EFFECTS OF LOGGING ON PHOSPHORUS POOLS IN A TROPICAL RAINFOREST OF BORNEO

N Imai[1, *], K Kitayama[1] & J Titin[2]

[1] *Laboratory of Forest Ecology, Graduate School of Agriculture, Kyoto University, Oiwake-cho, Kitashirakawa, Sakyo-ku, Kyoto 606-8502, Japan*
[2] *Forest Research Centre, Sabah Forestry Department, 90715 Sandakan, Sabah, PO Box 1407, Malaysia*

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IMAI N, KITAYAMA K & TITIN J. 2012. Effects of logging on phosphorus pools in a tropical rainforest of Borneo. We quantified the amount of various phosphorus (P) fractions in a tropical lowland rainforest of Borneo and estimated the potential effects of selective logging on the P availability during the following regrowth period through the export of P as timber. Ecosystem pools of P (sum of aboveground vegetation, standing litter, roots and soils to 1 m deep) and of simultaneously quantified nitrogen (N) and carbon (C) were 3.4, 11.5 and 365 Mg ha^{-1} respectively. Only 2.6% of the total ecosystem P was in the aboveground vegetation, unlike C (61%) and N (16%). Soil P largely consisted of recalcitrant occluded fractions (78–91%) and only 4% was labile (bicarbonate-extractable). The concentration of labile organic P, acid phosphatase activity and fine root biomass were greatest in the topsoil (top 5 cm) and decreased with depth, suggesting that the supply of P to plants took place mainly in the topsoil. The amount of total P which was exported out as timber from the ecosystem by heavy selective logging was estimated at 24.0 kg ha^{-1}, while the amount of labile P in the topsoil was 12.8 kg ha^{-1}, indicating that the labile P might become deficient by more than 12 kg ha^{-1} for biomass recovery. Our results imply that excessive logging can induce P-limitation of post-logging biomass recovery.

Keywords: Acid phosphatase activity, carbon, nitrogen, nutrient limitation, selective logging, soil phosphorus fractionation

IMAI N, KITAYAMA K & TITIN J. 2012. Kesan pembalakan terhadap himpunan fosforus di dalam hutan hujan tropika di Borneo. Kami menilai kuantiti pelbagai pecahan fosforus (P) di dalam hutan pamah hujan tropika di Borneo dan menganggar kesan tebangan memilih melalui pengeksportan P dalam bentuk balak terhadap P tersedia semasa pertumbuhan semula. Himpunan P dalam ekosistem (jumlah vegetasi atas tanah, sarap pokok dirian, akar dan tanah sehingga kedalaman 1 m) serta jumlah nitrogen (N) dan karbon (C) yang dinilai serentak adalah masing-masing 3.4, 11.5 dan 365 Mg ha^{-1}. Cuma 2.6% daripada jumlah P ekosistem terdapat di vegetasi atas tanah berbanding C dan N yang masing-masing sebanyak 61% dan 16%. Sebahagian besar P tanah terdiri daripada pecahan terperangkap yang rekalsitran (78–91%) dan cuma 4% adalah labil (bikarbonat terekstrakan). Kepekatan P organik labil, aktiviti asid fosfatase dan biojisim akar halus paling tinggi pada lapisan tanah atas (5 cm) dan berkurangan dengan kedalaman tanah. Ini mencadangkan yang bekalan P kepada tumbuhan berlaku kebanyakannya pada lapisan tanah atas. Jumlah P yang dieksport keluar daripada ekosistem sebagai kayu melalui penebangan memilih yang giat dianggarkan sebanyak 24.0 kg ha^{-1} manakala jumlah P labil pada lapisan tanah atas ialah 12.8 kg ha^{-1}. Ini menunjukkan yang P labil mungkin akan berkurangan lebih daripada 12 kg ha^{-1} untuk pemulihan biojisim. Keputusan menunjukkan yang penebangan keterlaluan boleh mengehadkan P dalam pemulihan biojisim selepas pembalakan.

INTRODUCTION

Selective logging of marketable large trees has been a major mode of commercial timber production in South-East Asian tropical rainforests. Logging, if uncontrolled, often damages more than 50% of the original forest biomass through soil disturbances by heavy machinery (Cannon et al. 1994, Pinard & Putz 1996, Bertault & Sist 1997, Sist et al. 1998). The patches of highly degraded forests following such unregulated selective logging occur extensively in the lowland, and forest degradation has become a major social and environmental concern in the South-East Asian tropics (ITTO 2006).

Sustainable forest management has been applied to natural production forests in Sabah, Malaysia (Kleine & Heuveldop 1993, Lagan et al. 2007). A management plan is set up based on the amount of annual allowable cut (Lagan et al. 2007). Allowable cut is a key concept for sustainable forest management because

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*E-mail: *inobuo@kais.kyoto-u.ac.jp*

guidelines based on the annual allowable cut ensure harvesting not more than the annual growth. This contributes to maintaining the amount of commercial timber at a sustainable level. Some individual-based growth models such as DIPSIM (Ong & Kleine 1995) and FORMIX3 (Huth & Ditzer 2001) were developed based on annual growth of commercial tree species or all tree species. These models examined forest dynamics with varying logging scenarios in order to determine an appropriate amount of allowable cut. However, the models and concept of the sustainability of timber harvesting do not take into account the nutrient loss from the ecosystem by timber harvesting. Nutrients pooled in aboveground vegetation will be exported out as timber from the ecosystem, and soil nutrients may be eroded by soil disturbances. The substantial loss of nutrients, especially phosphorus (P), from the tropical rainforest ecosystem may induce the limitation of forest regrowth following logging (Amir et al. 1989, Nussbaum et al. 1995, Gehring et al. 1999, Campo & Vázquez-Yanes 2004, Davidson et al. 2004, Lawrence et al. 2007). However, it has not been strictly estimated how much nutrients will be removed from a forest by selective logging.

Phosphorus is considered to be the element most commonly limiting productivity of humid tropical forests on weathered soils (Vitousek 1984, Hedin 2004, Reich & Oleksyn 2004). Soil P can be characterised based on chemically defined fractions which differ from one another in their availability for plants. Phosphorus availability to plants depends on the pool size of a labile P fraction but not of an occluded P fraction (Walker & Syers 1976). Heavily weathered tropical soils are known to contain low levels of labile P and total P but are dominated by occluded P and recalcitrant organic P fractions (Cross & Schlesinger 1995). Under the circumstances, if heavy logging occurs, aboveground P will be exported out as timber from the ecosystem and the supply of a comparable amount of labile P in soils is necessary for biomass recovery after the logging. If the amount of biomass P removed from the ecosystem is considerably larger than the pool size of labile P in soils, a slow post-logging biomass recovery may be induced due to deficiency of plant-available P in soils. The relationship between the amounts of labile P in soils and biomass P that will be removed from the ecosystem is crucial for the understanding of P availability to plants in the following regrowth period.

The concentration and pool size of soil P fractions in tropical soils have been well documented with regard to the effects of soil age (Crews et al. 1995, Kitayama et al. 2004), substrate (Cross & Schlesinger 1995, Kitayama et al. 2000), topography (Tiessen et al. 1994a, Chacón et al. 2005) and human disturbances (Garcia-Montiel et al. 2000, Lawrence & Schlesinger 2001, Frizano et al. 2003, Lawrence et al. 2007), but these studies usually focused on P fractions in the topsoil (see Frizano et al. 2002). Labile P pools may also exist in subsoil horizons because portions of labile P are supplied through weathering of bedrock. Given that fine roots can often be found in deep soils in tropical rainforests (Schenk & Jackson 2002), measurements of the concentration and amount of soil P fractions across horizon including deep soils are primarily needed for a comprehensive understanding of P availability to plants.

The amount of biomass P that will be removed from the ecosystem by selective logging can be estimated by multiplying the concentration of P in each of the different parts (i.e. leaf, branch and stem) by its corresponding biomass that will be removed. Leaf P in terms of the concentrations and biomass have been well studied (Amir & Mona 1990, Hughes et al. 1999, Wright et al. 2004, 2005, Hidaka & Kitayama 2009), but the P in woody parts, which may function as an important reservoir of P because of the generally greater biomass in woody parts than in leaves, has not been well quantified. Measurements of the concentration and amount of P in each of the different parts and the total amount of P in the aboveground biomass are still few in the neotropics (Kauffman et al. 1995, Hughes et al. 1999, Johnson et al. 2001, Feldpausch et al. 2004) and are unknown in South-East Asian tropical forests. This contrasts with the other elements affecting the global climate such as carbon (C) and nitrogen (N) in which these pools in vegetation have been measured elsewhere across the tropics (Rodin & Bazilevich 1967).

The aims of this study were to quantify the amount of P in the forest ecosystem (aboveground vegetation, standing litter, roots and soils including subsoil horizons) and to examine how selective logging affects P pools in a tropical lowland rainforest. We used a sequential extraction procedure for estimating soil P. We studied the pool sizes of vegetation and soil P only, and could not determine the fluxes between different soil P pools by which the post-logging P pool might be replenished. Since the pool size of a labile P fraction can become a surrogate of soil P availability as Crews et al. (1995) and Kitayama and Aiba (2002) have demonstrated, we considered the pool size of labile P as a critical indicator of soil P availability to plants.

MATERIALS AND METHODS

Study site

This study was carried out in Deramakot Forest Reserve, a 55,083 ha forest located in Sabah, Malaysia (5° 22' N, 117 °25' E). The climate is maritime equatorial. The mean monthly temperature is 27 °C with little seasonal variation. The annual precipitation is 3500 mm, with no pronounced dry season (Kleine & Heuveldop 1993). The region is characterised by tertiary sedimentary rocks. Soils are mainly Acrisols that are generally poor in nutrients, well drained and easily eroded. The altitude is between 130 and 300 m asl. The vegetation is mixed dipterocarp lowland tropical rainforest.

Deramakot is divided into 135 compartments of varying sizes (approximately 500 ha each). A total of 17 compartments (3473 ha) are reserved for conservation (not to produce logs), while the remaining compartments are designated to sustainably produce timber using reduced-impact logging with planned rotation period of 40 years (Lagan et al. 2007).

Biomass estimation

A 2 ha permanent plot (100 × 200 m), consisting of 10 × 10 m subplots, was established in a primary forest located within the conservation area. Most of the plot was on flat ridge and gentle slope and it included three steep valleys. The difference between the highest and lowest points in the plot was 45.8 m. We computed slope inclination of a 10 × 10 m subplot by approximating the ground surface to a plane, applying the least square regression to three-dimensional coordinates of the four corners (Yamakura et al. 1995, Itoh et al. 2003). We then classified subplots as flat ridge (2.1–10°), and gentle (10–30°) and steep (30–43.7°) slopes. The numbers of subplots in flat ridge, gentle and steep slopes were 27, 123 and 50 respectively.

All trees ≥ 10 cm diameter at breast height (dbh) within the 2 ha plot were measured. We also established 100 subplots (5 × 5 m) within the 2 ha plot (allocated alternately to each 10 × 10 m subplot) and measured dbh of small trees with 5–10 cm dbh. Buttressed trees were measured 50 cm above protrusions. We collected voucher specimens from trees that could not easily be identified *in situ*. Specimens taken were identified at the herbarium of the Forest Research Centre, Sabah Forestry Department, Sandakan. Samples that could not be identified to species were distinguished as morphospecies.

The heights of trees were measured in a 0.2 ha plot (40 × 50 m) in the gentle slope within the 2 ha plot using a digital hypsometer. The relationship between dbh (D) and tree height (H) was regressed using a hyperbolic allometric equation (Ogawa 1969):

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

where A and H* are regression constants. Aboveground biomass was estimated from an empirical allometric relationship reported for a tropical lowland dipterocarp forest in East Kalimantan, Indonesia (Yamakura et al. 1986):

$$Ws = 0.02903(D^2H)^{0.9813}$$
$$Wb = 0.1192\ Ws^{1.059}$$

and

$$Wl = 0.09146\ (Ws + Wb)^{0.7266} \qquad (2)$$

where Ws, Wb and Wl are the dry mass of the trunk, branches and leaves of a tree respectively. Aboveground biomass is the sum of Ws, Wb and Wl. In the calculation of Ws in equation 2, the estimated H from equation 1 was used instead of H.

Coarse-root biomass (Wr) was estimated from an allometric relationship reported for a tropical lowland dipterocarp forest in Peninsular Malaysia (Niiyama et al. 2010):

$$Wr = 0.023D^{2.59}$$

Sampling of vegetation components

To estimate the amounts of C, N and P in aboveground vegetation, we collected the samples of fully expanded healthy sun-exposed leaves, bark and wood from canopy dominant species. Seven canopy dominant species, defined as species with ≥ 3% in relative basal area (BA) were collected: six *Shorea* species of Dipterocarpaceae (*Shorea atrinervosa*, *S. exelliptica*, *S. foxworthyi*, *S. macroptera*, *S. multiflora*, *S. parvifolia*) and one Anacardiaceae species (*Gluta wallichii*). The sum of BA of these seven species (11.5 m^2 ha^{-1}) attained 33.5% of total BA (34.2 m^2 ha^{-1}). Three trees were sampled from each of the seven species. Sun leaves were collected from the crown tops using a slingshot. From the same individual tree, bark and wood samples were extracted using a chisel and an increment borer at 1 m height above the ground. Wood core samples were taken from the sapwood area that is within 3 cm from the bark. We collected at least three sun leaves, at least two samples of bark and wood per individual tree, and combined samples by individual tree. In the laboratory, leaves were wiped and all samples were oven dried at 70 °C for three days and finely ground.

Soil sampling

We randomly excavated three soil pits down to 1 m deep under closed canopy at each of the three topographic positions (i.e. flat ridge, and gentle and steep slopes) within the 2 ha plot (nine soil pits in total). Soil samples were collected from two O horizons (O1 and O2 horizon) and four mineral soil layers (A, AB, B1 and Bt horizons). The O1 horizon represents Oi horizon comprising freshly-fallen litter (twigs < 2 cm girth, leaf and other fractions ≥ approximately 1 cm^2), and the O2 horizon represents Oe and Oa horizons comprising more fragmented fractions with an accumulation of fine roots. The O horizons were sampled at three random points around each pit using a circular frame (23 cm diameter). At the same sampling point below the O horizons, A horizon (0–5 cm deep) was collected vertically with a 5 cm deep core sampler (diameter 37 mm). For each of the O1, O2 and A horizons, three samples per pit were combined to one composite sample (i.e. 3 composites × 3 topographic positions = 9 composites per horizon). The other three horizons below 5 cm (AB, B1 and Bt horizons) were collected horizontally from the wall of soil pit using the same core sampler. For each of the AB, B1 and Bt horizons, 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 × 3 topographic positions = 3 composites per horizon). The boundaries of A–AB, AB–B1 and B1–Bt horizon were 5, 16.4 ± 5.5 and 41.1 ± 6.5 cm deep respectively.

Samples of O horizons were sorted into living roots, twigs and leaves. The other mineral soil layers were sorted into living roots and soils. All living roots < 2 mm diameter were manually collected and gently rinsed with deionised water. Roots with dark coloured tissues and rotten bark were considered dead and discarded. Each composite soil was immediately stored in a refrigerator at 4 °C until analysis. Twig and leaf litter, and fine roots were oven dried at 70 °C for three days, weighed and finely ground. Our estimation of the amount of C, N and P in the ecosystem did not include coarse woody debris (≥ 2 cm girth), trees < 5 cm dbh, herbs and lianas.

Chemical analysis

Soil pH was determined in a 1:2 fresh soil to deionised water. Inorganic and organic phosphorus (Pi and Po) were sequentially extracted following the method of Tiessen and Moir (1993) with 0.5 M $NaHCO_3$ (adjusted to pH 8.5 with NaOH), 0.1 M NaOH, and 1.0 M HCl. Samples of 1 g of fresh soil were weighed into 50 ml polypropylene centrifuge tubes for the extraction. We omitted the step using anion-exchange resin to extract the most labile Pi, and started from the bicarbonate ($NaHCO_3$) stage. We assume that resin Pi is fully a subset of bicarbonate Pi. Bicarbonate-extractable P encompasses both inorganic (CO_3-Pi) and organic (CO_3-Po) fractions, and is considered as the most labile fraction of P in this study. Hydroxide (NaOH)-extractable P is assumed to represent the iron and aluminium surface-bound inorganic P (OH-Pi) and the partially stabilised organic P in soil organic matter (OH-Po). It is considered less readily available for organisms but non-occluded. The 1.0 M HCl-extractable P is assumed as inorganic P bound with calcium in primary minerals such as apatite (Ca-Pi). Extracts of bicarbonate and hydroxide solutions contained both Pi and Po. Pi was determined after precipitating organic matter by acidifying subsample solutions to pH 1.5 with 0.9 M H_2SO_4. The concentration of Pi was determined colorimetrically on a spectrophotometer at 712 nm by the molybdate–ascorbic acid procedure of Murphy and Riley (1962). Total P (Pi plus Po) was determined on an inductively coupled plasma emission spectrophotometry. The concentration of Po was determined as the total P minus Pi. Residual P, considered as highly recalcitrant occluded Pi, was calculated as the difference between acid-digestible total P (see below) and the sum of all extraction steps in the above.

We determined the concentrations of total C, N and P in the powdered sample of vegetation (sun leaves, bark and wood of canopy dominants and fine root) and belowground components (soil and litter). The C, N and P concentrations of wood were used as substitutes for the values of coarse roots. Soil subsamples were oven dried at 105 °C for more than 48 hours to determine gravimetric water content. The concentrations of total C and N in samples were determined by the dry combustion method with an N–C analyser. To measure the concentrations of the total P, subsamples of 0.2 g were weighed and digested on a block digester with concentrated H_2SO_4 and H_2O_2. Digestion was repeated until the solution became clear. Digests were filtered through Whatman 2 V filter paper and made up to 50 ml with deionised water. The concentration of P in the digests was determined on an inductively coupled plasma emission spectrophotometry. The amounts of C, N and P in each component on an area basis were calculated by multiplying the mass of each component by its corresponding weight-basis concentration.

To estimate Po mineralisation in soils, acid phosphatase activity was determined by the p-nitrophenyl phosphate (pNP) method (Tabatabai & Bremner 1969). About 5.0 g of fresh soils were added to 50 ml 50 mM acetate buffer solution (pH 5.0) and briefly shaken by hand. We added 0.5 ml of the mixture to a 1.5 ml Eppendorf tube that contained 0.5 ml of 50 mM pNP-substrate solution or acetate buffer (sample control). Tubes were incubated at 25 °C for two hours, centrifuged, and then 0.5 ml of the supernatant in each tube was transferred to a bottle containing 0.1 ml of 1.0 M NaOH to terminate the reaction and cause colour change. The solution was brought to a volume of 5 ml using deionised water and the pNP released was determined spectrophotometrically by measuring the absorbance of the solution at 410 nm.

Estimation of logging effects on the C, N and P pools

To evaluate the logging effects on C, N and P pools, we calculated the changes of aboveground C, N and P pools assuming a hypothetical selective logging in the primary forest. The magnitude of harvest usually ranged from a few to 20 trees per hectare. If uncontrolled, it usually reduces more than 50% of the aboveground biomass of the original stand (Pinard & Putz 1996, Bertault & Sist 1997, Sist et al. 1998). In the forests nearby Deramakot where heavy selective logging has been applied, mean aboveground biomass is decreased by 64% compared with neighbouring primary forests (Seino et al. 2005). Such a decline of forest biomass encompasses the amount of both harvested timber and collaterally killed trees during road constructions and loggings. In the Bornean rainforest subjected to heavy selective loggings, exported volume ranged from 51.2 to 54.0% of felled volume (remaining felled trees may be converted into necromass) (Bertault & Sist 1997). Branches and leaves attached to felled commercial trees usually are cut off from the trees and left in the forests. We, therefore, assume that the logging, which reduces 60% of the original aboveground biomass and leaves behind branches, leaves and 50% mass of stem in the forest, is a typical unregulated heavy selective logging in this region. We applied simple logging scenarios with different intensities (reduced 20–60% of the aboveground biomass of the primary forest studied) and harvest treatments (left nothing, left all branches and leaves, or left all branches, leaves and 50% stem mass in the forest after logging).

Statistical analysis

Comparison of the soil chemical properties (pH, acid phosphatase activity, concentrations of P fractions and total C, N and P) among horizons were tested by analysis of variance (ANOVA). ANOVA was also used to compare the concentrations of total C, N and P between vegetation components (leaf, bark, wood and fine root). When the ANOVA p value was < 0.05, the Tukey-Kramer post-hoc test was performed to determine which pairs of means differed significantly.

RESULTS

Biomass

Estimated aboveground biomass attained 449 Mg ha^{-1}, with 98.8% of aboveground biomass accounting for by stem and branch while only

1.2% by leaf (Table 1). A small number of canopy trees accounted for a large proportion of aboveground biomass; for example, trees > 60 cm dbh accounted for only 1.6% of total number of trees but 48.5% of aboveground biomass. Fine-root biomass attained 30 Mg ha^{-1} and 70% of fine-root biomass concentrated in the topsoil (O and A horizons) (Table 2). Estimated coarse-root biomass was about three times larger than fine-root biomass (102 Mg ha^{-1}). Standing litter (leaf and twig) attained 15 Mg ha^{-1}, with a relatively large amount of fragmented leafy fractions at O2 horizon. Accordingly, total biomass (the sum of aboveground biomass, fine- and coarse-root biomass and standing litter mass) attained 597 Mg ha^{-1}, with 75% of total biomass accounted for by aboveground vegetation (Tables 1 and 2).

Concentrations and pools of C, N and P

Mean concentration of C in vegetation component (leaf, bark, wood and fine root) varied from 45.2 to 50.6% and was relatively higher in aboveground components (leaf, bark and wood) than in fine root (Table 3). In contrast, N and P concentrations were higher in leaf, while intermediate in fine root, and lower in bark and wood. The N concentration ranged from 0.40 to 1.90% while P concentration ranged from 0.019 to 0.062%. Foliar N/P ratio (results not shown) in our forest was 31.5 ± 4.4 (n = 7), and this value was closer to the upper limit in forests worldwide (McGroddy et al. 2004).

The C, N and P concentrations in soils decreased from surface to deep horizon, but the magnitude of decline differed between elements. Soil organic C concentration drastically decreased with depth, ranging from 36.7% in O1 to 0.2% in Bt. Soil total N concentration gradually decreased with depth (range 1.14 to 0.05%). Soil total P concentration was higher in O horizons (0.038%) than in the mineral soils (A to Bt), but total P concentration in mineral soils was nearly constant regardless of horizon (0.025–0.027%).

Most of soil organic C was stored in the surface horizons, but that of the total P was in a deeper horizon, while total N showed an intermediate pattern (Table 4). For example, C, N and P pools in the deepest Bt horizon accounted for 24, 45 and 61% of total pool in soils respectively. The C, N and P pools in the entire ecosystem (the sum of aboveground vegetation, standing

Table 1 Aboveground and coarse-root biomass and tree density in a lowland tropical rain forest of Deramakot, Borneo

Soil	Tree density (No. ha^{-1})	Aboveground biomass (Mg ha^{-1})				Coarse-root biomass (Mg ha^{-1})
		Total	Stem	Branch	Leaf	
5–10 cm	892.0	13.5	11.3	1.6	0.5	3.2
10–30 cm	501.5	87.0	73.2	12.0	1.8	18.7
30–60 cm	79.0	131.0	109.3	20.1	1.5	28.1
> 60 cm	24.0	218.0	179.8	36.6	1.6	51.8
Total	1496.5	449.4	373.6	70.3	5.4	101.8

Table 2 Mean (± SD) of fine-root (< 2 mm in diameter) biomass and density, standing litter mass, bulk density, pH (H_2O) and acid phosphatase activity in a lowland tropical rainforest of Deramakot, Borneo

Parameter	O1	O2	A	AB	BI	Bt	Total
Fine-root biomass (Mg ha^{-1})		0.4 ± 0.3	21.0 ± 4.7	3.8 ± 1.5	2.5 ± 1.2	2.7 ± 1.8	30.4
Leaf litter mass (Mg ha^{-1})	4.7 ± 0.4	7.7 ± 1.4	–	–	–	–	12.4
Twig litter mass (Mg ha^{-1})	1.5 ± 0.8	1.5 ± 0.4	–	–	–	–	3.0
Fine-root density (mg cm^{-3})			41.9 ± 9.5	3.5 ± 0.8	1.0 ± 0.4	0.5 ± 0.3	–
Bulk density (g cm^{-3})			0.8 ± 0.06	1.2 ± 0.03	1.3 ± 0.09	1.4 ± 0.05	–
pH (H_2O)			3.40 a ± 0.12	3.71 b ± 0.02	3.83 bc ± 0.01	3.86 c ±0.03	–
Acid phosphatase (µmol *p*NP g^{-1} hour^{-1})			6.68 a ± 0.87	2.60 b ± 0.37	0.77 c ± 0.16	0.51 c ±0.13	–

Soil horizons having the same letter did not differ significantly at $p < 0.05$

Table 3 Mean (± SD) concentrations of carbon (C), nitrogen (N) and phosphorus (P) of aboveground vegetation and soils by component in a lowland tropical rainforest of Deramakot, Borneo

Parameter	C (%)	N (%)	P (%)
Vegetation component			
Leaf	50.6 a ± 2.7	1.90 a ± 0.14	0.062 a ± 0.012
Bark	48.6 a ± 2.7	0.57 c ± 0.05	0.023 b ± 0.003
Wood	49.1 a ± 0.7	0.40 c ± 0.04	0.019 b ± 0.002
Fine root	45.2 b ± 4.4	1.38 b ± 0.32	0.052 a ± 0.004
Soil horizon			
O1	36.7 a ± 1.4	1.14 a ± 0.07	0.038 a ± 0.005
O2	23.3 b ± 9.6	1.00 a ± 0.31	0.038 a ± 0.003
A	3.6 c ± 0.55	0.23 b ± 0.02	0.027 b ± 0.002
AB	1.4 c ± 0.15	0.11 b ± 0.001	0.026 b ± 0.001
B1	0.6 c ± 0.08	0.07 b ± 0.001	0.025 b ± 0.001
Bt	0.2 c ± 0.02	0.05 b ± 0.002	0.025 b ± 0.001
Other component			
Twig in O horizons	42.1 ± 1.0	0.8 ± 0.15	0.032 ± 0.005

Vegetation components and soil horizons having the same letter did not differ significantly at $p < 0.05$

litter, roots and soils) were 365, 11.5 and 3.4 Mg ha^{-1} respectively. Most of the C was stored in aboveground vegetation, but P was stored in soils, while N showed an intermediate pattern. The C, N and P pools in the aboveground vegetation accounted for 61, 16 and 2.6% of the total ecosystem pool respectively.

Phosphorus fractionation

The mineral soils were highly acidic and soil pH increased with depth (Table 2). Acid phosphatase activity was highest in the A horizon and decreased with depth. Regardless of horizon, mean concentration of total phosphorus (T-P) varied within a narrow range of 245–268 μg g^{-1} (Table 5). These T-P values were closer to the values in some Bornean lowland tropical soils (Burghouts et al. 1998, Kitayama et al. 2000, Paoli & Curran 2007). Most phosphorus was found in the occluded fraction (78–91% of T-P), presumably due to the effects of soil weathering. A total of 11% of T-P (range 7–19%) was accounted for by organic fraction (Table 5). Only 4% (range 2.8–5.5%) of T-P was found in the most labile bicarbonate Pi and Po fractions (Table 5). The stock of most labile bicarbonate Pi and Po was 130 kg ha^{-1} in soils down to 1 m deep.

Logging effects on the C, N and P pools

Estimated amounts of C, N and P that are exported out as timber from the primary forest through logging, which are based on Table 4 and the three logging scenarios, are shown in Figure 1. Exported amounts of C, N and P increased linearly with increasing logging intensity. A scenario which did not leave any component of logged trees in the forest exported larger amounts of C, N and P than a scenario which left behind branches and leaves or a scenario which left branches, leaves and 50% mass of stem in the forest (i.e. the most common practice). When heavy selective logging occurred, which reduced 60% of the original aboveground biomass and leaf branches, leaves and 50% mass of stem in the forest, a total of 24 kg P ha^{-1} would be exported out as timber from the ecosystem. This exported amount was more than twice the amount of plant-available P in the topsoil (O and A horizons) (Figure 1); the stock of bicarbonate Pi and Po in the topsoil (O and A horizons) were 1.3 and 10.5 kg ha^{-1} (Tables 4 and 5) respectively (total P in O horizon was assumed as the labile Po fraction).

Table 4 The amounts of carbon (C), nitrogen (N) and phosphorus (P) of the aboveground vegetation, roots and soils by components in a lowland tropical rainforest of Deramakot, Borneo

Parameter	C (Mg ha^{-1})	N (kg ha^{-1})	P (kg ha^{-1})
Aboveground vegetation			
> 60 cm	107.0	894.2	42.4
30–60 cm	65.5	555.9	26.2
10–30 cm	43.1	377.4	17.6
5–10 cm	6.6	62.1	2.8
Total	222.3	1889.7	89.0
Fine root			
O2	0.2	5.0	0.2
A	9.5	288.8	10.9
AB	1.7	51.9	2.0
B1	1.1	34.8	1.3
Bt	1.2	37.5	1.4
Total	13.7	418.0	15.7
Coarse root	50.0	406.4	19.5
Soil horizon			
O1	2.4	65.9	2.3
O2	2.4	88.6	3.4
A	15.1	981.4	112.7
AB	19.1	1472.5	362.2
B1	20.8	2269.9	809.6
Bt	19.2	3934.4	2009.9
Total	79.0	8812.8	3300.1
Ecosystem total	365.0	11526.8	3424.3

Table 5 Mean (± SD) concentrations and amounts of phosphorus (P) fraction by horizons in a lowland tropical rainforest of Deramakot, Borneo

Soil horizon	CO_3^-		OH^-		Ca-Pi	Occl-Pi	T-P
	Pi	Po	Pi	Po			
Concentration (µg g^{-1})							
A	3.2 a ± 0.10	11.5 a ± 3.7	5.6 a ± 0.34	38.8 a ± 12.6	2.0 a ± 0.22	207.9 ± 66	268.4 ± 17.1
AB	2.8 b ± 0.17	4.5 ab ± 2.8	5.2 a ± 0.10	14.4 b ± 5.4	1.4 b ± 0.01	233.9 ± 193	262.2 ± 14.0
B1	2.7 b ± 0.03	6.5 ab ± 0.1	4.5 b ± 0.11	17.8 b ± 1.9	1.1 b c ± 0.08	222.8 ± 31	246.3 ± 3.4
Bt	2.6 b ± 0.12	7.6 b ± 0.9	4.2 b ± 0.09	14.2 b ± 3.9	1.1 c ± 0.06	215.5 ± 79	245.1 ± 11.4
Percentage to T-P (%)							
A	1.2 ± 0.08	4.2 ± 1.1	2.1 ± 0.1	14.3 ± 3.8	0.8 ± 0.03	77.6 ± 5.0	
AB	1.1 ± 0.01	1.7 ± 1.1	2.0 ± 0.13	5.6 ± 2.2	0.5 ± 0.02	89.1 ± .3	
B1	1.1 ± 0.02	2.6 ± 0.1	1.8 ± 0.04	7.2 ± 0.7	0.5 ± 0.04	90.5 ± 0.8	
Bt	1.1 ± 0.05	3.1 ± 0.3	1.7 ± 0.05	5.8 ± 1.4	0.4 ± 0.04	87.9 ± 1.1	
Amount (kg ha^{-1})							
A	1.3	4.8	2.3	16.3	0.9	87.2	112.7
AB	3.8	6.2	7.1	19.9	1.9	323.1	362.2
B1	8.9	21.3	14.9	58.6	3.7	732.4	809.6
Bt	21.4	62.5	34.3	116.4	8.6	1766.8	2009.9
Total	35.5	94.8	58.7	211.2	15.1	2909.5	3294.4

Soil horizons sharing the same letters did not differ significantly at $p < 0.05$. Bicarbonate-extractable organic and inorganic P = CO_3-Po and CO_3-Pi respectively, hydroxide-extractable organic and inorganic P = OH-Po and OH-Pi respectively, 1 M HCl extractable P = Ca-Pi, residual P = Occl-Pi, total P = T-P

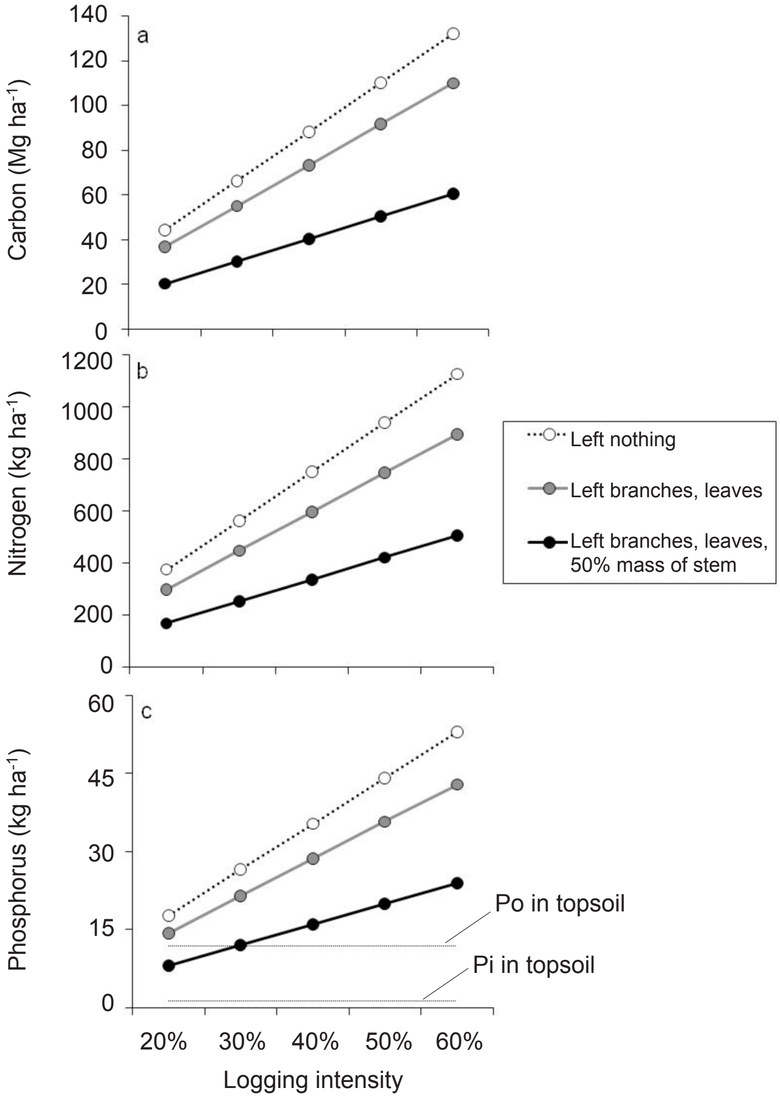

Figure 1 Estimated amounts of (a) carbon (b) nitrogen and (c) phosphorus that are exported out as timber through logging with different logging intensities (20–60% reduction of the aboveground biomass of the original stand) and harvest treatments (left nothing, left branches and leaves, and left branches, leaves and 50% mass of stem in the forests after the logging). This figure simultaneously shows the amount of bicarbonate-extractable inorganic P (Pi) and organic P (Po) pooled in the topsoil (O and A horizon).

DISCUSSION

The amount of total P which is exported out as timber from the ecosystem is estimated to be 24 kg ha^{-1} when heavy selective logging (which reduces 60% of the aboveground biomass of the original stand and leave branches, leaves, and 50% mass of stem in the forest) occurs in a primary tropical forest of Deramakot, Borneo. The supply of a comparable amount of plant available P in soils is necessary for biomass recovery after the logging. Cumulative amount of the most labile bicarbonate P in soils (130 kg ha^{-1}) was greater than the harvested amount of T-P (24 kg ha^{-1}). However, plants may not be able to access the entire labile P pools because most of labile P is pooled in deeper horizons where plant roots exist sparsely. For example, the deepest Bt horizon (approximately 0.4–1 m deep) accounted for 64% of labile P pool but only 9% of fine-root biomass (Tables 2 and 5). Phosphorus uptake by plants, therefore, may depend mainly on the supply of labile P in the topsoil where plant roots exist abundantly. The amount of bicarbonate labile P in the topsoil (O and A horizons) was estimated at

11.8 kg ha^{-1} (Tables 4 and 5). The balance between the exported amount and the initial labile P pools in the topsoil (12.2 kg P ha^{-1}) was the amount deficient for biomass recovery for a first approximation (Figure 1). Although this calculation was based on the pool size of P fractions only, our estimate was legitimate because the pool size of labile P has been described as a surrogate of soil P availability to plants (Crews et al. 1995, Kitayama & Aiba 2002, Paoli et al. 2005).

Organic matter (Po) mineralisation in the topsoil is an especially important process for providing available P to plants in tropical soils (Tiessen et al. 1994b). Acid phosphatase activity was the highest in the topsoil and dramatically decreased with depth. A large amount of root biomass (70%) was found in the topsoil in this study plot. A dense root mat is known to be an effective strategy for P acquisition in the tropics (Laclau et al. 2004, Powers et al. 2005). Stark and Jordan (1978) demonstrated that less than 1% of ^{32}P passed through root mat into the soils. Such a closed, effective P acquisition system may occur in our forest because a high foliar N/P ratio represents the efficient use of P (relative to N) by trees, mostly due to the low availability of P in soils (McGroddy et al. 2004, Hidaka & Kitayama 2009). However, heavy selective logging, which causes serious skidding damage (Pinard et al. 2000, Sist et al. 2003), may collapse such effective P acquisition system in the topsoil. The amount of deficient labile P for biomass recovery can therefore be higher than 12.2 kg ha^{-1}. Such a substantial deficiency of plant available P in soils may induce a slow post-logging biomass recovery (Lawrence et al. 2007).

Some studies expected that the translocation of P from subsoil through deep rooting, which is called nutrient pumping, may contribute to sustaining productivity and continuing biomass accumulation of tropical secondary forest (Lawrence & Schlesinger 2001, Feldpausch et al. 2004, Lawrence et al. 2007). However, extending fine roots through the subsoil is a costly process because P is quickly depleted in the rhizosphere (the immediate vicinity of roots) and the diffusion of P is extremely slow in soils. Therefore, deep rooting for scavenging P may not necessarily be an adaptive mechanism to acquire P in tropical secondary forest. Indeed, fine-root biomass in the subsoil is usually lower in a secondary forest than in a primary forest (e.g. Jaramillo et al. 2003). Therefore, where deep rooting is limited by such reason or recurrent destructive logging and other environmental factors (i.e. most common case in tropical secondary forests), P-limitation to forest regrowth may occur.

Heavy selective logging will also export a total of 505 kg N ha^{-1} out as timber from the ecosystem (Figure 1). Such an exported amount of total N is substantial, but N may not limit forest regrowth following selective logging in tropical lowland forests. Dinitrogen (N_2) fixation is an important process to add N to the ecosystem. Tropical lowland forests show higher N_2 fixation rate and higher abundance of N_2-fixing trees compared with forests at a high latitude (Houlton et al. 2008). The symbiotic N_2 fixation rate by trees in lowland tropical forests was estimated to be 20–40 kg N ha^{-1} $year^{-1}$ (Houlton et al. 2008). Another estimation of biological N_2 fixation rate (the sum of symbiotic and non-symbiotic N_2 fixation) in tropical evergreen forests ranged from 14.7 to 36.1 kg N ha^{-1} $year^{-1}$ (Cleveland et al. 1999). Given the amounts of litterfall N input which have been reported in Bornean lowland tropical rainforests as 58.4 (Mirmanto et al. 1999), 79.7 (Moran et al. 2000) and 81 kg N ha^{-1} $year^{-1}$ (Proctor et al. 1983), such N_2 fixation rates (approximately 15–40 kg N ha^{-1} $year^{-1}$) are considerable. Phosphorus frequently limits productivity of tropical lowland forests on weathered soils, while N has been considered to be relatively abundant in most tropical lowland forests but not in tropical montane (Tanner et al. 1998) or temperate forests (Martinelli et al. 1999). Therefore, if heavy selective loggings occur recurrently in such tropical lowland forests and then plant available nutrients in soils dramatically decrease, the biomass recovery may be more susceptible to P-limitation than to N-limitation.

Our analysis demonstrates that labile P (including biomass P) is rather localised within a forest. Furthermore, such localised P is susceptible to logging because a primary tropical forest stores a half of total aboveground biomass in trees ≥ 60 cm dbh (which often demarcates a minimum dbh for logging) (Table 1) and keeps the soil organic matter with concentrated Po and phosphatase activity in the topsoil. Thus, even if foresters comply with forestry guidelines, substantial effects of harvesting on the P dynamics are inevitable. Our results cautions against excessive logging because of a possibility of inducing P-limitation in the following regrowth period. Minimising the harvest volume and collateral damages in order to reduce P export is, therefore, another principal requirement for achieving sustainable forest management.

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