DBH < 40 cm	169	306
40 cm \leq DBH	95	121
All classes	801	1213
Dipterocarps		
10 cm \leq DBH < 20 cm	91	174
20 cm \leq DBH < 40 cm	39	87
40 cm \leq DBH	59	76
All classes	189	337
Non-dipterocarps		
10 cm \leq DBH < 20 cm	446	612
20 cm \leq DBH < 40 cm	130	219
40 cm \leq DBH	36	45
All classes	612	876

rates of dipterocarps in both sites and non-dipterocarps in the sedimentary site tended to decrease with increasing trunk diameter, while those of non-dipterocarps in the volcanic site tended to increase (Table 6).

DISCUSSION

Plant-available P can be derived from the following three processes: solubilization of the labile Pi (P extracted by NaHCO_3 and NaOH), solubilization of primary minerals (i.e. Ca-Pi) and mineralization of Po (Cross and Schlesinger 1995, Johnson et al. 2003). The soils in the volcanic site contain greater concentrations of all above three fractions especially for the surface layer (0–5 cm in depth) (Table 2), in which the density of active fine roots was greatest

Table 5. Relative growth rates of stem diameters (RGR) for all species, dipterocarps and non-dipterocarps in the Tawau Hills Park (volcanic site) and the Deramakot Forest Reserve (sedimentary site). Differences between the study sites were tested with Mann–Whitney U-statistics. SE and P indicate the standard error and the degree of significance (*, $P < 0.005$; **, $P < 0.0005$), respectively.

	Volcanic RGR ($\text{cm cm}^{-1} \text{ year}^{-1}$)	SE	Sedimentary RGR ($\text{cm cm}^{-1} \text{ year}^{-1}$)	SE	P
All species					
10 cm \leq DBH < 20 cm	0.011	0.001	0.010	0.000	0.35
20 cm \leq DBH < 40 cm	0.011	0.001	0.012	0.001	0.50
40 cm \leq DBH	0.010	0.001	0.009	0.001	0.70
All classes	0.011	0.001	0.010	0.000	0.16
Dipterocarps					
10 cm \leq DBH < 20 cm	0.019	0.002	0.012	0.001	**
20 cm \leq DBH < 40 cm	0.016	0.003	0.012	0.001	0.09
40 cm \leq DBH	0.011	0.001	0.009	0.001	0.55
All classes	0.015	0.001	0.012	0.001	*
Non-dipterocarps					
10 cm \leq DBH < 20 cm	0.010	0.001	0.010	0.000	0.86
20 cm \leq DBH < 40 cm	0.009	0.001	0.010	0.000	0.87
40 cm \leq DBH	0.007	0.003	0.006	0.001	0.36
All classes	0.009	0.001	0.009	0.000	0.75

Table 6. Mean annual mortality rates (m) for all species, dipterocarps and non-dipterocarps in the Tawau Hills Park (volcanic site) and the Deramakot Forest Reserve (sedimentary site). CI and Sig. indicate the 95% confidence intervals of m and the degree of significance (*, the 95% confidence intervals of m in the two sites do not overlap), respectively.

	Volcanic m (% year $^{-1}$)	CI	Sedimentary m (% year $^{-1}$)	CI	Sig.
All species					
10 cm \leq DBH < 20 cm	3.1	3.6–2.7	1.8	2.1–1.5	*
20 cm \leq DBH < 40 cm	3.3	4.3–2.5	1.7	2.0–1.4	*
40 cm \leq DBH	2.3	3.5–1.5	0.9	1.8–0.4	
All classes	3.1	3.5–2.7	1.6	1.9–1.4	*
Dipterocarps					
10 cm \leq DBH < 20 cm	4.7	6.4–3.3	2.2	3.2–1.5	*
20 cm \leq DBH < 40 cm	2.0	4.0–0.9	1.9	2.5–1.4	
40 cm \leq DBH	1.1	2.3–0.5	0.7	1.9–0.2	
All classes	2.9	3.8–2.2	1.5	2.0–1.0	*
Non-dipterocarps					
10 cm \leq DBH < 20 cm	2.8	3.4–2.4	1.7	2.1–1.3	*
20 cm \leq DBH < 40 cm	3.7	4.9–2.7	1.6	2.0–1.4	*
40 cm \leq DBH	4.7	7.7–2.6	1.2	3.0–0.3	
All classes	3.1	3.6–2.7	1.7	2.0–1.4	*

(Matsushima *unpublished data* for the volcanic site; Imai et al. 2010 for the sedimentary site). This suggests that P availability to plants is much greater in the volcanic site than in the sedimentary site. The elevated P concentrations of the soils in the volcanic site are definitely related to the andesitic volcanic ash of ca. 27,000 years ago.

The soils in the volcanic site demonstrated also ex-

tremely higher concentrations of inorganic N ($\text{NH}_4 - \text{N}$ and $\text{NO}_3 - \text{N}$) than those in the sedimentary site (Table 2). Greater P availability in the volcanic site may link with greater inorganic N probably through greater microbial N mineralization and nitrification activities. Such co-variation of N and P availabilities was suggested by Elser et al. (2007). N and P are the essential elements for plants, and frequently

limit primary production of forest ecosystems (Elser et al. 2007, Harpole et al. 2011). Our results indicated that soils in the volcanic site showed greater availability of these elements than those in the sedimentary site. In the following, we discuss how the differences in soil-nutrient availabilities are associated with tree turnover.

We found that dipterocarps in the volcanic site demonstrated the greater RGR than those in the sedimentary site at the smallest size class (Table 4). Light conditions in the understory can co-vary with soil nutrient availability (Coomes and Grubb 2000; Russo et al. 2012), and therefore nutrient and light may be involved in the greater RGR of the volcanic site. We found that the ratio of trees with shaded crown (i.e. CPI = 1) was almost the same in both sites for dipterocarps under 40 cm DBH (Table 3, Fig. 1). Although CPI as a surrogate of relative light condition cannot actually elucidate the absolute light intensity of the understory layer in the volcanic site, our results strongly suggest that the greater RGR of small dipterocarps in the volcanic site can be associated with the greater nutrient availabilities. More robust light measurement needs to support our suggestion in the near future.

Interestingly, the difference in RGR of dipterocarps between the sites was not significant at the larger size classes (DBH \geq 20 cm) (Table 5). Fertilization experiments (Wright et al. 2011, Alvarez-Clare et al. 2013) and comparative studies using natural gradients of soil nutrient availability (Ashton and Hall 1992, Nilus 2004) also demonstrated the same pattern among tropical lowland forests; small-sized trees increased RGR with increasing soil nutrient concentrations whereas large-sized trees did not. These results suggest that RGR of small-sized trees responds to soil fertility more drastically than that of large-sized trees, (but see Russo et al. 2005), and that the growth of small-sized trees has an important role for determining the variation of tree growth rate among Bornean rain forests reflecting nutrient availability. The reason why RGR of small-sized trees shows a greater response to soil fertility is not known. Functional traits and environmental conditions of individual trees can vary in relation to tree size and soil nutrient availability, which might be essential for understanding the underlying mechanisms to explain the size-specific response of tree growth rates to soil nutrient availability.

On the other hand, RGR of non-dipterocarps did not differ between the sites at the smallest size class (and greater classes also) (Table 5, and Fig. 2) despite the considerable difference in soil N and P concentrations (Table 2). These results imply that the growth of non-dipterocarp trees in the understory is limited by light and that there is no interaction of light and nutrients for them.

Contrary to RGR, mean annual mortality rates tended to be greater in the volcanic site than in the sedimentary site at all size classes for all phylogenetic groups (all species, dipterocarps and non-dipterocarps) (Table 6). This supports the idea that soil characteristics influence tree mortality irrespective of the tree size among the tropical tree communities (Nilus 2004, Russo et al. 2005). Furthermore, in our results, annual mortality rates of dipterocarps in both sites and non-dipterocarps in the sedimentary site tended to decrease with increasing trunk diameter, while those of non-dipterocarps in the volcanic site tended to increase (Table 6). Previous studies reported that tree mortality did not change with trunk diameter for trees over 10 cm DBH among tropical forests (Lieberman and Lieberman 1987, Swaine et al. 1987, Condit et al. 1993, Milton et al. 1994, Nilus 2004, Russo et al. 2005). These results imply that the relationship between tree mortality and the size is unclear among tropical forests, and that it may change depending on phylogenetic groups.

Overall, the greater growth and mortality rates in the volcanic site than in the sedimentary site (Table 5 and 6) indicate a greater tree turnover in the volcanic site, which might be associated with the high soil N and P availabilities (Table 2). Furthermore, the greater growth rate of the volcanic site was size- and phylogeny-specific because only small-sized dipterocarps (10 cm \leq DBH < 20 cm) demonstrated a significantly greater growth rate. The structure and function of tropical rain forests are intimately related to the turnover of tree populations. Our study suggests that small-sized dipterocarps have an important role to control the overall population dynamics as a function of N and P availabilities; this may be one of the mechanisms that underlie the variation of the structure and function of lowland tropical rain forests with varying soil fertility. Our suggestion needs to be substantiated by a further study with an emphasis on the size- and phylogenetic specific tree dynamics.

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