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Soil phosphorus fractionation and phosphorus-use efficiencies of tropical rainforests along altitudinal gradients of Mount Kinabalu, Borneo

Abstract We studied soil phosphorus (P) fractionation and P-use efficiencies (PUEs) of rainforests along altitudinal gradients (700–3100 m) on two types of parental rocks (sedimentary versus ultrabasic) on Mount Kinabalu, Borneo. Sedimentary rocks were known to contain more quartz (which does not adsorb P) than ultrabasic rocks. The pool (top 30 cm) of total P was always greater on sedimentary (ranging from 34.9 to 72.6 g m^{-2}) than on ultrabasic (9.0–29.2 g m^{-2}) rocks at comparable altitudes. Accordingly, the pools of organic P and labile inorganic P were always greater on sedimentary than on ultrabasic rocks. The pool of primary mineral, calcium P increased upslope from 1.7 to 4.3 g m^{-2} on sedimentary rock, suggesting that the altitudinal sequence of the sites reflected a decreasing magnitude of soil weathering upslope. The pool of calcium P on ultrabasic rock did not vary consistently with altitude (1.2–2.8 g m^{-2}), probably reflecting the greater between-site variability of primary mineral P in parent rocks. When all sites were compared, the pool of most labile, bicarbonate-extracted inorganic P increased (ranging from 0.02 to 1.85 g m^{-2}) with increasing calcium P. Calcium P was therefore considered to be an important P source to the biota on Kinabalu. Gross patterns in the variation of PUE (indexed as the reciprocal of the P concentration in litter) were best explained by the pool size of actively cycling P (total P minus occluded inorganic P). PUE, however, demonstrated distinct altitudinal patterns to generate an intricate conrol of P use pattern by soil P pools and altitude.

Key words Ecosystem control · Litterfall · Nutrient-use efficiency · Parent materials · Soil phosphorus fractionation

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Introduction

The primary source of phosphorus (P) in terrestrial ecosystems is the weathering of minerals found in parent rock materials (Lajtha and Schlesinger 1988). P can ultimately control net primary production (NPP) and the decay of organic matter either directly or through interactions with nitrogen (N) in P-deficient ecosystems (Walker and Syers 1976; Cole and Heil 1981; Pastor et al. 1984; Tate and Salcedo 1988; Crews et al. 1995; Herbert and Fownes 1995). Ecosystem processes of lowland tropical rainforests on some deeply weathered skeletal soils are limited by P (e.g., Vitousek 1984; Vitousek and Sanford 1986; Tiessen et al. 1994; Raaimakers et al. 1995; Sollins 1998). However, the extent of such P-deficient rainforests is still unknown.

Vitousek and Sanford (1986) have demonstrated that soil fertility can vary considerably with soil type in the lowland tropics. Moreover, in comparison to lowland tropical rainforests, upland rainforests are believed to be limited by N due to slow mineralization of organic matter (Grubb 1977; Vitousek and Sanford 1986; Tanner et al. 1990, 1992, 1998). These results imply that the pattern and control of nutrient cycling in tropical rainforests vary in a landscape context, but on old substrates, the nutrient limitation shifts from P to N with increasing altitude on single mountain slopes (Tanner et al. 1998). Evidence to support these hypotheses is, however, circumstantial, and has been obtained mainly from the element concentration in litterfall (Vitousek 1984; Tanner et al. 1998). We are not aware of any research that has investigated the type and quantity of soil P fractions, and the

variation of P-use in the above-ground processes in climax tropical rainforests on single mountain slopes (cf. the study on a new tropical volcano by Schlesinger et al. 1998). Our aims are thus to determine the pools of soil P fractions, and to estimate the magnitude of P limitation in NPP in relation to the soil P status on a single mountain slope.

Model of soil P transformation and hypotheses

According to the model of Walker and Syers (1976), as has been substantiated by Crews et al. (1995), primary mineral calcium phosphate (Ca-P) in parent rock is released into soil solution, and is taken up directly by plants and soil microbes or sorbed to become iron and aluminum phosphate minerals. These secondary iron and aluminum phosphate minerals may be labile (non-occluded), and dissolve further to enter biological cycles. Secondary mineral P that is not taken up by organisms, however, is increasingly occluded by iron and aluminum oxides in weathered soils, the products of which are chemically recalcitrant and with low bioavailability. The P utilized by organisms may be recycled as inorganic P (Pi), or incorporated into recalcitrant organic matter as organic P (Po). Dissolved Pi that is removed by organisms can be replenished from non-occluded labile Pi (iron and aluminum phosphate), which is in turn very slowly replenished from Ca-P or recalcitrant Pi or Po (Tate 1984; Tate and Salcedo 1988). This dissolution-desorption process of Pi is geochemical, and dependent on the types and amount of secondary clay minerals. Tiessen et al. (1994) demonstrated that soil P could be fractionated differently in response to the abundance of iron oxides along a sequence of topographies; oxidizing upper sites contained abundant iron oxides and thus less soluble Pi, while chemically reducing lower sites had less oxides and more soluble Pi.

Conversion of Po to Pi, on the other hand, is predominantly biological (biological mineralization by microbes), and in old ecosystems where the soil P pools are occupied by a greater proportion of Po, most soluble Pi is produced through this process (Tate 1984). However, net mineralization of Po depends on the availability of Pi to microbes. If decomposing substrates have a large C/P ratio and soil microbes are under starvation condition, mineralized Pi can be immobilized (Tate and Salcedo 1988). Thus, P itself can control accumulation of soil organic matter (Tate 1984; Tate and Salcedo 1988).

Our study sites (as will be described in detail) form a matrix of four altitudes and two geological substrates (sedimentary versus ultrabasic rocks) on Mount Kinabalu, Borneo. Soils on both substrates are more deeply weathered at lower than at higher altitudes (Kitayama 1992; Kitayama et al. 1998b) due to the warmer lowland climate. The two substrates represent different primary minerals which reflect different weatherability, and different secondary minerals in derived soils which presumably reflect different sorbing capacities for P. Sedimentary rocks on Kinabalu (e.g., sandstone and siltstone) generally contain abundant quartz (Jacobson 1970) which is inert to sorb P. Ultrabasic rocks weather faster, and contain much less silicon, but more iron and magnesium; derived soils are believed to contain richer iron oxides that are reactive with P.

We predict that on Kinabalu: (1) Ca-P, non-occluded P, and total P in soil decrease downslope, while Po and occluded P increase proportionately, reflecting increasing weathering intensity on both rocks; (2) availability of P (e.g., the pool of labile Pi) is greater on sedimentary than on ultrabasic rocks at the same altitudes because sedimentary rocks contain more quartz inert to P; (3) variation in P-use efficiency (PUE) of the rainforests reflects the availability of Pi in the rhizosphere in relation to altitude and geology.

Materials and methods

Study areas

The eight study sites were located on a south slope of Mount Kinabalu (4095 m, 6°05' N, 160°33' E) (Table 1). The four elevations are about 700, 1700, 2700, and 3100 m above sea level. A permanent plot was set up on a gentle slope at each site (varying area ranging from 1 ha at 700 m to 0.09 ha at 3100 m; Aiba and Kitayama 1999). Climate is humid tropical with a constant monthly mean air temperatures throughout the year. Mean annual air temperature is 27.5°C at 0 m, and decreases at a lapse rate of 0.55°C per 100 m (Kitayama 1992). Mean annual rainfall is ample at all sites ranging from 2000 to 3000 mm without any marked dry spell (Table 1). The biomass and stature of the forests are comparable between substrates at 700 m, but become increasingly dissimilar from each other upslope with a sharper decline on ultrabasic rock (Table 1; Aiba and Kitayama 1999).

The geological ages of the two substrates are similar to each other. Sedimentary rock consists of argillite, sandstone, and siltstone of the Trusmadi Formation that was deposited in the pelagic basin during the Eocene, and folded in the Miocene. Sandstone and siltstone contain >50% quartz (Jacobson 1970). The geology of the uppermost "sedimentary" site is actually granite which contains about 60% SiO_2. Ultrabasic rock intruded at depth in the upper Cretaceous, and was emplaced by faulting in the Miocene; it consists of serpentinite and serpentinized peridotite, and contains about 41% SiO_2, about 36% MgO and about 4% FeO (Jacobson 1970). The concentration of primary mineral P in the parent rock at each site is unknown.

Soil chemical analyses

Four soil pits, subjectively selected under closed canopy, were excavated to saprolite at each site in July 1996. The excavation at 700 m was stopped at 1 m depth. We collected a bulk soil sample from each horizon for chemical analysis. We then combined the same amounts (fresh weight) of soils from the corresponding horizons of the four pits at each site to produce composite samples. Composites were produced to allow a complete P-fractionation analysis on all horizons for all sites by reducing the number of soil samples. In addition, duplicate soil cores were collected from the middle of each horizon with a core sampler of known volume. Each composite sample by horizon was manually homogenized, with stones and roots removed, and immediately stored in a refrigerator at 4°C.

Within 2 weeks of the field sampling, we weighed 1.5 g of field-moist soils in duplicate into 50-ml polypropylene centrifuge tubes. Pi and Po were sequentially extracted following the method

Table 1 Description of the eight study sites on Mount Kinabalu, Borneo. Annual rainfall values are based on 1 year of measurement from November 1995 to October 1996 using data-logger systems established at sedimentary sites (the value of 3100 m is actually from 3300 m). Rainfall values at ultrabasic sites are assumed to be the same as comparable sedimentary sites

Site(m)	Actual altitude (m)	Annual rainfall (mm)	Forest stature[a] (m)	Above-ground biomass[a] (kg m^{-2})	Forest type
Sites on sedimentary rock					
700	650	2509	46.8	48.1	Hill dipterocarp rainforest
1700	1560	2714	30.0	28.0	Lower montane rainforest
2700	2590	2085	20.6	29.5	Upper montane rainforest
3100[b]	3080	3285	15.0	20.7	Subalpine forest
Sites on ultrabasic rock					
700	700	2509	65.4	54.2	Hill dipterocarp rainforest
1700	1860	2714	22.6	21.3	Lower montane rainforest
2700	2700	2085	14.2	10.8	Upper montane rainforest
3100	3050	3285	6.1	1.9	Subalpine forest/scrub

[a] Quantitative vegetation data after Aiba and Kitayama (1999)
[b] Actually underlain by granitic rock

of Tiessen and Moir (1993) using the following solutions (30 ml volume) in order: 0.5 M NaHCO$_3$ (adjusted to pH 8.5 with NaOH); 0.1 M NaOH; 1 M HCl; concentrated hot HCl; and, concentrated H$_2$SO$_4$. We omitted the step using anion-exchange resin to extract the most labile Pi, and started from the bicarbonate stage; we assumed that resin Pi is fully a subset of bicarbonate (NaHCO$_3$) Pi. Extracts of the NaHCO$_3$, NaOH, and hot-HCl solutions contained both Pi and Po; Pi in these extracts was determined after precipitating organic matter by acidifying subsample solutions to pH 1.5 with 0.9 M H$_2$SO$_4$. Other subsamples of the extracts were autoclaved with ammonium persulfate and 0.9 M H$_2$SO$_4$ to convert Po into Pi; this gave the total P. The concentration of Po in each extract was determined as the total P minus Pi. The concentration of Pi was determined using the Murphy-Riley method (Murphy and Riley 1962) on a spectrophotometer at 712 nm at pH 4.5.

All organic fractions (bicarbonate, hydroxide, and hot HCl) were summed as Po which may include different availabilities. The Pi extracted with 1 M HCl is defined as Ca-associated primary mineral P (Ca-P). The hot-HCl-extracted Pi, and the residue after hot HCl were summed as highly recalcitrant occluded Pi.

Subsamples of the field-moist soils were oven-dried at 105°C for 3 days to determine gravimetric soil moisture contents. The amounts of P fractions on an area basis were converted from the weight basis concentrations and bulk densities. Organic carbon (C) was determined on field-moist soils by the Walkley-Black wet digestion method (Nelson and Sommers 1982). Total N was digested by the micro Kjeldahl procedure, and determined as NH$_4$-N colorimetrically on a Burkard SFA-2 autoanalyzer. Soil pH was determined on a slurry of 1:1 fresh soil to H$_2$O.

Pi extraction with buried ion exchange resin

The ion exchange resin method was used in situ to estimate the supply rate of available Pi. We weighed 8 g of moist anion-cation mixed-bed resin (Bio-Rad, AG 501-X8, 20–50 mesh) into rings made of PVC pipe (40 mm orifice, 5 mm high), which were subsequently wrapped in acid-washed nylon stocking. At each site, we selected five positions, widely spaced under closed canopy on a gentle slope, and marked each with a PVC pipe. One ring was buried horizontally at 5 cm depth near each pipe by carefully cutting one section of the surface soil so as not to disturb the soil structure (i.e., five rings per site). At 700 m, the rings were further placed in 1-mm stainless steel mesh (tightly folded as a 10×10 cm bag) to protect them from termites. Resins were retrieved after 30–40 days. We repeated the placement of resins five times at regular intervals in 1 year from December 1996 to October 1997.

Collected resins were rinsed with ultra-pure water until free of soil particles, air-dried for 7 days, weighed, and extracted with 40 ml extracting solution (2 M KCl in 0.1 M HCl) by shaking for 30 min. The concentration of Pi in the extracts was determined by the same method as soil Pi, and expressed on an air-dry resin weight basis. The mean concentration of five positions over five placements was calculated to represent the annual supply of labile Pi at each site.

Litterfall P and PUE

A total of 20 traps (each with a 0.5-m^2 opening) were set up 1 m above the ground at 10-m intervals along two parallel 100-m lines at each of the four lower sites (700 and 1700 m), while 10 traps were similarly set up along two 50-m lines at each of the four upper sites (2700 and 3100 m). The contents of the litter traps were collected biweekly, oven-dried at 70°C for 3 days to determine mass by trap, and combined for chemical analyses. Annual mass of litterfall was calculated based on the 1-year measurement from 25 March 1996 to 24 March 1997.

Biweekly litterfall demonstrated distinct seasonality during the year. Therefore, we selected two sets of fallen litter under two extreme seasonal conditions for chemical analyses: one from April 1996 representing a high litterfall flux (corresponding to a drier season), and the other from January 1997 representing a low litterfall flux (a wetter season). Ground litter samples of 0.2 g were weighed in duplicate, and digested in a block digester with concentrated H$_2$SO$_4$ and 30% H$_2$O$_2$. The amounts of P in the digests were determined colorimetrically using the same method as for soil Pi. The annual fluxes of P that return to the soils through litterfall were determined as annual litterfall mass multiplied by the mean P concentrations of duplicates over the two seasons.

We calculated PUE as the ratio of annual litterfall mass to its annual P content (Vitousek 1982). PUE values were plotted against the annual amounts of Pi exchanged with buried resins, and the pool sizes of bicarbonate Pi and actively cycling P in the rhizosphere (defined as 30 cm deep). Actively cycling P was defined as total P minus occluded Pi, which might indicate the size of the P pool that could enter a biological cycle. In this procedure, we included hot-HCl-extracted Po (which may be chemically recalcitrant) in active P, because this fraction might also contain bioavailable particulate organic matter (Tiessen and Moir 1993). The non-linear relationships between PUE and pool sizes (Silver 1994) were fitted to a double exponential decay equation:

$$Y = a \times e^{(-bX)} + c \times e^{(-dX)}$$

where a, b, c, d are constants, Y=PUE, and X=pool size.

Table 2 Concentrations ($\mu g\ g^{-1}$) of soil phosphorus fractions on Mount Kinabalu. Means of two replicates on an oven dry weight basis (*CO₃-Pi* bicarbonate-extractable inorganic P, *OH-Pi* hydroxide-extractable inorganic P, *Ca-Pi* diluted-HCl-extractable Pi, *Occl-Pi* occluded inorganic P, *Po* organic P, *T-P* total phosphorus)

Site (m)	Depth (cm)	CO₃-Pi	OH-Pi	Ca-Pi	Occl-Pi	Po	T-P
Sedimentary substrate							
700	0–5	1.05	18.14	2.44	62.15	96.86	180.64
	5–15	0.18	13.88	5.52	56.04	72.56	148.18
	15–50	0.00	30.90	4.83	65.42	82.09	183.24
	50–100	0.00	0.00	3.78	56.03	48.24	108.05
1700	0–10	37.04	34.49	12.85	134.78	198.12	417.28
	10–18	2.00	5.87	3.03	48.41	99.14	158.45
	18–34	0.50	0.00	2.32	27.13	60.11	90.06
	34–58	0.00	0.00	8.32	37.52	47.94	93.78
2700	0–9	23.35	69.65	23.22	109.78	134.06	360.06
	9–17	3.42	20.98	7.61	86.82	81.00	199.83
	17–36	0.83	12.24	8.28	121.42	102.63	245.40
3100	0–2	23.44	67.42	29.14	76.95	94.37	291.32
	2–15	14.71	48.03	28.79	88.51	59.34	239.38
	15–43	9.08	44.96	28.09	81.85	84.43	248.41
Ultrabasic substrate							
700	0–5	4.14	41.45	15.85	6.18	78.52	146.14
	5–15	0.15	34.59	5.80	4.56	67.08	112.18
	15–50	0.19	11.67	4.64	5.14	43.09	64.73
	50–100	0.04	0.00	4.09	4.09	12.12	20.34
1700	0–4	0.91	5.58	2.41	46.47	13.85	69.22
	4–24	0.00	0.00	6.09	23.17	5.34	34.60
	24–49	0.06	0.00	7.59	3.32	16.82	27.79
2700	0–3	1.79	22.89	7.45	106.83	68.15	207.11
	3–18	1.51	9.11	6.06	62.83	24.58	104.09
	18–24	0.59	0.00	32.11	26.27	54.65	113.62
3100	0–16	0.33	0.00	1.37	17.85	32.12	51.67
	16–24	0.00	0.00	13.24	5.34	37.72	56.30

All chemical analyses were conducted at the chemistry laboratory of the Forest Research Center, Sabah, Malaysia. Internal standard samples were included in every batch to check the consistency of analyses. We analyzed validated foliar and soil samples sent from the Finnish Forestry Research Institute and results of total N and P were all within 10% of the mean for each sample. Results of all chemical analyses are reported as a mean of two replicates.

Results

Concentrations of soil P fractions varied widely across altitudes and geological substrates (Table 2). The concentrations of bicarbonate and hydroxide Pi in analogous horizons were greater on sedimentary than on ultrabasic rocks at comparable altitudes (except at 700 m). Moreover, the concentration of total P was always greater on sedimentary than on ultrabasic rocks at comparable altitudes. Greater amounts of bicarbonate Pi were found in upper horizons in all cases, suggesting effects of P pumping from lower horizons by plants, and consequently the importance of upper horizons in supplying the most labile Pi to plants. The concentrations of primary mineral Pi (Ca-Pi) were ample in the bottom mineral horizons, which were close to the saprolites, except at the two lowest sites. The concentrations of occluded Pi tended to be greater in the upper horizons, but other than that there were no consistent patterns across altitudes and substrates. The concentrations of Po were highest in the uppermost horizons at all sites (except for the 3100-m ultrabasic site), but showed no other consistent variation across horizons.

There were marked altitudinal trends in area-basis P content in the topsoil rhizosphere (30 cm) where most fine roots were found (Table 3). The pools of Ca-Pi and the most labile, bicarbonate Pi tended to increase with increasing elevation on sedimentary rock, but did not vary consistently on ultrabasic rock. However, there were no consistent patterns in total P across altitudes on either rock type, contrary to our prediction. On the other hand, total P in topsoils was always greater on sedimentary than on ultrabasic rocks at comparable altitudes. The amounts of organic C and total N in topsoils increased fivefold with increasing elevation on sedimentary rock, but did not consistently change on ultrabasic rock (Table 3). There were no parallel changes in organic C, total N and Po; instead, extremely large C to Po ratios exceeding 1000 were found at the 3100-m sedimentary site and the 1700-m and 2700-m ultrabasic sites.

The ratio of hydroxide-extractable (less labile) to bicarbonate-extractable (more labile) Po increased with increasing elevation on ultrabasic rock, but decreased on sedimentary rock (Fig. 1). Similarly, the ratio of hot-HCl-extractable (less labile) to bicarbonate-extractable (more labile) Po increased on ultrabasic rock, but de-
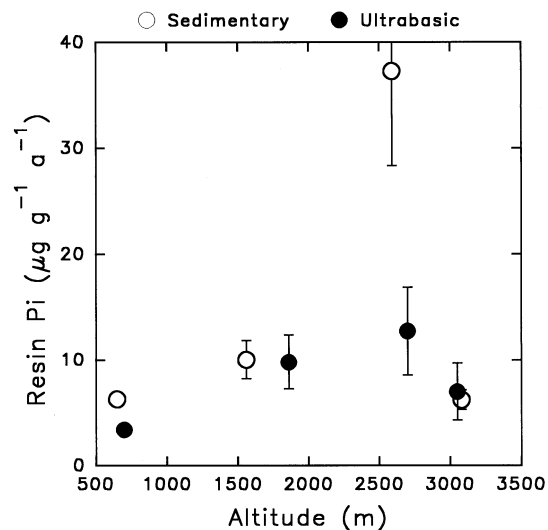
Table 3 Amounts of organic carbon (*O-C*), total nitrogen (*T-N*), and phosphorus fractions (see legend to Table 2 for abbreviations) in topsoils (30 cm), and ratios of organic carbon to organic phosphorus (*C/Po*) and total nitrogen to organic phosphorus (*N/Po*)

Site (m)	O-C (kg m^{-2})	T-N (kg m^{-2})	CO$_3$-Pi (g m^{-2})	OH-Pi (g m^{-2})	Ca-Pi (g m^{-2})	Occl-Pi (g m^{-2})	Po (g m^{-2})	T-P (g m^{-2})	C/Po	N/Po
Sedimentary substrate
700	3.53	0.38	0.07	8.40	1.71	22.19	28.99	61.36	122	13
1700	7.57	0.40	0.68	0.88	0.84	10.66	21.81	34.87	344	18
2700	14.0	0.88	1.65	7.41	3.10	31.16	29.24	72.57	484	30
3100	18.7	1.14	1.85	7.16	4.26	12.61	11.27	37.15	1702	104
Ultrabasic substrate
700	5.62	0.49	0.22	7.50	2.07	1.60	17.79	29.19	312	27
1700	5.72	0.40	0.02	0.11	1.58	4.93	2.32	8.97	2862	202
2700	8.42	0.64	0.23	1.33	2.76	10.11	7.04	21.47	1203	92
3100	6.67	0.50	0.05	0.00	1.22	3.07	7.68	12.02	833	62
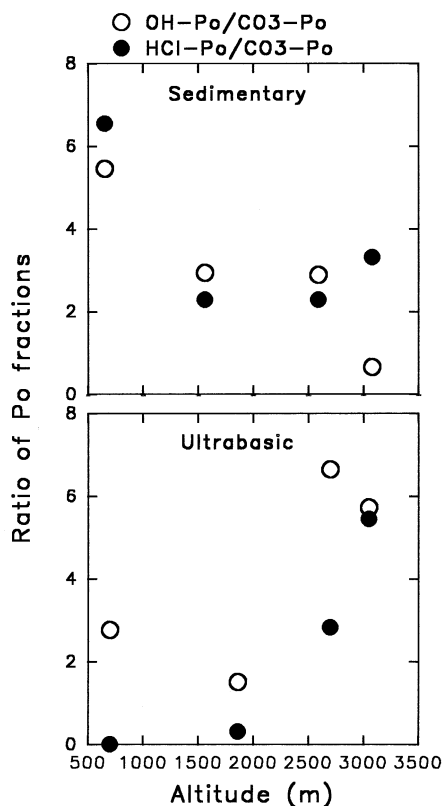
Fig. 1 Ratios of hydroxide-extractable to bicarbonate-extractable organic phosphorus (*open circles*), and ratios of hot-HCl-extractable to bicarbonate-extractable organic phosphorus (*solid circles*) along altitudinal gradients on Mount Kinabalu on sedimentary (**a**) and ultrabasic (**b**) rock

Fig. 2 Amount of soil Pi (µg g^{-1}resin year^{-1}) exchanged with buried ion exchange resins. Means (±SD) of five replicates per single site over five placements in 1 year from November 1996 to October 1997 are shown. Error bars (SD) are included to indicate within-site heterogeneity (*open circles* sedimentary sites, *solid circles* ultrabasic sites)

creased on sedimentary rock (Fig. 1). These altitudinal patterns indicated that changes in the proportion of recalcitrant to labile Po contrasted between the two geological substrates; the proportions of recalcitrant Po increased upslope on ultrabasic rock, but decreased on sedimentary rock.

The amount of Pi that was exchanged with buried resins increased from the lowest to middle altitudes, and then declined at the highest altitude; this pattern was con-

sistent on both substrates (Fig. 2). Approximately four- to sixfold greater amounts of soluble Pi were exchanged at middle than at the lowest altitude on both substrates.

Annual litterfall decreased with increasing elevation on both substrates (Table 4). The amounts were similar between the two substrates at 700 m, but the difference between the substrates increased with increasing altitude. The annual amounts of P that returned to the soils through litterfall decreased with elevation from 368 to 182 mg m^{-2} year^{-1} on sedimentary rock, and from 395 to 8 mg m^{-2} year^{-1} on ultrabasic rock (Table 4). The contribution of P by reproductive organs was high at the 700-m ultrabasic site (data not shown) due to an extremely high flux of flower/fruit litter during a rare masting event in 1996 (Kitayama et. al. 1998a). The contribution of P by the litter fraction that passes through a 2-mm mesh (i.e., dust) was disproportionately greater than those of the

Table 4 Annual litterfall (g m^{-2} year^{-1}), and amount (mg m^{-2} year^{-1}) of phosphorus contained in the litterfall, collected from 25 March 1996 to 24 March 1997 on Mount Kinabalu. Litterfall data are the means (SD in parentheses) of annual litterfall in 10–20 traps

	Sedimentary				Ultrabasic			
	700	1700	2700	3100	700	1700	2700	3100
Litterfall	1194 (279)	850 (244)	557 (162)	640 (162)	1199 (344)	660 (163)	635 (156)	189 (106)
Phosphorus	368	197	154	182	395	57	51	8
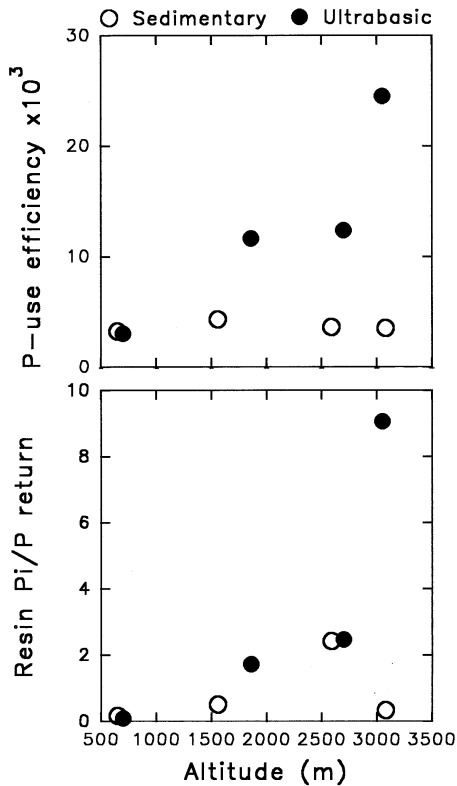
Fig. 3 Phosphorus-use efficiency of rainforests (**a**), and the ratios of buried-resin-exchanged phosphorus to phosphorus return through litterfall (**b**) on altitudinal gradients of Mount Kinabalu (*open circles* sedimentary sites, *solid circles* ultrabasic sites)

Fig. 4 Relationships between the phosphorus-use efficiency of rainforests (natural log) and the pool of bicarbonate inorganic phosphorus (CO$_3$-P) versus the pool of actively cycling phosphorus (total active P) on Mount Kinabalu. Curves were fitted using a double exponential decay model (*open circles* sedimentary sites, *solid circles* ultrabasic sites; *$P<0.05$)

other organs at all sites (unpublished data), indicating the importance of dust in ecosystem nutrient cycling.

PUE in above-ground NPP increased greatly with increasing elevation on ultrabasic rock, but remained low on sedimentary rock (Fig. 3). The ratios of resin-exchanged Pi to P return demonstrated similar altitudinal patterns as PUE; the ratio increased greatly with elevation on ultrabasic rock, but was consistently low on sedimentary rock (Fig. 3).

PUE values (log) decreased exponentially with increasing pools of available soil P when both substrates were combined (Fig. 4). The pool of actively cycling P (total P minus occluded Pi) was a better predictor of PUE than the pool of bicarbonate Pi (r^2=0.582, P=0.028 versus r^2=0.292, P=0.167). PUE values did not vary consistently with resin-exchanged Pi (r^2=0.022, P=0.726; data not shown).
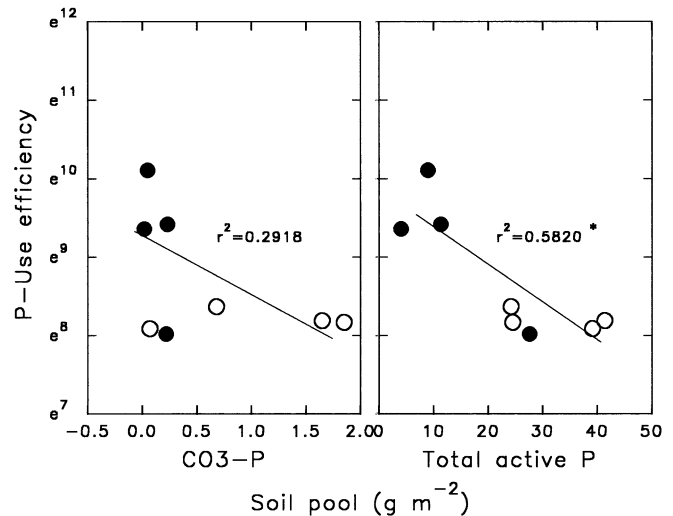
Discussion

Soil P fractionation

The pools of soil P fractions varied considerably across altitude and substrate, some in the manner we anticipated, but not in all cases. As predicted, both bicarbonate Pi and Ca-Pi increased with increasing altitude on sedimentary rock (Table 3). The altitudinal sequence of sedimentary sites thus seems to represent a direction of P fractionation associated with parent rock weathering (more weathered at lower sites). However, these fractions did not vary consistently on ultrabasic rock. Possibly, the altitudinal effects of ultrabasic sites are confounded by greater among-site variability of parent materials.

The pools (area-basis) of P fractions at all sedimentary sites and the lowest ultrabasic site are in the range reported from Amazonian rainforests on highly weathered acid leached soils in Venezuela (Tiessen et al. 1994) and from tropical forests on sandy acidic soils in Cameroon (Newbery et al. 1997). Resin+alkali-extractable Pi, Po, and total P in Venezuela range from 5.7 to 9.7, 6 to 12, and 17 to 39 g m^{-2}, respectively (to depths of 30–40 cm, calculated from Tiessen et al. 1994). Labile Pi, labile Po, and total P in Cameroon range from 0.9 to 1.1, 1.0 to

1.3, and 8.6 to 12.3 g m^{-2}, respectively (to a depth of 6 cm; Newbery et al. 1997). The use of different categories of P fractions from different depths does not allow direct comparison, but these values and ours are within the same order of magnitude. Labile Pi, Po, and total P pools in the three upper ultrabasic sites (particularly the 1700-m site) appear to be more impoverished than those of the Venezuelan and Cameroon forests.

The most striking difference from the Venezuelan and Cameroon sites (and in part old Hawaii sites of Crews et al. 1995) is the presence of the Ca-Pi fraction in our sites irrespective of altitude and substrate. The persistence of primary mineral Ca-Pi, which is also not expected from the model of Walker and Syers (1976), indicates that a terminal stage of pedogenesis has not been reached on Mount Kinabalu.

Closely parallel changes between bicarbonate Pi and Ca-Pi fractions (Table 3) indicate a significant contribution of bioavailable P from Ca-Pi. It should be noted that our bicarbonate fraction represents a pool of the most labile Pi that includes the resin Pi and bicarbonate Pi of the original method. We suggest that the pool of Ca-Pi is an important P source to the biota on Mt Kinabalu, especially at putatively less-weathered upper sedimentary sites. In contrast, the mineralization of Po was thought to be the major source of Pi to the biota in Venezuela where the Ca-Pi pool is depleted (Tiessen et al. 1994).

The persistent presence of non-occluded Pi and Po across altitudes and substrates also departed from our predictions. The persistence of non-occluded Pi in aged soils was also found in a chronosequential study in Hawaii (Crews et al. 1995). These authors suggested that plants symbiotic with mycorrhizae might dissolve occluded P under severe conditions of P deficiency, and reintroduce Pi to active P cycling. This mechanism is possible in our case, as has also been found by Tiessen et al. (1994) in Venezuelan rainforests. The infection rate by ectomycorrhizae was high, particularly at middle-elevation ultrabasic sites where total and labile P pools were among the lowest (K. Iwamoto, personal communication). Alternatively, the possibility of soil profile rejuvenation through the cycle of leaching and weathering cannot be dismissed.

Implications for above-ground vegetation processes

When the two substrates (that are drastically different in P pool) are combined, the overall pattern of PUE could be explained by the pool of actively cycling P (total P minus occluded Pi). The three upland sites on ultrabasic rock are highly P limited with a mere 4–10 g m^{-2} of the total soil P that may actively enter biological cycles, whereas all other sites contain pools greater than 24 g m^{-2}. We suggest that the pool size of active P is the primary determinant of the magnitude of P limitation on Kinabalu.

High PUEs are thought to indicate a P limitation to NPP and, conversely, less efficient forests occur at sites where available P is abundant (Vitousek 1982; Silver 1994). Do then the PUE patterns obtained on Kinabalu (Fig. 3) reflect soil P status alone? PUE on sedimentary rock did not decrease with increasing altitude although the pools of labile bicarbonate and primary mineral Pi increased. Conversely, PUE on ultrabasic rock increased steadily with altitude although labile and primary mineral Pi did not vary consistently. It seems that net effect of increasing altitude increase PUE per unit available soil P. The pattern of soil P fractions alone could not explain the altitudinal variation in PUE.

Even if the altitudinal sequence of sedimentary sites represents weathering intensity, current climate conditions (particularly thermal) also change with altitude. Consequently, patterns of P uptake by plants and biological adaptations to utilize labile and recalcitrant P are concurrently related to both the magnitude of soil weathering and current climate. More importantly, direct climatic constraints (primarily decreasing air temperature) on net assimilation per se are superimposed on altitudinal gradients. Thus, the interpretation of PUE variations is complex. As one plausible mechanism, the nutrient acquisition potential appears to be greater at P-limited sites owing to denser fine roots. The biomass of fine roots increased threefold with altitude on ultrabasic rock (K. Kitayama, unpublished data); this adaptation could improve the recycling of P, and increase PUE. Other mechanisms may also be involved (e.g., greater resorption efficiency before shedding leaves; Chapin 1980), but we have no direct evidence for these.

Earlier studies used the pool of available Pi as the best predictor of P limitation (e.g., Silver 1994). Surprisingly, the gross supply rates of soluble Pi (i.e., that exchanged with buried ion exchange resins) could not explain the variation in PUE. It is possible that the resins buried near the soil surface cannot trap net-available Pi to plants, nor available Pi at depth, while they may effectively estimate the gross supply rate near the surface and/or the mineralization efficiency of surface organic matter. Indeed, the correspondingly greater ratios of resin-exchanged Pi to P return with increasing PUE (Fig. 3) indicate that organic matter is more efficiently mineralized in these P-limited systems.

The suggested increasing efficiency of C mineralization with increasing elevation (=decreasing temperature) is inconsistent with the theory of decomposition kinetics that predicts exponentially decreasing rate constants with decreasing temperature (Johnson and Thornley 1985). If other factors are not limiting, the rate of C mineralization is also temperature dependent, and should decrease exponentially with decreasing temperature (e.g., Ellert and Bettany 1992). Possible mechanisms that can explain the relatively abundant supply of soluble P (besides the contribution from primary mineral Ca-Pi) despite colder temperatures at higher altitudes include mycorrhizal fungi symbiotic to plant roots, or cleaving of ester P from organic matter by extracellular enzymes from roots and microbes. The extremely high C to Po ratios at the sites where resin-exchanged Pi is high relative to bicar-

bonate Pi may indicate active cleavage of ester P from organic matter with extracellular phosphatase enzymes by roots and microbes (Tate 1984; Crews et al. 1995; Macklon et al. 1997). Other supporting evidence is the correspondingly high N/Po ratio at these sites suggesting active cleaving of P from organic matter relative to N release through mineralization (Table 3). The role of symbiotic fungi needs to be substantiated in the future.

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