PHOSPHORUS EFFICIENCY OF BORNEAN RAIN FOREST PRODUCTIVITY: EVIDENCE AGAINST THE UNIMODAL EFFICIENCY HYPOTHESIS

Gary D. Paoli,[1,4] Lisa M. Curran,[2] and Donald R. Zak[1,3]

[1]*Department of Ecology and Evolutionary Biology, University of Michigan, 830 N. University Avenue, Ann Arbor, Michigan 48109 USA*
[2]*Yale School of Forestry and Environmental Studies, 205 Prospect Street, New Haven, Connecticut 06511 USA*
[3]*School of Natural Resources and Environment, University of Michigan, Ann Arbor, Michigan 48109 USA*

Abstract. Plant communities on nutrient-poor soils are thought to use nutrients more efficiently to produce biomass than plant communities on nutrient-rich soils. Yet, increased efficiency with declining soil nutrients has not been demonstrated empirically in lowland tropical rain forests, where plant growth is thought to be strongly limited by soil nutrients, especially phosphorus (P). We tested for higher P uptake and use efficiency across a 16-fold soil P gradient in lowland Borneo by measuring the P content of aboveground net primary productivity (fine litter production plus new tree growth; ANPP) for 24 months. Extractable soil P was positively related to litter production, tree growth, and ANPP. Efficiency of P response (ANPP/available soil P), uptake (P uptake/available soil P), and use (ANPP/P uptake) increased monotonically with declining soil P and was significantly higher on P-rich soil than P-poor soil. Increased P uptake and use efficiency with declining soil P enabled higher than expected plant productivity on low P soils and thus strongly influenced spatial patterns of aboveground productivity throughout this lowland landscape.

A complementary P use efficiency index, the integrated canopy P (P_c) use efficiency of production (ANPP/P_c × residence time of P_c), was similar across the P gradient, but underlying dynamics varied significantly with soil P: on rich soils, ANPP/P_c was high and P_c residence time was low, while the converse held on poor soils. These contrasting strategies enabled rapid tree growth on nutrient-rich soils, where P limitation is relatively weak, and higher P conservation on nutrient-poor soils, where P limitation is relatively strong. The occurrence of contrasting P use strategies on high and low P soils has important implications for understanding spatial patterns of aboveground productivity, P cycling, and canopy tree species composition across the P gradient.

Key words: ANPP; Dipterocarpaceae; ectomycorrhizae; Indonesia; Kalimantan; parent material; phenotypic plasticity; phosphorus; response, uptake and use efficiency; trade off.

INTRODUCTION

Over the past two decades, plant nutrient use efficiency (NUE) has emerged as a central concept for understanding how declining resources determine spatial patterns of aboveground productivity, litter chemistry, and nutrient cycling in terrestrial ecosystems (Chapin 1980, Vitousek 1982). The fundamental tenet of NUE theory is that plant communities on nutrient-poor soils are less productive, but more efficient in their use of nutrients than communities on nutrient-rich soils. Species-level comparisons in temperate ecosystems support many key predictions of this theory—dominant plants on nutrient-poor soils tend to have lower maximum growth rates, low tissue nutrient concentrations, and leaf traits correlated with high plant-level NUE (Chapin 1980, Aerts 1998, Aerts and Chapin 1999). Likewise, community-level studies in a variety of temperate systems where the NUE of aboveground

net primary productivity (litter production plus tree growth; ANPP) was quantified have shown that nitrogen use efficiency (dry weight of ANPP per N content) increases as soil N availability declines (Gray and Schlesinger 1983, Pastor et al. 1984, Berendse et al. 1987).

In contrast to temperate ecosystems, few comprehensive studies of plant NUE have been conducted in diverse lowland tropical rain forests. Previous lowland studies have focused exclusively on the NUE of fine-litter production (Vitousek 1984, Silver 1994, Kitayama et al. 2000), which represents only 57–78% of ANPP in mature lowland forests (Clark et al. 2001*a*), and rarely quantified soil nutrients directly. The NUE of litter and tree growth components of ANPP in lowland forests have been quantified only in experimental model communities with one species of canopy dominant (Hiremath and Ewel 2001). Consequently, it is unknown to what extent increased plant NUE serves to maintain high ANPP in lowland tropical forests, where nutrient limitations to plant growth are considered widespread (Cuevas and Medina 1988, Ashton and

Fig. 1. Hypothetical relationship between soil nutrient availability and (A) productivity and (B) nutrient response efficiency. The curve in panel A depicts how ecosystem productivity varies with nutrient availability, where R_{min} on the x-axis represents the minimum nutrient requirement to achieve positive growth. The nutrient response efficiency curve in panel B depicts the ratio of productivity to nutrient availability at a range of resource levels. For resource levels $R1$–$R4$ on the x-axis, response efficiency is the slope of the line in panel A from the origin to the corresponding point on the productivity curve. (The figure is adapted from Pastor and Bridgham [1999].)
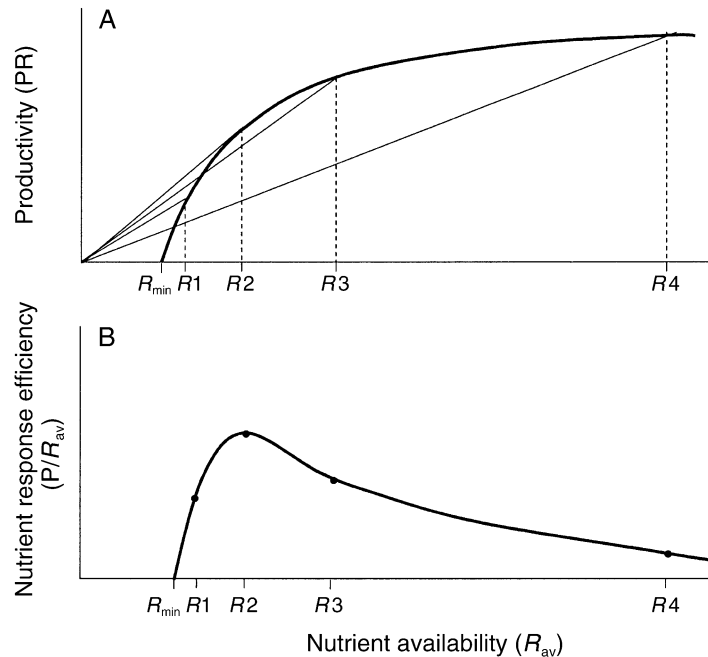
Hall 1992, Baker et al. 2003) and diverse species assemblages might create qualitatively different relationships than in temperate systems dominated by fewer species. The present study addresses this research need by quantifying the community-level phosphorus (P) uptake and use efficiency of litter production and tree growth across a 16-fold P gradient in species-rich lowland Bornean rain forest.

Ecological studies on the efficiency of plant nutrient uptake and use span multiple levels of biological organization—from leaves to ecosystems—and use a corresponding diversity of terminology (Grubb 1989). Even the usage of common terms, such as nutrient use efficiency, may differ among authors, leading to fundamental disagreement over interpretation of the same data (e.g., Knopps et al. 1997, Vitousek 1997). Bridgham et al. (1995) resolved much of this ambiguity by defining three distinct types of nutrient efficiency and explaining how variation in these parameters determine changes in aboveground productivity across nutrient gradients. Bridgham et al. (1995) define nutrient response efficiency as ecosystem productivity (PR) per quantity of nutrients in the soil (R_{av}). Nutrient response efficiency is defined by the relationship between ecosystem productivity and soil nutrient availability (Fig. 1A); the slope from the origin to any point on the productivity curve depicts how response efficiency changes with soil nutrients (Fig. 1B). Bridgham et al. (1995) then define nutrient uptake efficiency as the proportion of available soil nutrients acquired by plants (R_{ac}/R_{av}) and nutrient use efficiency as total net primary productivity (PR) per quantity of nutrients acquired during the same period (R_{ac}). Thus defined, nutrient response efficiency is the product of nutrient uptake and use efficiency:

$$\text{nutrient response efficiency} = \frac{PR}{R_{av}} = \frac{R_{ac}}{R_{av}} \times \frac{PR}{R_{ac}}. \quad (1)$$

A decline in ecosystem productivity with decreasing soil nutrients can thus be mitigated if nutrient response efficiency (PR/R_{av}) increases through more efficient nutrient uptake (R_{ac}/R_{av}), nutrient use (PR/R_{ac}) or both.

Nutrient response efficiency is thought to increase as nutrients decline in natural systems, but the form of this relationship and its appropriate quantification is contentious (Knopps et al. 1997, Vitousek 1997, Pastor and Bridgham 1999). Vitousek's (1982) formulation implied that NUE increases monotonically as resources decline, but this assumption is unrealistic as nutrients approach zero. Bridgham et al. (1995) countered that along nutrient gradients with a nutrient-poor extreme, efficiency is more likely to be unimodal, because on the poorest soils nutrient supply becomes inadequate to maintain plant growth for all but a few extremely stress-tolerant plant species. Bridgham et al. (1995) confirmed the prediction of unimodal response efficiency in nutrient-poor peatlands of North Carolina, using the litterfall NUE index of Vitousek (1982). Pastor and Bridgham (1999) also demonstrated mathematically that response efficiency across broad gradients is necessarily unimodal if two assumptions hold: (1) productivity is a positive, saturating function of resource availability; and (2) a resource threshold (R_{min}) greater than zero is required for positive net production (both properties depicted in Fig. 1).

Whether in most natural systems response efficiency increases unimodally or monotonically along nutrient gradients has important biological implications. From an ecosystem perspective, unimodal response efficiency implies that the severity of soil nutrient limitation on the poorest soils exceeds the capacity of the most efficient species to further adjust nutrient use and acquisition strategies and resist resource-based declines in productivity. Plant productivity on such soils will, consequently, be extremely low. From a community perspective, unimodal efficiency implies that changes in community membership along the nutrient gradient are likely to be determined by different ecological processes on opposite sides of the efficiency peak. At points to the right of the peak, where response efficiency increases with declining nutrients, shifts in community composition likely reflect the balance between ecological trade-offs of growth potential and nutrient conservation; community membership to the left of the peak likely reflects plant tolerance to extreme nutrient scarcity. Despite the potential importance of unimodal response efficiency in determining ecological patterns, and despite mathematical proof that response efficiency must be unimodal across broad gradients (Pastor and Bridgham 1999), unimodal efficiency has been tested for in only one natural system that did not examine tree growth (Bridgham et al. 1995). Thus, the generality of unimodal efficiency is unclear.

In this study, we quantify the community-level P uptake and use efficiency of rain forest trees across a 16-fold soil P gradient in lowland Borneo to test for evidence of increased efficiency with declining soil P, and to determine the form of this functional relationship. We focus on soil P given evidence for P limitations on plant growth in lowland forests (Vitousek 1984, Mirmanto et al. 1999, Baker at al. 2003) and documented covariation between soil P and plant species distributions throughout the tropics (Sollins 1998, Potts et al. 2002). We use the analytical framework of Bridgham et al. (1995) and Pastor and Bridgham (1999) because it enables (1) an unbiased statistical test of the form of the response efficiency curve, which suffers from autocorrelated axes; and (2) the decomposition of response efficiency into its component uptake and use efficiencies, which are controlled by different plant traits. We also compare strategies of canopy P allocation and use across the P gradient, and its relationship with productivity, by quantifying the integrated canopy P use efficiency (CPUE) of production. Integrated CPUE measures the cumulative net primary production earned per unit P investment in the canopy summed over its lifetime in the canopy. This parameter is a fundamental attribute of plant resource use strategy, reflecting the balance between contradictory pressures to minimize P losses via death of photosynthetic structures and maximizing plant growth potential. Variation in integrated CPUE and the plant traits underlying it, e.g., net assimilation rates, leaf lifespan, and nutrient resorption proficiency from leaves, have important implications for understanding spatial patterns of ecosystem dynamics and species distributions across nutrient gradients.

We test three hypotheses: (1) the P response efficiency of ANPP in lowland Bornean rain forest varies unimodally with soil P; (2) unimodal P response efficiency reflects underlying unimodal patterns of P uptake and P use efficiency across the P gradient; and (3) integrated CPUE increases with declining soil P, reflecting the joint effects of longer leaf life spans and canopy P residence times on P-poor soils.

METHODS

Study site

Our study was conducted at the Cabang Panti Research Station (~ 15 km^2) in Gunung Palung National Park (GPNP; 90 000 ha) in West Kalimantan, Indonesia ($1°00'–1°20'$ S, $109°–110°25'$ E). Annual rainfall at GPNP is 4125 ± 950 mm (mean $\pm$ SD for 1985–2002), with marked interannual variation corresponding to El Niño Southern Oscillation (ENSO) events. The core of the park contains two interconnected mountain peaks (1080 m and 1116 m above sea level [a.s.l.]), with western slopes that form a ridge system demarcating the watershed of the research site.

GPNP contains a diversity of distinctive lowland forest formations including peat swamps, freshwater swamps, and mixed dipterocarp forest on well-drained mineral soils up to ~ 300 m a.s.l. (Cannon and Leighton 2004). Underlying the well-drained lowlands is a variety of parent materials, including recent alluvial deposits, fine- to coarse-grained sedimentary rocks, and granite. Alluvial deposits are restricted to river banks from 5–15 m a.s.l. along the western river bank. Extending eastward up the mountain slopes to 40–140 m a.s.l. is a heterogeneous zone of sedimentary rock, beyond which forest is underlain by granite. Total soil N and cation content is significantly higher in alluvium than granite soils, and sedimentary soils are intermediate; soil texture is similar throughout the study area (G. D. Paoli, L. M. Curran, and D. R. Zak, *unpublished manuscript*). Local topography differs among parent materials, most notably between the largely flat alluvium at the base of the mountain and the sedimentary and granite substrates, which include narrow stream channels, broad gullys, gradual to steep slopes, and ridges and plateaus of various form. Soil depth is greater on the alluvium and sedimentary substrates than throughout the granite (G. Paoli, *personal observation*).

The lowland flora of GPNP is extremely species rich, reflecting the variety of parent materials and its influence on the species composition of woody plants (Cannon and Leighton 2004; G. D. Paoli, L. M. Curran, and D. R. Zak, *unpublished manuscript*). Forests on different parent materials share a number of plant families in common, but they differ markedly in species com-

position. The alluvium and sedimentary substrates share only 15% of their woody plant species ($\geq$10 cm dbh) in common with the granite (22% in common with each other), and only two species, *Strombosia ceylanica* Gardner (Olacaceae) and *Dipterocarpus sublamellatus* Foxworthy (Dipterocarpaceae), are among the 10 most abundant species on all three parent materials (Cannon and Leighton 2004). G. D. Paoli, L. M. Curran, and D. R. Zak (*unpublished manuscript*) found that turnover in dominant species of the Dipterocarpcaeae, which compose 61–79% of canopy tree basal area in lowland GPNP (Curran and Leighton 2000), was most strongly related to soil P. Soils of the alluvium and granite thus represent extremes of a habitat gradient and support distinct woody plant communities, especially in the canopy tree stratum.

The soil P gradient at GPNP covaries with elevation and other soil nutrients; however, three lines of evidence suggest that soil P is the stronger determinant of ecological patterns. First, continuous monitoring of climate throughout the elevational gradient from February 2000 to March 2001 showed no significant variation in rainfall volume or frequency, or maximum and minimum temperature (G. Paoli, *unpublished data*). This suggests that rainfall and temperature influences on productivity are similar throughout the lowland watershed. Second, extractable surface soil P is a better predictor of litter production, tree growth, and ANPP throughout the watershed than any single exchangeable or total nutrient parameter, or multivariate combinations thereof (Paoli 2004). Third, extractable soil P explains >70% of the covariation between soil factors and dipterocarp species composition throughout the watershed (G. D. Paoli, L. M. Curran, and D. R. Zak, *unpublished manuscript*). These findings suggest that soil P exerts stronger control on plant community structure and ecosystem dynamics throughout the study area than elevation or other edaphic factors.

Methodological approach

A complete accounting of ecosystem productivity and nutrient dynamics across this gradient requires measuring above- and belowground patterns of biomass increment, turnover, and nutrient content. However, as a first approximation of ecosystem-level patterns, we focus on aboveground dynamics and draw tentative conclusions based on these findings.

To examine how aboveground net primary productivity (ANPP) and P efficiency varies with soil P, three parameters are required: ANPP, P uptake by plants, and soil P content. It is extremely difficult to measure community-level nutrient uptake in intact natural communities, so we estimated total P uptake indirectly as the sum of P contained in fine litter production and new wood. This estimation relies on the assumption that P used for aboveground litter production and new wood is offset by an equal quantity acquired from soil during the same period.

A complete accounting of ANPP in large-stature tropical forests also presents unique challenges (Clark et al. 2001*b*), especially if all ANPP components are measured, including fine litter production, biomass increment, and biomass losses through herbivory, volatilization, and leaching. Here, we measured two components of ANPP—fine litter (leaves, reproductive material, and miscellaneous material <2 cm diameter) and live biomass increment—because these fractions compose 84–92% of ANPP in lowland tropical forests (data in Clark et al. 2001*a*).

To quantify ANPP and soil P pools, we established 30 circular plots of 30 m diameter (0.071 ha) between 5 and 240 m a.s.l. (study area ~340 ha). Ten plots were located on alluvial soils, eight on sedimentary soils, and 12 on granite soils (total sample area = 2.12 ha). Within each substrate, plots were positioned randomly with the requirement that recent gaps represented <30% of total plot area. Median distance between plots was 678 m (range 51–1747 m).

Soil sampling and P analysis

Soil samples were collected from surface (0–20 cm) and subsoil (40–50) layers. Using a stratified random design, six sampling points were positioned in each plot (5–24 m between points), and five soil cores (2 cm diameter) were collected at each point—one at the center and four at 2 m in cardinal directions. The five surface cores at each point were bulked (N = 6 surface samples/plot), as were all subsoil cores (N = 1 subsoil sample/plot). Soils were air dried, lightly ground, and sieved to remove particles >2 mm. The mineral fraction ($\leq$2 mm) was subsampled (~150 g), and stored in polythene bags for transport to the USA for analysis.

Extractable soil P was assayed using the Olsen method. We extracted 3 g of soil with 50 mL of 0.5 mol/L $NaHCO_3$. Total P was determined by digesting 500 mg of finely ground soil in sequential additions of concentrated hydroflouric acid, hydrochloric acid and hydrogen peroxide (Bowman 1990). Phosphorus concentration was determined colorimetrically using an ascorbic acid-molybdate complex measured at 880 nm on a MiltonRoy Spectronic20 spectrophotometer (Milton Roy, Ivyland, Pennsylvania, USA).

In most tropical soils, the total P pool is dominated by fractions unavailable to plants. Olsen extractable P, however, represents a relatively labile fraction of soil P adsorbed to mineral and organic surfaces of soil colloids. We analyzed P efficiency in relation to Olsen and total P, but present results of Olsen P only, as both were similar. In plant ecological studies, soil P concentration (μg/g) is a valid relative index of availability only if soil bulk density is uniform across sites. We instead use soil P content (kg P/ha) as a relative index of available P, computed as the product of P concentration (μg/g), bulk density (g/cm^3), and sampling depth (cm). Bulk density was estimated using Rawl's (1983) regression method, based on soil organic matter, sand, and clay

content. We also present soil P in μg/g for comparison with other sites.

Aboveground productivity

Total ANPP, defined as fine litter production plus live biomass increment, was monitored from March 1999 until March 2001 within all 30 plots.

Aboveground live biomass increment.—To quantify live biomass increment, all stems $\geq$10 cm dbh ($N = 1150$) were tagged, and diameter growth was monitored over 24 months. Stems <20 cm dbh ($N = 665$) were measured using a diameter tape and permanent red paint to mark the point of initial measurement; stems $\geq$20 cm dbh ($N = 485$) were fit with dendrometer bands made in the field using steel banding (modified from Brady 1944 and Liming 1957). Bands were installed in November 1998 and allowed four months to settle before initial measurements were taken in March 1999. Final growth measurements were taken 24 months later in March 2001.

Aboveground biomass increment was estimated following Clark et al. (2001a). Net increment in each plot was defined as the cumulative growth of all trees that survived through the observation interval plus the cumulative biomass of ingrowth of new recruits (trees $\geq$10 cm dbh) beyond the 10 cm dbh threshold (i.e., cumulative net biomass >10 cm dbh of new recruits). Choosing an appropriate allometric equation is critical to estimate biomass change from diameter increment. Brown's (1997) moist forest equation $Y = \exp(-2.134 + 2.53 \times \ln[D])$, designed for sites with annual rainfall of 1500–4000 mm and a distinct dry season, best matched the climate and forest structure of GPNP (Paoli 2004). Liana biomass increment was estimated using the equation of Putz (1983).

Aboveground fine litter production.—The moist forest equation of Brown (1997) estimates increments of stem wood, branches, and leaf biomass for individual trees. However, if initial and final measurements are widely spaced in time (24 months in our case), much leaf and twig biomass is produced and shed during the measurement interval and, therefore, unaccounted for in the regression estimate (Clark et al. 2001b). We therefore measured fine litter production directly and added this to regression estimates of biomass increment to estimate total ANPP.

Aboveground fine litter production was quantified using eight 0.49-m^2 litter traps made from polyester cloth of an extremely fine mesh (~0.3 mm) suspended 1 m above ground on wooden poles. All 240 traps were collected bimonthly. Contents were dried at 70°C for three days and then sorted into four fractions: leaf and leaf fragments ($\geq$1 cm), fine woody debris (<2 cm diameter), reproductive parts and residual fine material. For each collection in each plot, the leaf fraction was sorted by trap, weighed separately, and then bulked; the remaining fractions were first bulked across traps and then weighed. Leaves were weighed separately by

trap to quantify within-plot spatial heterogeneity in a separate study (G. Paoli, *unpublished manuscript*).

The relationship between ANPP and soil P content was analyzed following Bridgham et al. (1995), which provides a novel, statistically unbiased test of both the direction (increase or decrease) and form (unimodal or monotonic) of the relationship between response efficiency and soil nutrients. ANPP is modeled as a function of soil P using a modified Michaelis-Menten equation to test for (1) a saturating relationship between soil P and ANPP; and (2) a positive *x*-intercept (i.e., minimum nutrient requirement >0). Together, these two traits indicate unimodal response efficiency (Fig. 1; Pastor and Bridgham 1999). The model is

$$PR = \frac{(P_{ex} - P_{min}) \times PR_{max}}{(P_{ex} - P_{min} + \alpha)} \qquad (2)$$

where PR is productivity, P_{ex} is extractable P, P_{min} is the estimated minimum P requirement for positive growth, PR_{max} is the production asymptote and α is the half-saturation constant. Eq. 2 was parameterized using field data for PR and P_{av} and nonlinear regression to estimate P_{min}, PR_{max} and α (using SPSS 10.0; SPSS Inc., Chicago, Illinois, USA). A negative *x*-intercept ($P_{min} < 0$) does not imply that positive net production could occur at levels of soil P $\leq$ 0; this is impossible biologically. Rather, it indicates that P deficiency at the low end of the soil P gradient is insufficient to drive net production toward zero.

Because the response efficiency curve (PR/P_{ex} vs. P_{ex} in Fig. 1B) is defined by the relationship between productivity and available P (Fig. 1A), we parameterized this curve by dividing the parameterized function of Eq. 2 by P_{ex} (Pastor and Bridgham 1999). The precise form of this curve is potentially affected by autocorrelation of axes, so we assessed autocorrelation with a randomization procedure. We shuffled the pairing of independent and dependent variables, recomputed the variance explained using the same function derived form Eq. 2 and then repeated the procedure 1000 times recording the frequency of observing a simulated $R^2 >$ observed R^2. We emphasize, however, that our primary test for unimodal response efficiency uses Eq. 2, which is not biased by autocorrelated axes.

P content of fine litter and biomass increment

Because P response efficiency is the product of P uptake and use efficiency (Eq. 1), we examined how variation in P response efficiency reflects these underlying parameters. This required estimating P uptake, defined here as the P content of fine litter and new wood.

P content of fine litter.—Chemical analyses of fine litter fractions were conducted at different temporal resolutions. For leaf litter, two consecutive collections (one month) were combined and then analyzed. For the woody debris and fine miscellaneous fraction, four consecutive collections (representing two months) were

TABLE 1. Extractable soil P in lowland rain forest on three contrasting parent materials at Gunung Palung National Park, Indonesia.

Parent material	P concentration (μg/g)		P content (kg/ha)	
	Surface (0–20 cm)	Subsoil (40–50 cm)	Surface (0–20 cm)	Subsoil (40–50 cm)
Alluvium	27.0[a] (0.9)***	4.7[a] (0.9)***	47.9[a] (2.9)***	11.9[a] (2.4)****
Sedimentary	9.9[b] (1.0)	2.2[b] (1.2)	21.6[b] (3.3)	4.8[b] (2.4)
Granite	5.3[c] (0.8)	0.6[b] (0.2)	12.1[c] (2.7)	1.6[b] (0.4)

Notes: Values are mean Olsen P in surface (0–20 cm) and subsoils (40–50 cm) surveyed in multiple 0.07-ha plots ($n = 6$ samples per plot) in each parent material (alluvium, $n = 10$; sedimentary, $n = 8$; granite, $n = 12$ plots), expressed on a mass and area basis (standard errors are reported in parentheses). Surface soils were compared using a two-factor nested ANOVA, with sample nested within plot; subsoils were compared using one-way ANOVA. Means with different superscript letters are significantly different (Scheffé test).

     *** $P < 0.001$; **** $P \leq 0.0001$.

combined and then analyzed. Reproductive material was not analyzed, because we focused on litter fractions representing an investment in plant growth structures, and because reproductive material was <2% of total fine litter during the 24-month period. Samples were ground in the field and a 30 g subsample was taken for analysis.

The dry combustion method (Allen 1989, Jones et al. 1990) was used to analyze litter chemistry. Tissues were ground in a Tecator mill, and 500-mg samples were combusted at 400°C in a muffle furnace for 5 h. Ash was dissolved in a 20-mL solution of 20% HCl and 18% HNO_3. The solution was diluted 2:1 and P concentration was determined colorimetrically as described for soils. Two replicate samples from the solution were measured and the mean recorded, unless replicates differed by >5%, in which case a third replicate was measured.

For all plots, the P litter content in each fraction was defined as the product of litter mass and P concentration for that period. The P content of each fraction was summed over the 24-month period and then summed across fractions to estimate total P content of fine litter.

P content of live biomass increment.—New stem wood production represents ~90% of the estimated biomass increment of mature lowland forests in southern Borneo (Yamakura et al. 1986). Thus, rather than measure the P content of new leaves, branches, and stem wood separately, we measured the P content of wood and used this to estimate the P content of biomass increment. This approach underestimates the actual quantity of P used to produce biomass by an amount equal to the percentage of biomass increment composed of stems and leaves times the difference in P content between wood and *senesced* stems and leaves (i.e., the quantity P lost in production of these tissues). Because stems and leaves represent <10% of biomass increment, and the difference in P content between leaf and wood tissue varied similarly along the gradient, the estimation method used here does not likely affects our results.

Within this national park, we were not permitted to harvest wood samples from all of the 30 plots. Rather, we collected wood samples from a random subsample of tree species in the alluvium ($N = 13$, 32–112 cm dbh), sedimentary ($N = 5$, 37–86 cm dbh) and granite habitats ($N = 12$, 42–96 cm dbh). Wood samples (~200 g) were collected from the outer 2 cm of sapwood at two points on opposite sides of the bole. Samples were oven dried and transported to the USA for analysis using the methods described for litterfall. Sapwood samples were then used to estimate the mean P concentration of wood from each habitat. Although wood sampling on sedimentary soils was limited, estimated wood P concentration in this habitat (0.01%) was intermediate between wood of the alluvium and granite, consistent with the intermediate P content of sedimentary soils (Table 1; Appendix). We consider this a tentative validation of estimated wood P on sedimentary soils, and therefore use this value in subsequent calculations. To estimate the P content of biomass increment in each plot, we multiplied plot-wide biomass increment times the wood P concentration for the appropriate habitat. P content of litter and biomass increment was summed to estimate P use and, by definition, P uptake.

Estimated P uptake was used to compute the efficiency P uptake (P uptake/P available) and use (ANPP/P uptake). The extractable P pool was used as an index of soil P availability. We modeled relationships between P uptake and P availability (uptake efficiency) and between ANPP and P uptake (use efficiency) by modifying Eq. 2 as in Bridgham et al. (1995). For P uptake efficiency, the productivity term (PR) was replaced with P uptake (P_{up}), so that

$$P_{up} = \frac{(P_{ex} - P_{min}) \times P_{up\text{-}max}}{(P_{ex} - P_{min} + \alpha)} \qquad (3)$$

where $P_{up\text{-}max}$ is the predicted asymptote of P uptake. For P use efficiency, production was modeled as a function of P uptake by replacing the P_{ex} term of Eq. 2 with P_{up} to obtain the following:

$$PR = \frac{(P_{up} - P_{min}) \times PR_{max}}{(P_{up} - P_{min} + \alpha)} \tag{4}$$

As with response efficiency, we tested for unimodal P uptake and use efficiency by testing for an asymptotic shape and positive x-intercept in the curves derived from Eqs. 3 and 4, respectively. Also as above, P uptake and use efficiency functions were estimated not by fitting new functions, but by dividing parameterized Eqs. 3 and 4 by P_{ex} and P_{up}, respectively. The same randomization procedure was used to assess autocorrelation of the relationships.

Integrated canopy P use efficiency

Canopy P (P_c) productivity, defined as the ratio of ANPP to P allocated to the canopy (ANPP/P_c), is a parameter widely used to quantify instantaneous photosynthetic returns to investment in canopy P (Harrington et al. 2001, Kitayama and Aiba 2001). However, this static measure is of limited value for understanding efficiency relationships, because canopy P is a dynamic property requiring continuous P investment as leaves senesce and are replaced, often at rates that vary with soil nutrients (Herbert and Fownes 1999). We therefore computed the integrated canopy P use efficiency (CPUE) of production, which is the product of canopy P productivity (ANPP/P_c) and canopy P residence time (cf. Cordell et al. 2001). This parameter integrates the productivity of P_c summed over its lifespan in the canopy.

Total P_c (g P/m²) was estimated as the product of canopy leaf area (m²/m²) and foliar P concentration per unit leaf area (g P/m²), and then scaled to kg P/ha. Canopy leaf area was estimated for 28 of the 30 plots by analyzing hemispherical canopy photographs taken at the end of the study. Photographs were taken at plot centers ~1 m above ground, digitized, and analyzed using Hemiview 2.0 software (Delta-T Devices, Burwell, Cambridge, UK) to estimate canopy leaf area. The P concentration of fresh adult leaves was quantified for 58 trees throughout the study area. Fresh leaves were collected either from trees climbed specifically for this purpose ($N = 14$) or opportunistically within <24 h of new tree falls ($N = 31$) or large limb breaks ($N = 13$). Seven to 24 (median = 9) fully expanded leaves per tree were collected randomly from the upper crown. Sampling among substrates was uneven (25 in alluvium, eight in sedimentary, 24 in granite). Leaves were pressed, dried at 70°C for three days, traced to determine leaf area, weighed, and then bulked into one sample per tree. Pre-and post-drying leaf area did not differ significantly for 12 species tested individually (G. D. Paoli, *unpublished data*). Phosphorus concentration was determined as for fine litter. Total P_c for each plot was computed as the product of canopy leaf area and mean leaf P concentration of the appropriate habitat. Canopy P productivity was computed as the ratio of ANPP to total P_c.

Canopy P residence time was estimated for each plot as the ratio of P_c (kg P/ha) to rate of P losses in leaf litter (kg P·ha⁻¹·yr⁻¹). This P loss rate combines the effects of variation in leaf lifespan and leaf litter P, which varies with the efficiency of P resorption. This approach assumes that P translocated from senescing leaves stays in the canopy and is not used for other physiological functions in the plant, and thus represents a conservative estimate of P residence time. The integrated CPUE of each plot (Mg dry mass/kg P_c) was then computed as the product of ANPP/P_c (Mg·ha⁻¹·yr⁻¹/kg P_c·ha⁻¹) and P_c residence time (years). We also estimated leaf lifespan to assess its influence on P_c residence time, defined as the ratio of standing leaf biomass to leaf litter production. Leaf biomass was estimated as the product of canopy leaf area and mean specific leaf mass (g/cm²; inverse of SLA) of the appropriate habitat (Paoli 2004).

Data analysis

Nonlinear modeling of P response, uptake and use efficiency was performed as described above. Comparisons among parent materials of soil P, productivity, and leaf canopy characteristics were conducted using one-way ANOVA, and nested two-factor ANOVA in the case of surface soil extractable P, with soil sample nested within plot. Significant differences between groups were tested using Scheffé's post hoc test. Litter production was compared using nested two-factor, repeated-measures ANOVA. Relationships between canopy characteristics and soil P were analyzed using standard linear and non-linear regression techniques. All analyses were performed using SPSS version 10.

RESULTS

Soil phosphorus

Soil P content differed markedly among parent materials, creating a 16-fold gradient of surface soil extractable P (kg/ha; Fig. 2A). In a rank order of plots from high to low extractable P, P-rich soils were mainly in the alluvium whereas P-poor soils were predominately found in the granite. Mean extractable P varied significantly among parent materials and was highest in the alluvium, intermediate in the sedimentary, and lowest in the granite (Table 1). Surface soil extractable P was positively related to total P ($r^2 = 0.462$, $P < 0.001$; Fig 2B), but the relationship was nonlinear. Subsoil extractable P varied similarly across parent materials (Table 1).

ANPP and P response efficiency

Aboveground net primary productivity (ANPP; kg·ha⁻¹·yr⁻¹) increased with soil P and was well described by Eq. 2 ($R^2 = 0.802$; Fig. 3A). Contrary to expectations, this relationship did not saturate and the predicted x-intercept (P_{min}) was negative (Fig 3A). Thus, P response efficiency—the ratio of ANPP to soil

P—increased monotonically, not unimodally, with declining P (Fig. 3D). P response efficiency was well described ($R^2 = 0.863$) by the curve derived from the function in Fig. 3A (see *Methods*). The form of the response efficiency curve as depicted (Fig. 3D) was not an artifact of autocorrelated axes (1000 randomizations; $P = 0.024$).

Aboveground productivity was significantly higher in the alluvium than sedimentary or granite habitats, reflecting a nearly two-fold difference in tree biomass increment between forest on the alluvium and other substrates (Table 2). Fine litter production also was significantly higher in the alluvium (Table 2), but the difference was smaller in absolute and relative terms, suggesting a stronger effect of soil P on tree growth than litter production.

P uptake efficiency

Total P uptake (kg P/ha) increased with the Olsen index of soil P and was well described ($R^2 = 0.904$) by Eq. 3 (Fig. 3B). The relationship was weakly non-linear but, again contrary to expectations, the predicted *x*-intercept (P_{min}) was negative. Thus, despite the breadth of the P gradient, the efficiency of P uptake—the ratio of acquired P to available P—also increased monotonically with declining P (Fig. 3E). As in the case of P response efficiency, this relationship was well described ($R^2 = 0.889$) by the curve derived from the function of Fig. 3B. The form of the relationship between P uptake efficiency and soil P (Fig. 3E) was not an artifact of autocorrelated axes (1000 randomizations; $P = 0.002$). P uptake efficiency varied significantly among parent materials and was lower in the alluvium than other substrates (Table 3).

P use efficiency

ANPP increased with P uptake and was well described ($R^2 = 0.866$) by the curve derived from Eq. 4 (Fig. 3C). The relationship was clearly linear over the four-fold range of P uptake and the predicted *x*-intercept was again negative. Thus, P use efficiency—the ratio of ANPP to P uptake—also increased monotonically with declining P uptake (Fig. 3F). As with P response and uptake efficiency, the form of the relationship between P use efficiency and P uptake was not an artifact of autocorrelated axes (1000 randomizations; $P = 0.048$). Phosphorus use efficiency varied significantly among parent materials, and was higher on P-poor granite soils than other substrates (Table 3).

The overall increase in P use efficiency with declining P uptake reflected higher efficiency in the production of both fine litter and wood on P-poor soils. The P efficiency of litter production (kg dry mass/kg litter P content) increased monotonically with declining P (Fig. 4) and was significantly higher in forest on granite than other substrates (Table 3). The P efficiency of wood production showed the same trend, and was on
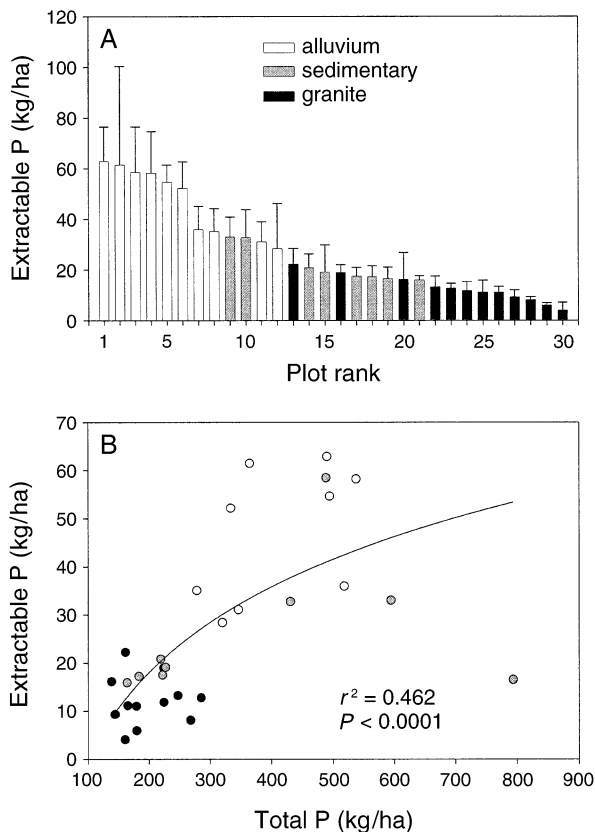

FIG. 2. (A) Gradient of Olsen extractable P content (mean + SE) in surface soils (0–20 cm), and (B) the relationship between surface soil extractable P and total P in lowland rain forest underlain by three parent materials at Gunung Palung National Park, Indonesia

average 22% higher on the granite substrate than the alluvium (Kruskal-Wallis test, $P = 0.102$; Table 3).

Integrated canopy P use efficiency

Total P_c (kg P/ha) was positively related to soil P (Fig. 5A) and significantly higher in the alluvium than other substrates (Table 4). This pattern reflected a trend toward higher leaf P concentrations (μg P/m^2 leaf area) on P-rich soils ($P = 0.057$; Table 4), not differences in leaf area, which did not vary significantly with substrate or soil P (Table 4; Fig. 5B). Estimated residence time of P_c declined with soil P (Fig. 5C) and was significantly shorter in the alluvium than other substrates (Table 4), reflecting shorter leaf life spans on P-rich soils (Fig. 5D). In contrast, canopy productivity (ANPP/P_c) increased with soil P (Fig. 5E) and was significantly higher in the alluvium than other substrates (Table 4). Consequently, integrated canopy P use efficiency (Mg ANPP/kg P_c), defined as the product of ANPP/P_c and P_c residence time, did not vary with substrate (Table 4) or soil P (Fig. 5F).

DISCUSSION

Three main objectives in this study were (1) to test for evidence that P response, uptake, and use efficiency
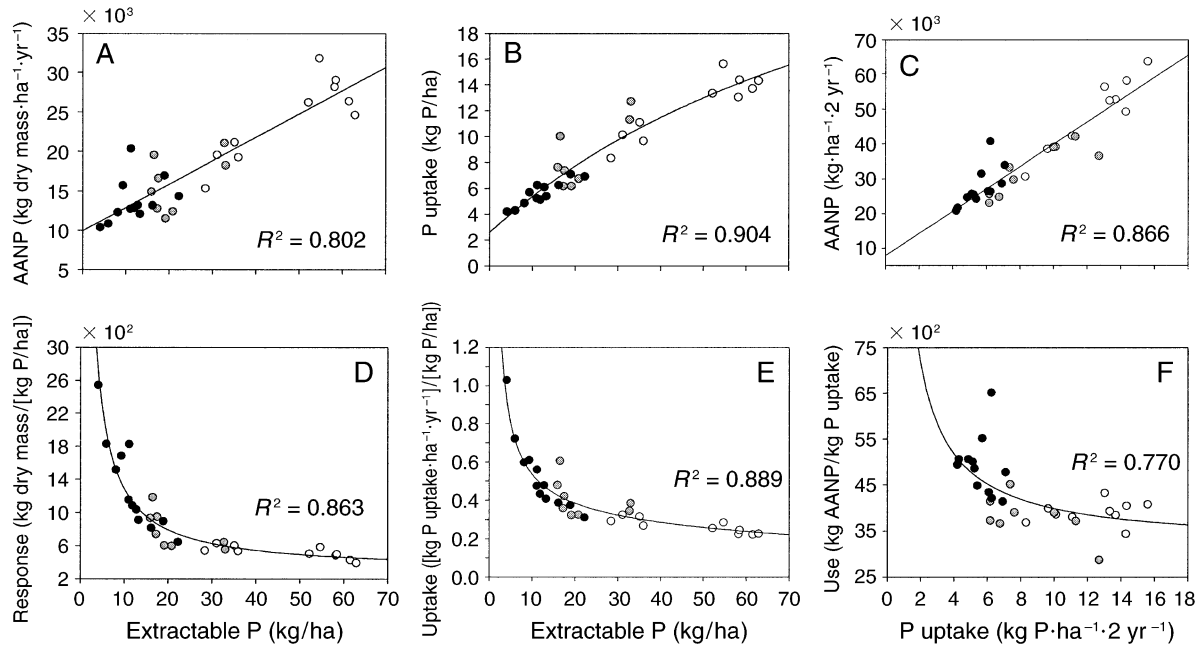
FIG. 3.   Variation in (A) aboveground net primary productivity, (B) P uptake, (C) P use, and the efficiencies of (D) P response, (E) P uptake, and (F) P use along a soil P gradient at Gunung Palung National Park, Indonesia. Curves in A, B, and C are modified Michaelis-Menten functions fit to the data using Eqs. 2, 3, and 4, respectively. Curves in D, E, and F were not fit to the data, but were derived from the functions defining curves in A, B, and C, respectively. In panels A, C, D, and F, note that the y-axis scale numbers must be multiplied by the power of ten shown to obtain actual values

increases with declining soil P in lowland tropical forest; (2) to determine the form of the relationships between P efficiency and soil P; and (3) to test for evidence of divergent canopy P use strategies across the P gradient. Phosphorus response efficiency increased significantly with declining soil P, but contrary to our expectation of a unimodal relationship, response efficiency increased monotonically across the 16-fold gradient. Increasing P response efficiency reflected monotonic increases in underlying efficiencies of P uptake and use as soil P declined, suggesting adjustments in plant strategy to enhance both P acquisition and its conversion to biomass. These findings provide direct evidence for increasing community-level efficiency

with declining P in lowland tropical forest, and suggest that unimodal response efficiency (Pastor and Bridgham 1999) may not be a general feature of lowland Bornean forests.

The integrated canopy P use efficiency (CPUE) of production did not vary systematically with soil P across the gradient, but underlying dynamics indicated divergent canopy P use strategies on contrasting soils. Plant communities on P-rich soils favored rapid growth at the expense of short leaf life spans and rapid canopy P turnover, while plant communities on P-poor soils used a more conservative P use strategy that favored long leaf life spans and low P loss rates at the expense of rapid growth. That integrated CPUE was similar on

TABLE 2.   Aboveground net primary productivity (ANPP) in lowland rain forest on three contrasting parent materials at Gunung Palung National Park, Indonesia.

Parent material	Litter production ($Mg \cdot ha^{-1} \cdot yr^{-1}$)	Aboveground tree biomass increment ($Mg \cdot ha^{-1} \cdot yr^{-1}$)	Total ANPP ($Mg \cdot ha^{-1} \cdot yr^{-1}$)
Alluvium	8.12[a] (0.24)****	16.0[a] (1.6)****	24.1[a] (1.6)****
Sedimentary	7.30[b] (0.65)	8.6[b] (1.9)	15.9[b] (1.2)
Granite	5.96[c] (0.18)	7.8[b] (0.8)	13.7[b] (0.8)

Notes: All parameters were monitored continuously over 24 months in multiple 0.07-ha plots in each parent material (alluvium, $n = 10$; sedimentary, $n = 8$; granite, $n = 12$ plots). All data are presented as means, with SE in parentheses. Tree biomass increment includes all stems ≥10 cm dbh. Litterfall was compared using two-way repeated-measures mixed-model ANOVA. Aboveground growth and total productivity were compared using one-way ANOVA. Total fine litter is the sum of leaves, twigs, and bark (<2 cm), and miscellaneous fine material (<1 cm). Means with different superscript letters are significantly different (Scheffé test).
    **** $P < 0.0001$.

TABLE 3. The efficiency of P uptake and use in lowland rain forest on three contrasting parent materials at Gunung Palung National Park, Indonesia.

Parent material	P uptake efficiency (kg P uptake· yr^{-1}/kg P·ha^{-1})	P use efficiency (kg dry mass/kg P)	P efficiency of wood production (kg dry mass/kg P)	P efficiency of litter production (kg dry mass/kg P)
Alluvium	0.266[a] (0.043)**	3898[a] (158)***	8656 (1493)	2275[a] (82)***
Sedimentary	0.405[b] (0.048)	3805[a] (177)	9621 (1121)	2410[a] (106)
Granite	0.532[b] (0.039)	4909[b] (144)	10 587 (870)	3016[b] (95)

Notes: Efficiency of P uptake is the ratio of P taken up to extractable P in surface soils. P use is the ratio of ANPP to P taken up by plants. P efficiency of wood and litter production is the ratio of dry mass to P content. All data are presented as means, with SE in parentheses. Efficiencies of P uptake, use, and litter production are means among multiple plots in each parent material (alluvium, $n = 10$; sedimentary, $n = 8$; granite, $n = 12$ plots) and were compared using one-way ANOVA. P efficiency of wood is the mean of multiple samples (alluvium, $n = 13$; sedimentary, $n = 5$; granite, $n = 12$ samples) and was compared using Kruskall-Wallis nonparametric test. Means with different superscript letters are significantly different (Scheffé test).

    ** $P < 0.01$; *** $P < 0.001$.

rich and poor soils appeared to reflect community-level trade-offs of equal magnitude between canopy P productivity (ANPP/kg P_c) and canopy P residence times across the gradient. Divergent canopy P use strategies on contrasting soils directly influence spatial patterns of ecosystem productivity, leaf litter chemistry, and possibly community composition across the P gradient.

Efficiency of P response, uptake, and use

Our finding that P response efficiency increased monotonically with declining P across the 16-fold gradient was inconsistent with our prediction of unimodal P response efficiency, and strongly determined patterns of ANPP throughout the watershed. For example, assuming a constant P response efficiency across the gradient based on the mean of the 15 most P-rich plots of Fig. 3D (~600 kg·ha^{-1}·yr^{-1}/kg soil P·ha^{-1}), predicted ANPP in the most P-poor plot of Fig. 3A (5 kg P·ha^{-1}) would be only 3 Mg·ha^{-1}·yr^{-1}. This value is less than one-third of observed ANPP in this plot. Thus, community-level changes in P response efficiency, and its underlying P uptake and use efficiencies, mitigated the effect of declining soil P on productivity and increased observed ANPP, especially on the poorest soils.

Bridgham et al. (1995) speculated that the declining segment of unimodal response efficiency might be observed only in extremely nutrient deficient ecosystems, such as the North Carolina peat swamps they studied. Thus, one possible explanation for the absence of unimodal response efficiency at GPNP is that, despite the breadth of the P gradient, the P content of poor granite soils is relatively high. In comparison to the P gradient quantified by Bridgham et al. (1995), the total P content of the poorest soils at GPNP is, indeed, 50% higher than that of the peat swamps they studied (~90 kg P/ha vs. 138 kg P/ha). However, in comparison to other tropical sites, the total P concentration of the poorest plots at GPNP (~60 μg/g) are lower than those reported across Borneo on sedimentary soils in Sabah, shale-derived soils in Brunei, and a variety of substrates in

Sarawak (Proctor et al. 1983, Burghouts 1993, Pendry and Proctor 1997). Moreover, total P concentrations of most granite soils at GPNP are only slightly higher than the poorest soils on highly weathered Tertiary sediments in Central Kalimantan (Mirmanto et al. 1999) and the extremely P-poor white-sand soils of caatinga forest in Venezuela (Herrera 1979). Thus, even though the P status of granite soils at GPNP is low by tropical standards, the severity of P deficiency was insufficient to cause a unimodal response efficiency. This suggest that, while it is impossible for response efficiency to increase monotonically without limits as nutrients decline, relatively few nutrient gradients, even in the P-deficient tropics, may include sufficiently poor extremes to cause unimodal response efficiency in natural communities.

Another possible explanation for the absence of unimodal response efficiency at GPNP is that, in contrast to the peat swamp communities studied by Bridgham et al. (1995), species turnover was continuous across
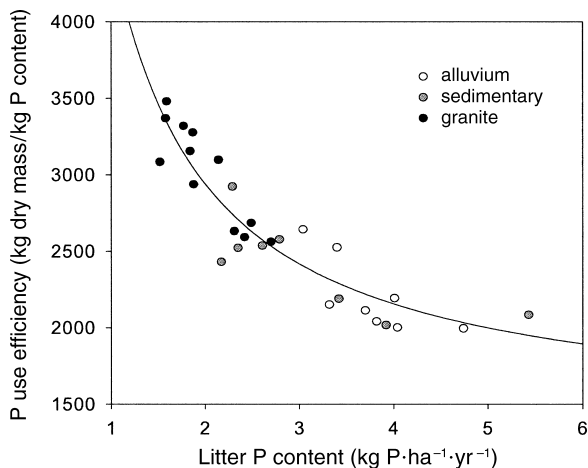

FIG. 4. The P use efficiency of litter production along a P gradient in lowland rain forest at Gunung Palung National Park, Indonesia
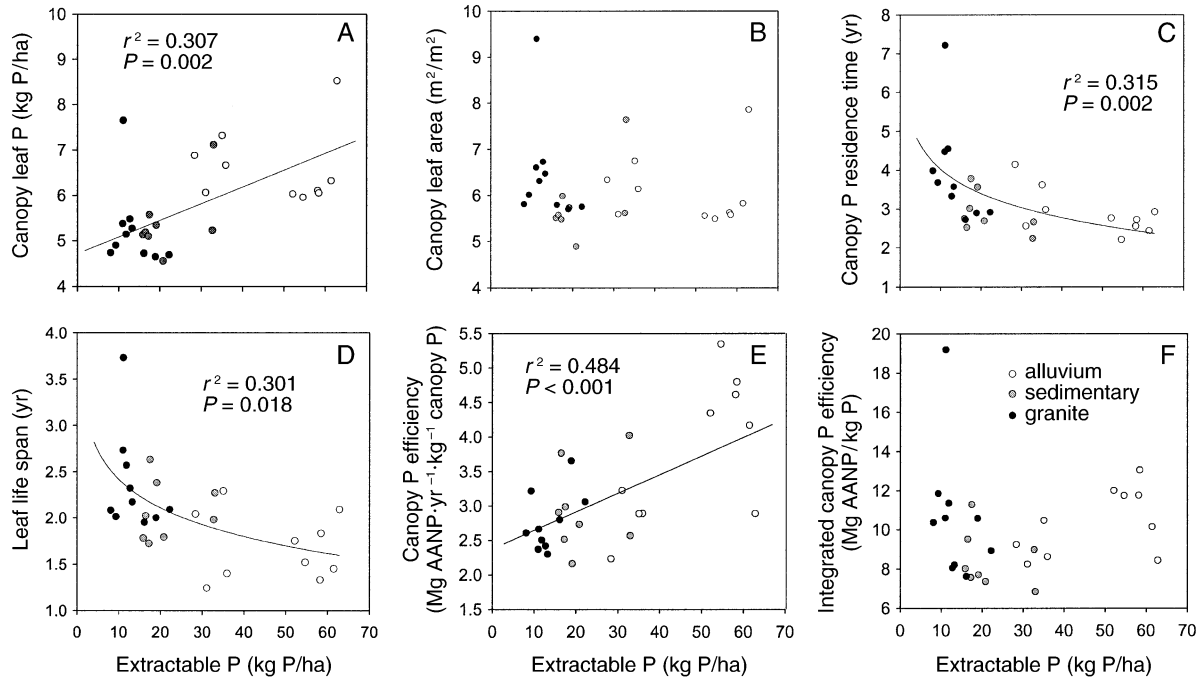
FIG. 5. The relationship between extractable soil P and (A) canopy leaf P, (B) canopy leaf area, (C) canopy P residence time, (D) leaf life span, (E) canopy P efficiency, and (F) integrated canopy P use efficiency in lowland rain forest at Gunung Palung National Park, Indonesia

the P gradient and may reflect the competitive replacement of relatively inefficient species by more efficient ones as soil P declined. Such a phenomenon would create a community-level pattern of monotonic increasing P response efficiency with declining P (Pastor and Bridgham 1999). In contrast to GPNP, low- and intermediate-P soils in the peat swamp studied by Bridgham et al. (1995) were dominated by communities that differed in stature (short vs. tall Pocosin) but not in species composition. Thus, the declining portion of the response efficiency curve observed by Bridgham et al. (1995) largely reflects a plastic, intraspecific phenotypic response to P deficiency. A similar plastic response was found by Lennon et al. (1985), who documented unimodal N response efficiency in sugar maple plantations along a soil N gradient using analytical

methods similar to those formulated by Bridgham et al. (1995). This suggests that in diverse plant communities, such as lowland tropical forests, where the species pool and, hence, variety of plant nutrient use strategies is relatively high, deterministic species replacement along nutrient gradients may render monotonic patterns of response efficiency more common than unimodal ones.

Our finding of monotonic response efficiency also indicates that the capacity of tropical plants to increase P uptake and use efficiency through physiological and other adjustments exceeded the severity of P limitations to growth. At GPNP, both P uptake and use efficiency increased significantly with declining P and together contributed to higher P response efficiency on poor soils (Figs. 3E and F). But, qualitatively, at low soil P,

TABLE 4. Canopy leaf characteristics in lowland rain forest on three contrasting parent materials.

Parent material	Leaf P content (μg/cm^2)	Canopy leaf area (m^2/m^2)	Canopy P mass (kg/ha)	Canopy P productivity (Mg ANPP/kg canopy P)	Canopy P residence time (yr)	Integrated canopy P efficiency (Mg dry mass/kg P)
Alluvium	11.3 (0.7)	6.07 (0.29)	6.6[a] (0.3)**	3.74[a] (0.24)*	2.89[a] (0.29)**	10.36 (0.75)
Sedimentary	9.9 (1.3)	5.80 (0.32)	5.4[b] (0.3)	2.95[ab] (0.27)	2.90[ab] (0.32)	8.39 (0.84)
Granite	8.9 (0.7)	6.46 (0.29)	5.3[b] (0.3)	2.76[b] (0.24)	3.93[b] (0.29)	10.66 (0.75)

Notes: Leaf P content is the mean among multiple trees within each parent material (alluvium, $n = 25$; sedimentary, $n = 8$; granite, $n = 24$ trees). All other parameters are means among multiple 0.07-ha plots (alluvium, $n = 10$; sedimentary, $n = 8$; granite, $n = 10$ plots). All data are means (with standard errors in parentheses) and were compared using one-way ANOVA. Differences in leaf P content were almost significant ($P = 0.057$). Means with different superscript letters are significantly different (Scheffé test).

 * $P < 0.05$; ** $P < 0.01$.

the pattern of increasing P uptake efficiency was more pronounced than P use. One possible explanation for relatively high P uptake efficiency at GPNP may be the prevalence of canopy tree species with ectomycorrhizal mutualisms. Members of the Dipterocarpaceae, the dominant family of canopy trees throughout Borneo, are obligate ectomycorrhizal plants (Smits 1994). Ectomycorrhizal fungi enhance plant acquisition of soil P through more extensive soil exploration and improved access to occluded, primary mineral, and organic forms of soil P (Dighton 1991, Fox and Comerford 1992*a, b,* Blum et al. 2002). Thus, the predominance of ectomycorrhizal canopy trees at GPNP and benefits of the mutualism may explain strongly increasing P uptake efficiency. Similar community-level NUE studies in other rain forest communities, particularly those where ectomycorrhizal plants are rare or absent, are necessary to assess whether monotonic increases in P uptake efficiency are a general feature of lowland tropical forests. Likewise, extending the P-poor end of the gradient at GPNP by including nutrient-poor peat swamp forests, which also occur at our site, would explore the generality of our findings on organic substrates.

Efficiency of canopy P use

Integrated canopy P use efficiency (CPUE) did not vary systematically across the P gradient. However, underlying strategies of canopy P conservation differed on P-rich and P-poor soils, resulting in divergent patterns of tree growth rate and canopy P cycling across the P gradient. Integrated CPUE estimates the cumulative net biomass earned by P investment in the canopy as the product of standing canopy P productivity (ANPP/kg P_c) and the residence time of P_c. Across the P gradient, estimated P_c residence time increased with declining soil P, and was on average 40% higher in forest on granite than the alluvium. However, canopy P productivity decreased with declining P and was on average 36% lower in forest on granite than the alluvium (Table 4; Fig. 5D). Thus, increased P_c residence time with declining P was completely offset by losses in P_c productivity, resulting in similar integrated CPUE across substrates and soil P conditions (Table 4; Fig. 5D). Notably, this finding conforms well to predictions made by Berendse and Aerts (1987) about an inverse relationship between whole-plant nutrient residence time and nutrient productivity, though here we focus on canopy P dynamics only.

Similar integrated CPUE across the P gradient, but variable P_c productivity and residence time, implies the occurrence of fundamentally divergent plant growth strategies on contrasting soils. The alluvium strategy enables rapid conversion of P_c to net biomass gain, favoring rapid aboveground growth at the expense of frequent canopy P replacement, while the granite strategy minimizes P_c losses by reducing the rate of P_c turnover at the expense of lower plant growth potential.

Changes in the efficiency of canopy P productivity (ANPP/kg P_c) across the gradient indicate that lower ANPP on poor soils was caused jointly by reduced soil P availability and more conservative canopy P use strategy. This implies a measure of abiotic and biotic control on ecosystem productivity.

Higher canopy P productivity on P-rich soils was related to higher leaf P concentrations and shorter leaf life spans (Table 4, Fig. 5D). These traits are positively correlated with maximum photosynthetic rates in tropical trees (Reich et al. 1991, Reich and Walters 1994, Raaimakers et al. 1995) and contributed directly to higher rates of tree growth in forest on alluvium. Higher canopy P residence time on granite soils resulted from longer leaf life spans (Fig. 5D) and lower leaf litter P concentrations (Fig. 4), the latter reflecting ~25% more efficient retranslocation of foliar P on granite soils prior to leaf senescence (Paoli 2004). These two traits are common mechanisms by which plants reduce nutrient losses and, accordingly, the minimum rate of nutrient supply required to survive (Aerts and Chapin 1999).

The occurrence of divergent canopy P use strategies on contrasting soils directly influences ecosystem-level, and potentially community-level, patterns across the P gradient. Higher rates of leaf turnover and leaf litter P concentrations on P-rich soils caused rates of P deposition through leaf litter that were on average ~80% higher in forest on alluvium than the granite (3.62 ± 0.18 vs. 2.01 ± 0.12 kg P·ha^{-1}·yr^{-1}; averages taken from Fig. 4). Higher P deposition rates and leaf litter P concentrations in the alluvium likely cause more rapid P return to soil through decomposition, thereby reinforcing spatial variation in soil P content due to underlying differences in geological substrate (Table 1).

From a community perspective, conservative P_c use strategies combined with higher P uptake efficiency on P-poor soils (Fig. 4) may be the cause of major shifts in tree species composition across the P gradient. Forests on the alluvium and granite substrates are dominated by different canopy tree species, whose distributions were significantly related to soil P (G. D. Paoli, L. M. Curran, and D. R. Zak, *unpublished manuscript*). Ecological studies in temperate plant communities have shown that trade-offs related to nutrient use strategy, especially maximum growth rate and minimum nutrient requirements, can be major determinants of species distributions across nutrient gradients (Aerts 1990, Berendse 1994). If community-level differences at GPNP reflect intrinsic differences between dominant species on rich vs. poor soils, then trade-offs related to nutrient use strategy may drive species turnover across the gradient. Alternatively, contrasting canopy P use strategies by plants on the alluvium and granite substrates may simply reflect a plastic phenotypic response to contrasting soil P levels, as found in *Metrosideros polymorpha* dominated montane rain forest along a P gradient in Hawaii (Herbert and Fownes 1999, Harrington et al. 2001). This distinction between intrinsic vs. phe-

notypic responses, and the interaction between them, has major implications for understanding the causes of species turnover across the P gradient and the relative importance of plant- vs. soil-mediated controls on ecosystem dynamics throughout GPNP. These subjects are important areas of future research.

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APPENDIX

A figure showing mean wood P content (%) vs. extractable soil P in lowland rain forest at Gunung Palung National Park, Indonesia, underlain by three parent materials, is presented in ESA's Electronic Data Archive: *Ecological Archives* E086-084-A1.