

Soil nutrients affect spatial patterns of aboveground biomass and emergent tree density in southwestern Borneo

Gary D. Paoli · Lisa M. Curran · J. W. F. Slik

Received: 3 January 2007 / Accepted: 18 October 2007 / Published online: 24 November 2007
© Springer-Verlag 2007

Abstract Studies on the relationship between soil fertility and aboveground biomass in lowland tropical forests have yielded conflicting results, reporting positive, negative and no effect of soil nutrients on aboveground biomass. Here, we quantify the impact of soil variation on the stand structure of mature Bornean forest throughout a lowland watershed (8–196 m a.s.l.) with uniform climate and heterogeneous soils. Categorical and bivariate methods were used to quantify the effects of (1) parent material differing in nutrient content (alluvium > sedimentary > granite) and (2) 27 soil parameters on tree density, size distribution, basal area and aboveground biomass. Trees ≥ 10 cm (diameter at breast height, dbh) were enumerated in 30 (0.16 ha)

plots (sample area = 4.8 ha). Six soil samples (0–20 cm) per plot were analyzed for physiochemical properties. Aboveground biomass was estimated using allometric equations. Across all plots, stem density averaged 521 ± 13 stems ha^{-1} , basal area 39.6 ± 1.4 m^2 ha^{-1} and aboveground biomass 518 ± 28 Mg ha^{-1} (mean \pm SE). Adjusted forest-wide aboveground biomass to account for apparent overestimation of large tree density (based on 69 0.3-ha transects; sample area = 20.7 ha) was 430 ± 25 Mg ha^{-1} . Stand structure did not vary significantly among substrates, but it did show a clear trend toward larger stature on nutrient-rich alluvium, with a higher density and larger maximum size of emergent trees. Across all plots, surface soil phosphorus (P), potassium, magnesium and percentage sand content were significantly related to stem density and/or aboveground biomass ($R_{\text{Pearson}} = 0.368$ – 0.416). In multiple linear regression, extractable P and percentage sand combined explained 31% of the aboveground biomass variance. Regression analyses on size classes showed that the abundance of emergent trees >120 cm dbh was positively related to soil P and exchangeable bases, whereas trees 60–90 cm dbh were negatively related to these factors. Soil fertility thus had a significant effect on both total aboveground biomass and its distribution among size classes.

Communicated by Detlef Schulze.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-007-0906-9) contains supplementary material, which is available to authorized users.

G. D. Paoli (✉)
Department of Ecology and Evolutionary Biology,
University of Michigan, 830 N. University Ave,
Ann Arbor, MI 48109, USA
e-mail: gary.paoli@gmail.com; hancur_lagi@yahoo.com

G. D. Paoli
Indonesian Resource Institute, Bogor, West Java, Indonesia

L. M. Curran
Yale School of Forestry and Environmental Studies,
205 Prospect Street, New Haven, CT 06511, USA
e-mail: lisa.curran@yale.edu

J. W. F. Slik
Nationaal Herbarium Nederland, Leiden University Branch,
PO Box 9514, Einsteinweg 2, 2300 RA Leiden, The Netherlands
e-mail: slik@nhn.leidenuniv.nl

Keywords Carbon sequestration · Dipterocarpaceae · Land use change · Nutrient limitation · Phosphorus

Introduction

The effect of soil fertility gradients on aboveground biomass of lowland tropical forest is an important, but poorly understood component aboveground biomass of ecological

variation in the tropics. Structural differences among major forest types on contrasting soils have been documented throughout the tropics (Richards 1952; Whitmore 1984), with lower aboveground biomass and higher stem densities in oligotrophic ecosystems, such as heath (kerangas) or caatinga forest on bleached sands or in peat swamp forest on deep organosols (Anderson 1964; Brunig 1974; Klinge and Herrera 1983). At a regional scale, however, these ecosystems are restricted to the nutrient-poor extreme of soil conditions present in the tropics and are, therefore, less extensive than upland forests on well-drained mineral soils, which also vary markedly in nutrient content (Vitousek and Sanford 1986; Tuomisto et al. 1995; Sollins 1998). Soil effects on plant species distributions and diversity in these upland forests has been well studied (Baillie et al. 1987; Clark et al. 1999; Potts et al. 2002; Phillips et al. 2003; Paoli et al. 2006), but few studies have quantified soil influences on forest structure (e.g. Laurance et al. 1999).

From an ecological perspective, the effect of soil nutrients on aboveground biomass merits greater attention because it is not straightforward to predict how biomass should covary with soil fertility. On rich soils, relaxed nutrient limitations on growth could increase the density and/or maximum size of trees, thereby leading to higher biomass on fertile sites. However, because forests on rich soils are more dynamic (Russo et al. 2005) and because mortality rates could increase faster than growth rates on rich soils, higher soil nutrients could lead to lower biomass with faster rates of turnover on rich sites.

Available empirical data supports both hypotheses. Laurance et al. (1999) reported positive effects of total soil nitrogen (N), carbon (C) and exchangeable bases on aboveground biomass across an approx. 1000-km² study area in Amazonia, and in Peru, DeWalt and Chave (2004) found higher aboveground biomass in forest on nutrient-rich entisols than in forest on nutrient-poor oxisols. In contrast, van Schaik and Mirmanto (1985) reported lower biomass and faster turnover rates in forest on phosphorus (P)-rich soils across a chronosequence of volcanic terraces in northern Sumatra, and DeWalt and Chave (2004) reported similar findings in a regional comparison among four Neotropical sites on contrasting soils. These contradictory reports, combined with evidence of no relationship between soil nutrients and aboveground biomass at other sites (Ashton and Hall 1992; DeWalt and Chave 2004), has led some to conclude that soil nutrients probably affect forest structure only in extreme cases (Vitousek and Sanford 1986; Proctor 1995).

Understanding the potential effects of soil nutrients on aboveground biomass would assist in refining models to quantify the impact of land use change on C emissions, especially from the tropics (Achard et al. 2002; van der Werf et al. 2004). Spatial patterns of land use change, and

associated changes in C storage and emissions, are non-random with respect to topography, soil nutrients and infrastructure (Nepstad et al. 2004; Soares-Filho et al. 2006). On the island of Borneo, for example, relatively fertile sites at lower elevations are targeted for agricultural conversion by farmers and for the establishment of industrial forestry plantations (McMorrow and Talip 2001; Curran et al. 2004). Any attempt at reconstructing the effects of recent land use change on aboveground C stocks on Borneo and elsewhere thus requires an understanding of how terrestrial C stocks vary with soil nutrients prior to disturbance (Malhi et al. 2006). The derivation of models to predict aboveground biomass as a continuous function of soil parameters (e.g. Laurance et al. 1999) will facilitate this process.

The four aims of our study were to: (1) estimate aboveground biomass in a mature lowland rain forest in south-western Borneo; (2) quantify effects of soil variation on stand structure and aboveground biomass; (3) derive a predictive equation of aboveground biomass based on soil variables; (4) place these findings in the context of regional soil variation across Borneo.

Methods and materials

Study site

This study was conducted at the Cabang Panti Research Station (total area approx. 15 km²) in Gunung Palung National Park (GPNP; 90,000 ha), West Kalimantan, Indonesia (1°00′–1°20′S, 109°00′–110°25′E). Mean annual rainfall is 4125 ± 950 mm (mean ± SD 1985–2002). Although there are no months in a year that average <100 mm rainfall in this aseasonal forest, a marked inter-annual variation in dry season severity does occur, with a 2- to 3-month period of <100 mm rainfall corresponding to the onset of the El Niño Southern Oscillation (ENSO).

In the center of the park are two mountain peaks, Mt. Palung (1070 m) and Mt. Panti (1130 m), whose western slopes form the watershed of the study site. Most of the major Bornean lowland forest types occur within the study site, including peat swamp, freshwater swamp, heath forest and lowland dipterocarp forest on well-drained mineral soils up to approximately 300 m a.s.l. (Cannon and Leighton 2004). Diverse geological substrates underlie the lowland forests in the study area, with raised alluvium from 5 to 15 m a.s.l. along banks of the Air Putih River (approx. 100 ha); sedimentary rock from 40 to 140 m a.s.l., which also contain localized patches of quartzite, and granite rock beyond this point to the summit of both peaks. Soil texture is similar across substrates, but soil nutrients are highest in the alluvium substrate and lowest in the granite (Paoli et al.

2006). Aboveground productivity, nutrient use efficiency, leaf traits and species composition vary markedly among substrates (Cannon and Leighton 2004; Paoli et al. 2005, 2006; Paoli 2006; Paoli and Curran 2007). The alluvium, sedimentary and granite-derived soils present at GPNP are widespread throughout Kalimantan (Indonesian Borneo), representing >63% of the total land area <500 m a.s.l. (RePPPProT 1986/1987).

Plot establishment and tree measurement

We combined intensive soil sampling within plots with extensive sampling throughout the watershed (approx. 340 ha) to capture the diverse physiographic and soil conditions present. Thirty 0.16-ha plots (40 × 40 m) were established between an elevation of 8 and 198 m (total sample area = 4.8 ha). This plot size was chosen to control within-plot heterogeneity, so that plots could be treated as homogeneous edaphic units and to permit replicated sampling within substrates of the heterogeneity present at this scale. Ten plots were established on alluvium, eight on sedimentary rock and 12 on granite.

The location of 0.16-ha plots were centered on and encompassed smaller 30-m diameter circular plots used to monitor forest dynamics in a separate study (Paoli et al. 2005; Paoli and Curran 2007). These circular plots were positioned randomly 30–150 m from permanent trails, with a decision rule that plots contain <30% of total area in recent gap (canopy ≤5 m height). If the proposed site had >30% of plot area in recent gap, then the plot center point was moved up to 10 m in any direction, starting with due north and moving clockwise. If the decision rule could be met using this procedure, then the plot site was accepted; if not, it was rejected. A total of three were rejected outright (two in the alluvium and one in the granite), six plots were accepted after repositioning and the rest were established at the randomly determined point. Distances among the 30 plots ranged from 51–1932 m (median = 835 m).

Because plots avoided large gaps, our method overestimated the density of large trees and, consequently, forest-wide aboveground biomass (Clark and Clark 2000; Chave et al. 2003). We account for this potential bias statistically by adjusting our estimate of forest-wide aboveground biomass using a separate, unbiased estimate of large tree density derived from 67 transects (100 × 30 m; sample area = 20.7 ha) stratified randomly throughout the study area (data from Curran and Leighton 2000; see Results).

Tree inventory methods are described in detail in Paoli and Curran (2007). The diameters of all woody stems ≥10 cm diameter at breast height ($n = 2516$) were measured at 130 cm above ground or 10 cm above buttresses or other deformities when present, using a 6-m ladder.

Estimating aboveground biomass

Two different allometric equations were used to estimate aboveground biomass based on diameter. First, the moist forest equation of Brown (1997) was used, which estimates live aboveground biomass as a function of diameter [$Y = \exp(-2.134 + 2.53 \ln D)$]. The moist rather than wet forest equation of Brown (1997) was chosen based on climatic and other considerations described thoroughly in Paoli and Curran (2007). We refer to this equation as the ‘Brown equation’.

For comparison, we then estimated aboveground biomass using the moist forest equation of Chave et al. (2005). This equation (hereafter the ‘Chave equation’) was derived from a larger data set than that used by Brown (1997) and estimates aboveground biomass as a function of diameter and wood specific gravity $\{Y = \rho \times \exp(-1.499 + 2.148 \ln(D) + 0.207 [\ln(D)]^2 - 0.0281 [\ln(D)]^3)\}$, where ρ = wood density (g cm^{-3}). Because we identified species in our plots for the Dipterocarpaceae only (approx. 19% of total stems), it was necessary to estimate wood specific densities (hereafter ‘wood density’) for this equation. To do so, we first tested for potential differences in wood density among substrates because soil fertility and aboveground productivity differ among substrates and because these factors are inversely related to wood density at a regional scale in Amazonia (Baker et al. 2004; Malhi et al. 2006).

Two methods were used. First, we computed community-level averages of wood density for each substrate based on dipterocarp trees only, weighted by basal area of each individual ($n = 467$). Wood densities were collated from Oey (1990) and the Food and Agriculture Organization (FAO) world agroforestry website (<http://www.worldagroforestry.org/Sea/Products/AFDbases/wd/>). Where a range of values or where ‘low, medium, high’ values were reported, the midpoint or medium value was used, respectively. Where wood density was unavailable for a species ($n = 39$), the average across all species in that genus in the corresponding habitat was applied. Community-level averages of dipterocarp wood density varied little across alluvium, sedimentary and granite substrates, averaging 0.656, 0.656 and 0.676 g cm^{-3} , respectively. These values are very similar to the mean reported by Chave et al. (2006) across 2456 tree species across Amazonia (0.645 g cm^{-3}).

Second, we computed community-level averages for each substrate based on a separate data set from the study area (Cannon and Leighton 2004) in which all trees >15 cm diameter at breast height (dbh) were identified to species or genus. For each tree, we assigned a genus average for wood density using the dataset of Slik (2006), in which the average across all species in genera present in Kalimantan, and for which wood density data are available, was computed for hundreds of genera. Genus level averages are highly

correlated with species-level values (72% of species wood density variance was explained by genus) and can be used as a reliable proxy when species-level data are unavailable (Chave et al. 2006; Slik 2006). We applied generic averages, rather than species values, because >95% of individuals in the data set were identified to genus. When individuals were weighted by basal area, community-level averages were again very similar across substrates, but they were 8–11% higher than for dipterocarps alone, averaging 0.721, 0.719 and 0.715 g cm⁻³ in the alluvium, sedimentary and granite, respectively. This method further suggests that wood density did not vary systematically with substrate.

In the final aboveground biomass estimate using the Chave equation we applied: (1) species-specific values of wood density for dipterocarps; and (2) the substrate averages estimated from Cannon and Leighton (2004) for all non-dipterocarps. Estimated aboveground biomass is presented for both equations, but for analyses of the relationship between aboveground biomass and soil nutrients or substrate, we use data from the Brown equation only, as it requires no assumptions about wood density for unidentified trees at our site (Paoli and Curran 2007).

Soil sampling

In all plots, physiochemical attributes of surface soils (0–20 cm) were quantified as described in Paoli et al. (2006). Six samples per plot (each a composite of five cores) were collected using a stratified random design. Soils were air dried, lightly ground and sieved to remove coarse particles (≥ 2 mm), which were weighed. Mineral soil <2 mm was subsampled in the field (approx. 150 g) and transported to the University of Michigan (USA) for analysis.

Potential long-term nutrient supply was estimated as total nutrient content, but since this parameter overestimates short-term availability for most nutrients, assays were also performed for exchangeable cations and extractable P, all of which are more labile. Total nutrients were quantified for C, N, P, K, Ca, Mg, Mn, Na, Al, Ni, Fe and Zn. Total C and N concentrations were measured by gas chromatography on 40-mg samples of finely ground soil oxidized at 700°C in a C–H–N analyzer (model NC2500; CE Instruments, Milan, Italy). Concentrations of remaining elements were determined following the digestion of 500 mg of finely ground soil in sequential additions of concentrated hydrogen fluoride (HF), hydrochloric acid (HCl) and hydrogen peroxide (H₂O₂) (following Bowman 1990). Total P concentration was measured using the Orthophosphate Procedure on the Alpkem Rapid Flow Auto Analyzer (RFA 3550; OI Analytical, College Station, TX). All other elements were measured using inductively coupled plasma (ICP) atomic emission spectrometry (Optima 3000; Perkin Elmer, Shelton, CT).

Extractable P was assayed using the Olsen method (Olsen et al. 1954) on 3-g samples and quantified using ICP methods. Exchangeable cations were measured using one composite sample per plot by combining approximately 5 g of soil from the six replicate samples. Subsamples of 10 g were shaken for 1 h in 100 ml of 1 M NH₄Ac (no pH adjustment) and equilibrated for 12 h before filtering and leaching with five successive additions of 20 ml extractant. The filtrate was analyzed using ICP. Texture was quantified on approximately 50-g samples using the hydrometer method. The coarse fraction (>2 mm) of soil samples removed by sifting was weighed separately to determine percentage ‘coarse fraction’ by mass. Some of the soil data used in the following analysis were originally presented in Paoli et al. (2006) and Paoli and Curran (2007).

Data analysis

One-way ANOVA was used to test for differences among substrates in terms of stem density, maximum stem diameter, basal area and aboveground biomass using the Scheffe post-hoc test. MANOVA was used to test for differences in stem density, basal area and aboveground biomass for different size classes using the Scheffe post-hoc test. Three separate bivariate analyses were performed to test for relationships between forest structure and soil factors or elevation. First, relationships between soil parameters and stem density, basal area and aboveground biomass were tested using the Pearson correlation. Second, multiple linear regression (MLR) was used to produce a predictive equation of aboveground biomass based on soil; stepwise forward selection was used with thresholds of $P \leq 0.05$ for parameters to enter the model and $P > 0.1$ to be removed. Third, a more detailed analysis was performed to test whether soil effects on stem density, basal area or aboveground biomass varied with tree size. In this analysis, principle components analysis (PCA) was used to describe major axes of soil variation separately for labile nutrients, total nutrients and soil texture. Stem density, basal area and biomass of each size class were regressed separately on these multivariate indices. Regression was performed for all 30 plots combined and for the subset of 17 plots on sedimentary and granite slopes only – referred to as ‘hill forest’. This was done to test whether soil effects detected across all substrates were also present on less extreme gradients.

Results

Forest structure

Forest structure varied markedly among plots, with stem density varying by 1.5-fold (431–656 trees ha⁻¹), basal

area by more than twofold ($27.2\text{--}60.3\text{ m}^2\text{ ha}^{-1}$) and estimated aboveground biomass by more than threefold based on the Brown equation ($300\text{--}983\text{ Mg ha}^{-1}$) or the Chave equation ($380\text{--}1230\text{ Mg ha}^{-1}$). Average stem density was $521 \pm 13\text{ stems ha}^{-1}$, basal area $39.6 \pm 1.4\text{ m}^2\text{ ha}^{-1}$ and aboveground biomass $518 \pm 28\text{ Mg ha}^{-1}$ based on the Brown equation and $622 \pm 33\text{ Mg ha}^{-1}$ based on the Chave equation (Table 1). Forest structure did not vary significantly with substrate, but a trend toward larger stature was present, with lower stem densities, higher basal area and aboveground biomass and larger maximum diameter on the alluvium (Table 1). Pooling data across plots on the same substrate, tree diameter in the top 2.5 percentile was significantly larger in the alluvium ($115 \pm 3\text{ cm}$) and sedimentary ($112 \pm 5\text{ cm}$) than in the granite ($94 \pm 2\text{ cm}$; one-way ANOVA, $F_{2,57} = 15.433$, $P < 0.001$, Scheffe post-hoc test).

Using MANOVA to test for differences by size class, stem density, basal area and aboveground biomass did not vary significantly among substrates (Table 2). However, when the alluvium and granite extremes of the gradient were compared, the highest aboveground biomass of medium-sized trees (50–90 cm dbh) was found to occur on the granite, whereas that of trees >90 cm dbh was on the alluvium (Table 2). When trees were grouped into diameter classes of 30-cm intervals (Fig. 1), a greater percentage of total biomass was contained in trees 60–90 cm dbh than in trees >90 cm dbh in forests on sedimentary (33 vs. 24%) and granite substrates (33 vs. 22%), whereas the reverse occurred on alluvium (22 vs. 32%). The greatest structural difference between forests on nutrient-rich alluvium and nutrient-poor granite was a 12-fold higher aboveground biomass of emergent trees >120 cm dbh (hereafter ‘emergent trees’) on the alluvium (145 ± 50 vs. $12 \pm 12\text{ Mg ha}^{-1}$). This reflected the higher tree density (6 ± 2 vs. $1 \pm 1\text{ ha}^{-1}$) and larger size of emergent trees in the alluvium (Tables 1, 2).

Soil effects on forest structure

Only six of the 27 soil parameters quantified were significantly correlated with one or more aspect of forest structure

(Table 3). Stem density was negatively correlated with extractable P and exchangeable Ca, whereas aboveground biomass was positively correlated with extractable P and exchangeable K and negatively correlated with percentage sand (Table 2). The aboveground biomass of emergent trees was strongly, positively correlated with extractable P, total P, and exchangeable K. Stepwise MLR produced a simple, two-parameter model to predict total aboveground biomass based on percentage sand and extractable P content in kg P ha^{-1} ($r^2 = 0.291$, $P = 0.012$): aboveground biomass = $881.34 + 2.66 \times P_{\text{exch}} - 665.71 \times \% \text{ sand}$.

Major soil gradients were described by PCA (Table 4). For labile nutrients, three axes described 66% of the variance, with Axis 1 representing a gradient of increasing extractable P and major base cations (Table 4). For total nutrients, three axes combined described 70% of the variance, representing a gradient of increasing major cations along Axis 1, and of increasing total C, N and P along Axis 2 (Table 4). The PCA of soil texture (including percentage coarse material) retained two axes that described 79% of the variance, with Axis 1 representing a gradient of increasingly coarse texture and Axis 2 a gradient of increasing clay content (Table 4).

Relationships between forest structure and soil PCA axes were similar whether stem density, basal area or biomass was considered, so only biomass relationships are shown in Table 5 [stem density and basal area results are available online in Appendices 1 and 2, respectively, in the [Electronic Supplementary Material \(ESM\)](#)]. Analyses by size class showed that soil nutrients significantly affected the distribution of aboveground biomass among size classes, especially canopy and emergent trees. The aboveground biomass of emergent trees increased significantly with PCA axes describing gradients of increasing extractable P and exchangeable cations, whereas that of trees 60–70 and 80–90 cm dbh decreased along these axes (Table 5). Similar relationships were observed for PCA axes describing gradients of total cations (Table 5).

The positive effect of nutrients on emergent trees, but negative effect on canopy trees (60–90 cm) also held (albeit

Table 1 Structural characteristics of lowland tropical forest on contrasting substrates at Gunung Palung National Park, Indonesia

Habitat	Density (stems ha^{-1})	Basal area ($\text{m}^2\text{ ha}^{-1}$)	Aboveground biomass (Mg ha^{-1})		Mean tree diameter (cm)	Maximum tree diameter (cm)
			Brown (1997)	Chave et al. (2004)		
Alluvium	500 ± 22	41.4 ± 2.7	564 ± 58	660 ± 72	24.7 ± 0.6	116.4 ± 6.2
Sedimentary rock	503 ± 18	40.3 ± 3.2	534 ± 63	641 ± 68	24.6 ± 0.6	111.3 ± 9.9
Granite	550 ± 23	37.8 ± 2.0	470 ± 32	577 ± 36	23.4 ± 0.7	100.5 ± 4.5
Overall	521 ± 13	39.6 ± 1.4	518 ± 28	622 ± 33	24.1 ± 0.4	108.7 ± 3.9

Woody stems $\geq 10\text{ cm dbh}$ were enumerated in 30 (0.16 ha) plots throughout a forested watershed (approx. 340 ha; 8–195 m a.s.l.) underlain by alluvium ($n = 10$), sedimentary rock ($n = 8$) and granite ($n = 12$). Aboveground biomass was estimated based on allometry using the ‘moist forest’ equations of Brown (1997) and Chave et al. (2005), where the latter incorporate specific wood density (see [Methods and materials](#)). None of the parameters varied significantly among substrates. Data are mean among plots $\pm 1\text{ SE}$

Table 2 Size class distribution of stems (≥ 10 cm dbh), basal area and aboveground biomass in lowland tropical forest at Gunung Palung National Park, Indonesia

Habitat	Size class (diameter at breast height, in cm)											
	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	100–110	110–120	>120
Stem density												
Alluvium	306 ± 16 (61.3)	95 ± 10 (19.0)	38 ± 5 (7.5)	24 ± 5 (4.8)	13 ± 3 (2.6)	4 ± 1 (0.8)	6 ± 2 (1.3)	3 ± 1 (0.6)	7 ± 3 (1.4)	2 ± 1 (0.4)	3 ± 1 (0.5)	6 ± 2* (1.1) a
Sedimentary rock	307 ± 17 (61.4)	91 ± 4 (18.1)	38 ± 4 (7.7)	23 ± 8 (4.5)	13 ± 2 (2.5)	11 ± 3 (2.2)	7 ± 1 (1.4)	5 ± 1 (0.9)	6 ± 2 (1.3)	1 ± 1 (0.2)	2 ± 2 (0.5)	3 ± 1* (0.7) ab
Granite	344 ± 18 (69.0)	96 ± 7 (19.3)	38 ± 5 (7.6)	22 ± 3 (4.5)	17 ± 4 (3.4)	8 ± 3 (1.7)	8 ± 1 (1.6)	7 ± 2 (1.5)	4 ± 1 (0.8)	2 ± 1 (0.3)	2 ± 1 (0.4)	1 ± 1* (0.1) b
Basal area												
Alluvium	4.8 ± 0.2 (11.6)	4.4 ± 0.5 (10.7)	3.6 ± 0.4 (8.6)	3.7 ± 0.7 (8.9)	3.1 ± 0.6 (7.6)	1.3 ± 0.5 (3.1)	2.7 ± 0.8 (6.6)	1.7 ± 0.6 (4.1)	4.7 ± 1.8 (11.4)	1.6 ± 0.8 (3.8)	2.4 ± 1.0 (5.8)	7.3 ± 2.5* (17.7) a
Sedimentary rock	4.7 ± 0.3 (11.6)	4.3 ± 0.2 (10.7)	3.5 ± 0.4 (8.8)	3.6 ± 1.1 (8.9)	3.0 ± 0.6 (7.4)	3.7 ± 1.0 (9.3)	3.1 ± 0.6 (7.7)	2.6 ± 0.6 (6.3)	4.3 ± 1.7 (10.8)	0.6 ± 0.6 (1.5)	2.3 ± 1.6 (5.7)	4.6 ± 1.8* (11.3) ab
Granite	5.2 ± 0.2 (13.6)	4.3 ± 0.3 (11.3)	3.5 ± 0.5 (9.2)	3.4 ± 0.5 (9.1)	4.2 ± 0.9 (10.9)	2.9 ± 1.0 (7.6)	3.5 ± 0.6 (9.2)	4.0 ± 1.1 (10.7)	2.8 ± 0.8 (7.5)	1.3 ± 0.7 (3.5)	2.2 ± 1.2 (5.8)	0.6 ± 0.6* (1.7) b
Biomass												
Alluvium	30 ± 2 (5.3)	37 ± 4 (6.5)	36 ± 4 (6.3)	41 ± 8 (7.3)	40 ± 8 (7.0)	18 ± 6 (3.2)	40 ± 12 (7.2)	27 ± 9 (4.8)	78 ± 30 (13.9)	28 ± 14 (5.0)	44 ± 18 (7.8)	145 ± 50* (25.7) a
Sedimentary rock	29 ± 2 (5.5)	36 ± 1 (6.7)	35 ± 4 (6.5)	40 ± 13 (7.6)	38 ± 7 (7.0)	52 ± 14 (9.7)	46 ± 9 (8.6)	40 ± 9 (7.5)	72 ± 28 (13.6)	11 ± 11 (2.0)	42 ± 30 (7.9)	93 ± 37* (17.4) ab
Granite	32 ± 2 (6.8)	35 ± 3 (7.4)	34 ± 5 (7.3)	39 ± 6 (8.2)	52 ± 12 (11.1)	40 ± 14 (8.4)	52 ± 9 (11.0)	64 ± 18 (13.6)	47 ± 13 (10.0)	23 ± 12 (4.9)	41 ± 23 (8.6)	12 ± 12* (2.6) b

Data are mean ± 1 SE per hectare. The percentage of total stem density, basal area and biomass in each size class is given in parentheses. Values followed by different letters within a column indicate significant differences ($*P \leq 0.05$) between substrates for that parameter

Stems were enumerated in 30 (0.16 ha) plots throughout a lowland watershed (approx. 340 ha, 8–195 m a.s.l.) underlain by alluvium ($n = 10$), sedimentary rock ($n = 8$), and granite ($n = 12$). Density, basal area and biomass did not vary significantly among substrates when considered as a whole using MANOVA ($P > 0.05$), but differences among substrates were significant for large emergent trees >120 cm dbh when size classes were analyzed separately (ANOVA followed by Scheffé's test). Biomass was estimated using the moist forest equation of Brown (1997)

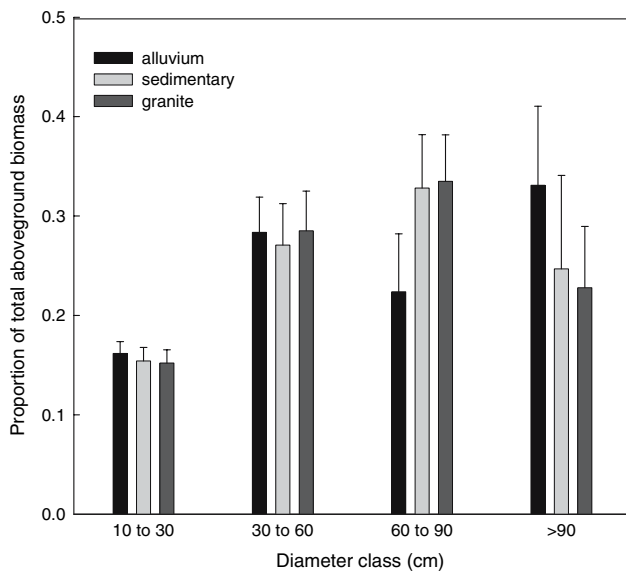


Fig. 1 Aboveground biomass of woody plants >10 cm diameter at breast height (dbh) by size class in mature lowland rain forest on three contrasting substrates at Gunung Palung National Park, Indonesia. Mean \pm SE across replicate 0.16-ha plots on alluvium ($n = 10$), sedimentary ($n = 8$) and granite-derived ($n = 12$) soils

more weakly) when analyses were restricted to plots in ‘hill forest’ on sedimentary and granite slopes: the density and aboveground biomass of medium trees decreased along Axis 1 of labile and total nutrients, whereas that of large trees 100–110 cm dbh increased (Table 5; online Appendices 1 and 2 in [ESM](#)).

Elevation weakly affected the density of trees 80–90 cm dbh, which increased with elevation, and that of emergent trees, which declined (Online Appendices 1 and 2 in [ESM](#)). Only four of 27 soil parameters were significantly correlated with elevation: extractable P (-0.713) and total C (-0.476), N (-0.388) and P (-0.513).

Forest-wide aboveground biomass

Forest-wide aboveground biomass averaged 518 ± 28 Mg ha $^{-1}$ using the Brown equation and 622 ± 33 Mg ha $^{-1}$ using the Chave equation (Table 1). These estimates are substantially higher than those of lowland Neotropical forests and partly reflect our systematic avoidance of large gaps in plot placement (see [Methods and materials](#)). This bias was partially accounted for statistically by comparing the estimated density of trees >100 cm dbh in our study with that of an unbiased sample based on 69 0.3-ha belts described in Curran and Leighton (2000). In comparison to this data set, our study overestimated the density of trees >100 cm dbh by 28% (6.7 ± 1.5 vs. 5.2 ± 1.1 ha $^{-1}$). Because density and biomass of trees >100 cm dbh were

strongly linearly related ($r^2 = 0.74$ for Brown, $r^2 = 0.67$ for Chave), we used the linear equations describing these relationships to revise estimated aboveground biomass of trees >100 cm dbh based on this lower density. Estimated aboveground biomass of trees >100 cm declined from 142 ± 32 to 102 ± 23 Mg ha $^{-1}$ using the Brown equation, and from 73 ± 14 to 58 ± 11 Mg ha $^{-1}$ using the Chave equation. This produced an adjusted overall forest-wide aboveground biomass equal to 478 ± 26 Mg ha $^{-1}$ based on Brown and 606 ± 31 Mg ha $^{-1}$ based on Chave.

Discussion

Forest structure across substrates

Variation in forest structure across substrates was surprisingly low at Gunung Palung despite marked differences in fertility. On rich alluvium, stem density was lower, basal area and aboveground biomass were higher and maximum tree diameter was larger, but the differences were significant only for emergent trees. Such structural similarity is surprising given the major differences in species composition, leaf traits, aboveground productivity and plant nutrient use strategy that occur across the gradient (Cannon and Leighton 2004; Paoli et al. 2005, 2006; Paoli 2006; Paoli and Curran 2007). However, it affirms speculation by DeWalt and Chave (2004) that forest structure may be less variable across soil gradients than community composition or ecosystem dynamics.

The greater abundance of emergent trees on nutrient-rich alluvium at GPNP reflects (1) demographic changes within a single widespread species and (2) compositional shifts linked to habitat partitioning by canopy trees. The emergent tree *Dipterocarpus sublamellatus* Foxw is the most common canopy tree on alluvium and granite at GPNP (Cannon and Leighton 2004; Paoli et al. 2006), but on alluvial soils compared to the granite, its density was 65% higher for stems ≥ 90 cm dbh (6.9 trees vs. 4.1 trees ha $^{-1}$) and nearly 400% higher for stems ≥ 120 cm dbh (0.5 trees vs. 1.9 trees ha $^{-1}$). The species did not attain a larger maximum size on the alluvium (108 ± 5 vs. 102 ± 5 cm dbh for the ten largest trees; independent sample t test, $P = 0.36$), but its higher density partially explains the higher biomass of emergent trees on the alluvium.

In addition, a suite of four emergent dipterocarp species in genus *Shorea* are strict specialists (*S. johorensis* and *S. gibbosa*) or significantly more abundant (*S. parvifolia* and *S. parvistipulata*) on nutrient-rich alluvium and sedimentary soils compared to the granite soil (Paoli et al. 2006). Individuals of these species comprised six of ten largest trees recorded in the alluvium, and nine of 20 largest trees throughout the watershed. Thus, larger stature on alluvium

Table 3 Correlations between physiochemical characteristics of soil (0–20 cm) and forest structure in lowland forest at Gunung Palung National Park, Indonesia

Soil parameter	Stem density	Basal area	Biomass	Biomass of trees >120 cm dbh
Labile nutrients				
P	−0.395*	0.239	0.375*	0.555**
K	−0.191	−0.124	0.368*	0.565**
Ca	−0.369*	−0.078	0.065	0.281
Mg	−0.106	0.180	0.063	0.333
Na	−0.130	0.002	0.066	0.141
Mn	−0.117	−0.207	0.124	−0.009
Ni	−0.208	−0.167	−0.238	−0.154
Zn	−0.140	−0.019	0.317	0.278
Fe	−0.048	0.273	0.350	0.339
Total nutrients				
C	−0.042	0.337	0.090	0.210
N	−0.137	0.217	0.279	0.324
P	−0.316	0.093	0.149	0.458*
K	−0.149	−0.195	0.235	0.120
Ca	−0.081	−0.106	−0.268	−0.136
Mg	−0.028	0.002	0.284	0.208
Na	−0.085	−0.277	0.350	0.274
Mn	−0.226	−0.213	−0.031	0.000
Ni	−0.113	−0.285	−0.293	−0.143
Zn	−0.104	0.015	0.227	0.135
Fe	−0.169	−0.127	−0.148	0.100
Soil texture				
% Sand	0.077	−0.116	−0.416*	−0.272
% Silt	−0.163	0.208	0.352	0.258
% Clay	0.125	−0.126	0.180	0.073
% Coarse material	0.062	−0.111	0.250	0.194
Soil acidity				
pH H ₂ O	0.077	−0.170	0.332	−0.400*
pH CaCl ₂	−0.010	−0.291	−0.217	−0.231

* $P > 0.05$, ** $P > 0.01$

Values indicate Pearson correlation coefficients

partly reflects compositional changes driven by a competitive advantage on rich soils for species with traits that promote rapid growth and large maximum size (Paoli et al. 2005; Paoli 2006).

These findings, combined with those of Ashton and Hall (1992), who linked taller stature on nutrient-rich, basalt soils in northern Borneo to differences in diameter–height relationships of dominant taxa on contrasting soils, illustrate that demographic changes within species and compositional shifts among them can lead to spatial patterning not only of floristic composition but also key ecosystem properties, such as biomass.

Relationships with soil nutrients

Although substrate had a limited impact on forest structure, total aboveground biomass and its distribution among size classes were significantly related to soil nutrients. In MLR,

extractable P and percentage sand together explained 29% of the variation in total aboveground biomass. Effects on emergent trees were even stronger – extractable P and exchangeable K each explained >30% of the variation in biomass of trees >120 cm dbh, and 44% when combined in MLR (results not shown). Higher densities of emergent trees on rich soils have been reported by Ashton and Hall (1992) in northern Borneo and by DeWalt and Chave (2004) in Peru. Our findings extend the generality of this pattern to southwestern Borneo and highlight soil P and K as candidate nutrients limiting the density of emergent trees on Borneo.

One unexpected finding of soil impacts on forest structure at GPNP was that the densities of mid- to upper-canopy trees (60–90 cm dbh) and emergent trees (>120 cm dbh) were inversely related to soil nutrients. Trees 60–90 cm dbh were significantly more abundant on nutrient-poor soils where emergent trees were relatively sparse. This

Table 4 Summary of factor loadings in principle components analysis (PCA) performed on soil factors in surface soils (0–20 cm) underlying lowland forest at Gunung Palung National Park, Indonesia

Soil parameter	Exchangeable nutrients			Total nutrients			Soil texture	
	Axis 1 (32.5%)	Axis 2 (18.1%)	Axis 3 (15.0%)	Axis 1 (33.1%)	Axis 2 (21.9%)	Axis 3 (14.2%)	Axis 1 (49.7%)	Axis 2 (29.4%)
C	–	–	–	–0.077	0.795*	–0.095	–	–
N	–	–	–	0.386*	0.801*	–0.162	–	–
P	0.794*	0.335	–0.050	0.517*	0.705*	0.339	–	–
K	0.778*	–0.096	0.325	0.760*	–0.170	–0.402*	–	–
Ca	0.799*	–0.083	0.213	0.478*	–0.351*	0.322	–	–
Mg	0.376*	–0.041	0.668*	0.768*	0.095	–0.200	–	–
Mn	0.453*	–0.747*	–0.188	0.860*	–0.085	0.021	–	–
Na	0.237	0.740*	–0.103	0.514*	–0.464*	–0.476*	–	–
Ni	0.164	0.479*	0.275	0.261	–0.481*	0.608*	–	–
Zn	0.719*	–0.190	–0.537*	0.591*	–0.059	–0.279	–	–
Fe	0.316	0.353	–0.582*	0.635*	0.131	0.658*	–	–
% Sand	–	–	–	–	–	–	–0.981*	0.077
% Silt	–	–	–	–	–	–	0.819*	–0.568*
% Clay	–	–	–	–	–	–	0.441*	0.776*
% Coarse material (>2 mm)	–	–	–	–	–	–	0.402*	0.495*

* $P \leq 0.05$ for parameters significantly correlated with that axis

Separate PCA were performed on (1) exchangeable cations and extractable P, (2) total nutrient assays following HF acid digestion and (3) soil texture, including percentage by weight of coarse material (>2 mm diameter). Total variance described by each axis is shown in parentheses

Table 5 Summary of linear regressions of soil factors and elevation on biomass of woody stems by size class in lowland forest at Gunung Palung National Park, Indonesia

Habitat	Size class (diameter at breast height, in cm)												Total
	10–20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100	100–110	110–120	>120	
Labile nutrients													
PCA Axis 1	NS	NS	NS	NS	NS	–*/NS	NS	–**/NS	NS	NS/+ (*)	NS	+***/NS	NS
PCA Axis 2	NS	NS	NS	NS	NS	NS	NS	–*/NS	NS	NS	NS	NS	NS
PCA Axis 3	NS	NS	NS	NS	NS	NS/–*	NS	NS	–(*)/NS	NS	NS	NS/+*	NS
Total nutrients													
PCA Axis 1	NS	NS	NS	NS	NS/–*	–**/–*	–*/NS	NS	NS	NS	NS	NS/+*	NS
PCA Axis 2	NS	NS	NS	NS	–(*)/NS	NS	NS	NS	NS	NS	NS	+(*)/NS	NS
PCA Axis 3	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	–***/–*	NS	–**/–*
Soil texture													
PCA Axis 1	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	+(*)/NS	NS/+ (*)	+*/+*
PCA Axis 2	NS	NS	NS	NS	NS	NS	NS	+*/NS	NS	NS	NS	NS	NS
Other													
Elevation	NS	NS	NS	NS	NS	NS	NS	+*/+***	NS	NS	NS	–(*)/NS	NS

(*) $0.05 < P \leq 0.1$, * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. NS, Not significant

Woody stems >10 cm dbh were enumerated in 30 (0.16 ha) plots throughout a lowland watershed (approx. 340 ha; 8–195 m a.s.l.) underlain by alluvium ($n = 10$ plots), sedimentary rock ($n = 8$) and granite ($n = 12$)

Separate regressions were performed for all plots combined and plots from hill forest only (sedimentary and granite). Results are shown separately if strength or direction of relationships differed, with all plots first, then hill plots only. Biomass was estimated using the moist forest equation of Brown (1997)

relationship could reflect the impact of more intense size asymmetric competition on rich soils, where local neighborhood competitive interactions (e.g. Stoll and Newbery 2005) may be more intense due to higher rates of plant growth (Paoli and Curran 2007) and thus competition for light.

Soil P influences on aboveground biomass at GPNP contrast findings in central Amazonia, where Laurance et al. (1999) reported a strong effect of soil N but no effect of P on aboveground biomass. This may reflect soil P differences between the study areas – extractable P ranged 16-fold at GPNP, but only twofold in Amazonia – or a general distinction between upland soils in Borneo and central/western Amazonia, wherein spatial patterns of productivity and species composition are controlled more strongly by P in Borneo (Baillie et al. 1987; Mirmanto et al. 1999; Potts et al. 2002; Paoli et al. 2005, 2006; Paoli and Curran 2007) and by N and base cations in Amazonia (Cuevas and Medina 1988; Tuomisto et al. 2003; Phillips et al. 2003; Duque et al. 2005). Data are insufficient to draw solid conclusions, but this possibility merits further consideration.

How do we reconcile conflicting reports of positive, negative or no effect of soil nutrients on aboveground biomass among this and other tropical studies? One possibility is that the soil–biomass relationship is scale-dependent. Higher aboveground biomass has been reported on poor soils at a regional scale (DeWalt and Chave 2004; Malhi et al. 2006), but on rich soils at a local scale (DeWalt and Chave 2004; data in Kitayama 1992; this study). Higher aboveground biomass on poor soils could arise at regional scales due to the formation of geographic gradients in plant life history traits, with slow-growing, long-lived species with a large maximum size and high wood density dominating poor soils (Aerts and Chapin 1999; Baker et al. 2004; King et al. 2005). In contrast, at local scales, such segregation of traits across gradients may be incomplete and/or offset on rich soils by the positive impact of increased productivity or shifts in resource allocation on aboveground biomass. This explanation is intuitive, but contrasting

patterns have been reported at regional (Ashton and Hall 1992) and local scales (van Schaik and Mirmanto 1986; van Noordwick and Hairah 1986), suggesting spatial scale alone is not the answer.

Another possibility is that the relationship between soil nutrients and aboveground biomass is unimodal. In this scenario, increasing soil nutrients at the nutrient-poor extreme increases aboveground biomass due to release from nutrient limitation and declining dominance by species with small stature and slow growth (Aerts and Chapin 1999). Eventually, an inflection point is reached, beyond which further nutrient increases reduce aboveground biomass, because productivity gains are more than offset by mortality losses due to increasing dominance by fast growing species with shorter lifespans (Berendse 1994; van Schaik and Mirmanto 1985). If the soil–biomass relationship is unimodal, then the results of a study will reflect the segment of the soil gradient that is sampled.

To test this, we collated data from studies on Borneo that quantified surface soil nutrients and basal area ≥ 10 cm dbh in mature forests. We found nine comparable sites to examine total P, and 14 sites for the sum of exchangeable K, Ca and Mg (Fig. 2). These data suggest a significant unimodal relationship between total P and basal area ($R^2 = 0.96$, $P < 0.001$, quadratic regression forced through the origin) and indicate that our study at GPNP surveyed low to moderate fertility soils along the ascending portion of the curve (Fig. 2a). In contrast, no relationship was found with exchangeable bases, but there was a positive trend among plots at Mt. Kinabalu (Kitayama 1992) and habitats at GPNP (Fig. 2b). More data are needed to assess the generality of a unimodal relationship between soil and aboveground biomass, yet Fig. 2a provides tentative support for the hypothesis.

Aboveground biomass in lowland Borneo

Our adjusted forest-wide estimate of aboveground biomass at GPNP is much higher than that reported for the Neotropics.

Fig. 2 Relationship between woody plant basal area >10 cm dbh and: **a** surface soil total P ($\mu\text{g g}^{-1}$), **b** the sum of surface soil exchangeable K, Ca and Mg ($\ln \text{cmol kg}^{-1}$) in mature lowland rain forest on Borneo

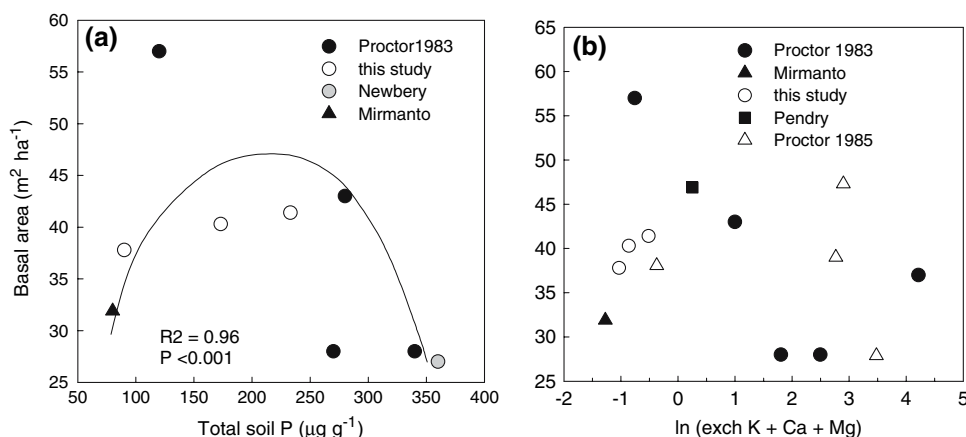


Table 6 Comparison of stem density (≥ 10 cm dbh) by size class between Bornean and Neotropical lowland forests

Location	Total stems ha^{-1}	Size class distribution (stems ha^{-1})						
		10–50	50–60	60–70	70–80	80–90	90–100	>100
Borneo ($n = 20$)	$554.3 \pm 27.0a$	$516.6 \pm 26.2a$	$12.2 \pm 0.9a$	$9.3 \pm 1.0a$	$5.8 \pm 0.9a$	$4.3 \pm 0.6a^{**}$	$2.4 \pm 0.5a$	$4.0 \pm 0.7a^*$
Neotropics ($n = 8$)	$541.8 \pm 51.9a$	$511.3 \pm 52.3a$	$13.9 \pm 1.8a$	$9.1 \pm 2.3a$	$2.8 \pm 1.2a$	$1.1 \pm 0.6b$	$2.1 \pm 0.9a$	$1.5 \pm 0.7b$

* $P \leq 0.05$; ** $P \leq 0.01$, indicates significance of differences

Data were extracted from published and unpublished literature. Comparisons were made between regions using Kruskal–Wallis test. Values followed by different letters are significantly different between locations for that size class. Raw data are available online in Appendix 3 in [ESM](#)

Our estimate of 478 Mg ha^{-1} using the Brown equation is 40% higher than the average across 227 plots in Amazonia (approx. 300 Mg ha^{-1}) and 32% higher than the mean of 27 ‘high biomass’ plots in slow-growing forests on poor soils of central and eastern Amazonia (327 Mg ha^{-1} ; Malhi et al. 2006). Previous estimates on Borneo range from 380 to 650 Mg ha^{-1} (422 ± 47 , median = 437; Proctor et al. 1983, 1988; Kitayama 1992; Kitayama and Aiba 2002; Palm et al. 2005), which is consistent with predictions by Brown et al. (1993, 2001) using calibrated GIS models incorporating climate, topography, soils and geology.

The higher aboveground biomass on Borneo appears to reflect differences in large and/or emergent tree densities on Borneo compared to the Neotropics. Stem densities on Borneo are twofold higher for trees 70–80 cm dbh, fourfold higher for trees 80–90 cm and nearly threefold higher for trees >100 cm (Table 6; Appendix 3 in [ESM](#)).

Higher densities of large trees on Borneo could reflect a higher productivity due to the warm, aseasonal insular climate (Schurr 2003; Running et al. 2004). However, Malhi et al. (2006) have shown that productivity and aboveground biomass are uncorrelated across Amazonia, suggesting that higher productivity on Borneo unlikely explains higher aboveground biomass. Alternatively, differences in stature could be linked to historical biogeographical factors that favored the predominance of ectomycorrhizal dipterocarps on Borneo but led to rarity of the family in the Neotropics (Ashton 1982; Hart et al. 1989; Curran 1994). Lowland Borneo is dominated by massive emergent trees in the Dipterocarpaceae (Ashton 1982; Whitmore 1984), which dominate the forest canopy (Curran and Leighton 2000), contributing, for example, 53 and 77% of aboveground biomass in the 60–80 cm and ≥ 80 cm dbh size classes, respectively, at GPNP (or 62% of total forest-wide aboveground biomass ≥ 10 cm dbh). A third possibility is that a milder disturbance regime on Borneo has enabled biomass accumulation over longer periods, leading to higher equilibrium biomass. At present, data are too few to evaluate which of these factors (or combination thereof) explains higher aboveground biomass on Borneo.

Land use change and carbon emissions

Our findings have two main implications for understanding C emissions resulting from deforestation, degradation and biomass burning across Borneo. Aboveground biomass and thus C stocks of intact lowland Bornean forest are very high, averaging approx. 425 Mg ha^{-1} across this and other studies (Proctor et al. 1983, 1988; Kitayama 1992; Kitayama and Aiba 2002; Palm et al. 2005). This is 30–40% higher than that of mature forest across lowland Amazonia (Malhi et al. 2006; Saatchi et al. 2007) and approximately threefold higher than that of Mato Grosso transitional forests in the arc of deforestation in Brazil (Morton et al. 2006; Saatchi et al. 2007). Thus, C emissions per hectare from upland forests on Borneo due to industrial oil palm plantations, fires and logging are likely to be higher than those of the Neotropics given the higher aboveground biomass on Borneo (Fuller and Fulk 2001; Siegert et al. 2001; Curran et al. 1999, 2004; Dennis and Colfer 2006).

Second, evidence for a significant relationship between soils and aboveground biomass, especially for emergent trees, indicates that spatial patterns of both forest conversion and aboveground biomass covary with soils. Modeling historical C emissions from past deforestation could thus be improved by the application of regionally appropriate ‘soil fertility functions’ to refine estimates of original aboveground biomass. Combinations of soil texture, P and exchangeable base cations hold significant potential for deriving such a function for Borneo, but broader regional sampling of soil nutrients and aboveground biomass is required.

Acknowledgments We are grateful to the Indonesian Institute of Sciences (LIPI) and the Department of Forest Protection and Nature Conservation (PHKA) for granting permission to conduct research in Indonesia. The research presented in this paper complies with the current laws of both Indonesia and the USA. We thank the Center for Research in Biology (PPB), for sponsorship and logistical support, and the students and faculty of Universitas Tanjungpura, for participating as our research counterparts. We thank C. Cannon and M. Leighton for use of the Gunung Palung floristic dataset to estimate specific wood densities across substrates, and Farizal, Hon, Tang and Morni for vital assistance in the field. A. Budiman, Sugarjito, N. Paliama and M. Sinaga

provided administrative support. Financial support for Gary D. Paoli from the Fulbright Indonesia Program and the University of Michigan; Lisa M. Curran from NASA Earth Science Program (NAG 511335 & 511161), the University of Michigan, the Yale School of Forestry and Environmental Studies and the Santa Fe Institute; and J. W. F. Slik from NWO-WOTRO (project grant nr.W84–573).

References

- Achard F, Eva HD, Stibig HJ, Mayaux P, Gallego J, Richards T, Malingreau JP (2002) Determination of deforestation rates of the world's humid tropical forests. *Science* 297:999–1002
- Aerts R, Chapin FS III (1999) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Adv Ecol Res* 30:1–67
- Anderson JAR (1964) The structure and development of the peat swamps of Sarawak and Brunei. *J Trop Geogr* 18:7–16
- Ashton PS (1982) Dipterocarpaceae. *Flora Malaesiana I* 9:237–552
- Ashton PS, Hall P (1992) Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *J Ecol* 60:305–324
- Baillie IC, Ashton PS, Court MN, Anderson JAR, Fitzpatrick EA, Tinsley J (1987) Site characteristics and the distribution of tree species in mixed dipterocarp forests on tertiary sediments in Central Sarawak, Malaysia. *J Trop Ecol* 3:201–220
- Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Lloyd J, Monteagudo A, Neill DA, Patino S, Pitman NCA, Silva JNM, Martinez RV (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob Chang Biol* 10:545–562
- Berendse F (1994) Competition between plant populations at low and high nutrient supplies. *Oikos* 71:253–260
- Bowman R (1990) A rapid method to determine total phosphorus in soils. *J Soil Sci Soc Am* 52:1301–1304
- Brown S (1997) Estimating biomass and biomass change of tropical forests: a primer. UN FAO Forestry Paper 134. Food and Agriculture Organization, Rome
- Brown S, Iverson LR, Prasad A, Liu D (1993) Geographical distributions of carbon in biomass and soils of tropical Asian forests. *Geocarto Int* 4:45–59
- Brown S, Iverson LR, Prasad A (2001) Geographical distribution of biomass carbon in tropical Southeast Asian forests: a database. Publication Number 4879. Environmental Sciences Division, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge
- Brunig EF (1974) Ecological studies in the kerangas forest of Sarawak and Brunei. Borneo Literature Bureau, Kuching
- Cannon C, Leighton M (2004) Tree species distributions across five habitats in a Bornean rainforest. *J Veg Sci* 15:257–266
- Chave J, Condit R, Lao S, Caspersen JP, Foster RB, Hubbell SP (2003) Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *J Ecol* 91:240–252
- Chave J, Condit R, Aguilar S, Hernandez A, Lao S, Perez R (2004) Error propagation and scaling for tropical forest biomass estimates. *Philos Trans R Soc Lond B* 35:409–420
- Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Folster H, Fromard F, Higuchi N, Kira T, Lescure JP, Nelson BW, Ogawa H, Puig H, Riera B, Yamakura T (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145:87–99
- Chave J, Muller-Landau HC, Baker TR, Easdale TA, ter Steege H, Webb CO (2006) Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. *Ecol Appl* 16:2356–2367
- Clark DB, Clark DA (2000) Landscape-scale variation in forest structure and biomass in a tropical rain forest. *For Ecol Manag* 137:185–198
- Clark D, Clark D, Read JM (1999) Edaphic factors and the landscape-scale distribution of rain forest trees. *Ecology* 80:2662–2675
- Cuevas E, Medina E (1988) Nutrient dynamics within Amazonian forests. II. Fine root growth, nutrient availability and leaf litter decomposition. *Oecologia* 76:222–235
- Curran LM (1994) The ecology and evolution of mast-fruiting in Bornean Dipterocarpaceae: a general ectomycorrhizal theory. PhD thesis, Princeton University, Princeton, MA
- Curran LM, Leighton M (2000) Vertebrate responses to spatio-temporal variation in seed production by mast-fruiting Bornean Dipterocarpaceae. *Ecol Monogr* 70:101–128
- Curran LM, Caniago I, Paoli G, Astiani D, Kusneti M, Leighton M, Nirarita CE, Haeruman H (1999) Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* 286:2184–2188
- Curran LM, Trigg SN, McDonald AK, Astiani D, Hardiono YM, Siregar P, Caniago I, Kasischke E (2004) Lowland forest loss in protected areas of Indonesian Borneo. *Science* 303:1000–1003
- Dennis RA, Colfer CP (2006) Impacts of land use and fire on the loss and degradation of lowland forest in 1983–2000 in East Kutai District, East Kalimantan, Indonesia. *Singapore J Trop Geogr* 27:30–48
- De Walt SJ, Chave J (2004) Structure and biomass of four lowland Neotropical forests. *Biotropica* 36:7–19
- Duque AJ, Duivenvoorden JF, Cavellier J, Sanchez M, Polania C, Leon A (2005) Ferns and Melastomataceae as indicators of vascular plant composition in rain forests of Colombian Amazonia. *Plant Ecol* 178:1–13
- Fuller DO, Fulk M (2001) Burned area in Kalimantan, Indonesia mapped with NOAA-AVHRR and Landsat TM imagery. *Int J Remote Sens* 22: 691–697
- Hart TB, Hart JA, Murphy PG (1989) Mono-dominant and species-rich forests of the humid tropics: causes for their occurrence. *Am Nat* 133:613–633
- King DA, Davies SJ, Supardi MNN, Tan S (2005) Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Funct Ecol* 19:445–453
- Kitayama K (1992) An altitudinal transect study of the vegetation of Mount Kinabalu, Borneo. *Vegetatio* 102:149–171
- Kitayama K, Aiba S (2002) Ecosystem structure and productivity of tropical rain forest along altitudinal gradients with contrasting soil phosphorus pools and Mount Kinabalu, Borneo. *J Ecol* 90:37–51
- Klinge H, Herrera R (1983) Phytomass structure of Amazonian caatinga ecosystems in Southern Venezuela I. Tall Amazon Caatinga. *Vegetatio* 53:65–84
- Laurance WF, Fearnside PM, Laurance SG, Delamonica P, Lovejoy TE, Rankin-de Merona JM, Chambers JQ, Gascon C (1999) Relationship between soils and Amazonian forest biomass: A landscape-scale study. *For Ecol Manag* 118:127–138
- Malhi Y, Wood D, Baker TR, Wright J, Phillips OL, Cochrane T, Meir P, Chave J, Almeida S, Arroyo L, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Monteagudo A, Neill DA, Vargas PN, Pitman NCA, Quesadas CA, Salamao R, Silva JNM, Lezama AT, Terborgh J, Vasquez R, Vinceti B (2006) The regional variation in above-ground live biomass in old-growth Amazonian forests. *Glob Chang Biol* 12:1107–1138
- McMorrow J, Talip MA (2001) Decline of forest area in Sabah, Malaysia: relationship to state policies, land code and land capability. *Glob Environ Chang* 11:217–230
- Mirmanto E, Proctor J, Green J, Nagy J, Suriantata L (1999) Effects of nitrogen and phosphorus fertilization in a lowland evergreen rainforest. *Philos Trans R Soc Lond B* 354:1825–1829
- Morton DC, DeFries RS, Shimabukuro YE, Anderson LO, Arai E, Espirito-Santo FD, Freitas R, Morissette J (2006) Cropland expan-

- sion changes deforestation dynamics in the southern Brazilian Amazon. *Proc Natl Acad Sci USA* 103:14637–14641
- Nepstad D, Lefebvre P, Da Silva UL, Schlesinger P, Solorzano L, Moutinho P, Ray DJ, Benito G (2004) Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. *Glob Chang Biol* 10:704–717
- Oey DS (1990) Berat jenis dari jenis-jenis kayu berat Indonesia dan pengertian beratnya kayu untuk keperluan praktek. Departemen Kehutanan Pengumuman nr. 13, Pusat dan Penelitian Pengembangan Hasil Hutan, Bogor, Indonesia
- Olsen SR, Cole CV, Watanabe FS, Dean LA (1954). Estimation of available phosphorus in soils by extraction with sodium bicarbonate. U.S. Dept Agric Circ 939
- Palm CA, van Noordwijk M, Woormer PL, Algre JC, Arévalo L, Castilla CE, Cordeiro DC, Hairiah K, Kotto-Same J, Moukam A, Parton WJ, Ricse A, Rodrigues V, Sitompul SM (2005) Carbon losses and sequestration after land use change in the humid tropics. In: Palm CA, Vosti SA, Sanchez PA, Ericksen PJ (eds) *Slash-and-burn agriculture: the search for alternatives*. Columbia University Press, New York, pp 41–63
- Paoli GD (2006) Divergent leaf traits among congeneric rain forest trees with contrasting habitat distributions. *J Trop Ecol* 22:397–408
- Paoli GD, Curran LM (2007) Soil nutrients limit fine litter production and tree growth in lowland tropical rain forest of southwestern Borneo. *Ecosystems* 10:503–518
- Paoli GD, Curran LM, Zak DR (2005) Phosphorus efficiency of above-ground productivity in Bornean rain forest: evidence against the unimodal efficiency hypothesis. *Ecology* 86:1548–1561
- Paoli GD, Curran LM, Zak DR (2006) Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. *J Ecol* 94:157–170
- Phillips OL, Vargas PN, Monteagudo AL, Cruz AP, Zans MC, Sanchez WG, Yli-Halla M, Rose S (2003) Habitat association among Amazonian tree species: a landscape-scale approach. *J Ecol* 91:757–775
- Potts MD, Ashton PS, Kaufman LS, Plotkin JB (2002) Habitat patterns in tropical rain forests: a comparison of 105 plots in northwest Borneo. *Ecology* 83:2782–2797
- Proctor J (1995) Rainforests and their soils. In: Primack RB, Lovejoy TE (eds) *Ecology, conservation and management of Southeast Asian rainforests*. Yale University Press, New Haven, pp 87–104
- Proctor J, Anderson JM, Chai P, Vallack HW (1983) Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. *J Ecol* 71:237–260
- Proctor J, Lee YF, Langley AM, Munro WRC, Nelson T (1988) Ecological Studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. I. Environment, forest structure and floristics. *J Ecol* 76:320–340
- Regional Physical Planning Program for Transmigration – RePPProT (1986/1987) Kalimantan, Borneo
- Richards PW (1952) *The tropical rain forest*. Cambridge University Press, Cambridge
- Running SW, Nemani RR, Heinsch FA, Zhao M, Reeves M, Hashimoto H (2004) A continuous satellite-derived measure of global terrestrial primary production. *Bioscience* 54:547–560
- Russo SE, Davies SJ, King DA, Tan S (2005) Soil-related performance variation and distributions of tree species in a Bornean rain forest. *J Ecol* 93:879–889
- Saatchi S, Houghton RA, Avala R, Yu Y, Soares JV (2007) Distribution of aboveground live biomass in the Amazon basin. *Glob Chang Biol* 13:816–837
- Schurr EAG (2003) Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation. *Ecology* 84:1165–1170
- Siegert F, Rueker G, Hinrichs A, Hoffman AA (2001) Increased damage from forest fires in logged forests during drought caused by El Niño. *Nature* 414:437–440
- Slik JWF (2006) Estimation of species-specific wood density from the genus average in Indonesian trees. *J Trop Ecol* 22:481–482
- Soares-Filho B, Nepstad DC, Curran LM, Cerqueira GC, Garcia RA, Ramos CA, Voll E, McDonald A, Lefebvre P, Schlesinger P (2006) Modelling conservation in the Amazon basin. *Nature* 440:520–523
- Sollins M (1998) Factors influencing species composition in tropical lowland rain forests: does soil matter? *Ecology* 79:23–30
- Stoll P, Newbery DM (2005) Evidence of species-specific neighborhood effects in the Dipterocarpaceae of a Bornean rain forest. *Ecology* 86:3048–3062
- Tuomisto H, Ruokolainen K, Kalliola R, Linna A, Danjoy W, Rodriguez Z (1995) Dissecting Amazonian biodiversity. *Science* 269:63–66
- Tuomisto H, Poulsen AD, Ruokolainen K, Moran RC, Quintana C, Celi J, Canas G (2003) Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecol Appl* 13:352–371
- van der Werf G, Randerson JT, Collatz GJ, Giglio L, Kasibhatia PS, Arellano AF Jr, Olsen SC, Kasischke ES (2004) Continental-scale partitioning of fire emissions during the 1997 to 2001 El Niño/La Niña period. *Science* 303:73–76
- van Noordwijk M, Hairah K (1986) Mycorrhizal infection in relation to soil pH and soil phosphorus content in a forest of northern Sumatra. *Plant Soil* 96:299–302
- van Schaik CP, Mirmanto E (1985) Spatial variation in the structure and litterfall of a Sumatran rain forest. *Biotropica* 17:196–205
- Vitousek PM, Sanford RL (1986) Nutrient cycling in moist tropical forests. *Annu Rev Ecol Syst* 17:137–167
- Whitmore TC (1984) *Tropical rain forests of the Far East*, 2nd edn. Oxford University Press, Oxford