



Plant Adaptation and Phosphorus Limitation in Tropical Forests: A Theoretical and Empirical Assessment

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ABSTRACT

Ecosystem dynamics are shaped by plant adaptation to environmental stress, yet the conditions under which this occurs remain poorly understood. We developed a theoretical framework to predict how strategies used by tropical trees to cope with low-phosphorus (P) availability (that is, traits related to P uptake, and use) influence growth under P limitation. We then tested this framework against data on tree species in Borneo and a meta-analysis of results from pantropical nutrient addition experiments. Our theoretical framework predicts that plant traits associated with low-P environments, including enhanced P allocation to leaves, efficient P resorption, and root phosphatase activity, alleviate the negative effects of P scarcity more strongly for “inefficiently” growing plants, represented by large trees and old-growth forests, compared with saplings or secondary forests. In

agreement with this prediction, changes in traits related to low-P environments increased the potential relative growth rate of large trees more than small trees in Borneo. Finally, theoretical expectation was supported by a meta-analysis which revealed stronger P limitation in saplings and secondary forests than in old-growth forests. Together, these findings provide a novel framework to interpret the relationship between resource constraints and plant performance and reinforce the importance of accounting for plant adaption to predict ecosystem responses to P limitation in tropical forests.

Key words: allocation; fertilization; meta-analysis; nutrient productivity; nutrient-use efficiency; residence time; trait-growth relationship; uptake.

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HIGHLIGHTS

- We theoretically examined the effects of plant adaption on growth under P limitation.
- The theory predicts that P scarcity more strongly affects small trees than large trees.

- Empirical data and a meta-analysis for tropical forests supported the prediction.

INTRODUCTION

Environmental stresses in natural ecosystems have been defined as “the external constraints which limit the rate of dry matter production of all or part of the vegetation” (Grime 2001). This definition emphasizes the impacts of the low or excess supply of light, water, or mineral nutrients. However, environmental stress is determined not only by the stressors themselves, but also the nature and properties of the plants (Bijlsma and Loeschcke 2005; Davis and others 2005; Kitayama 2005). Indeed, plant adaptation (here narrowly defined as physiological mechanisms to maintain/enhance individual carbon gain or growth, which eventually maintains or enhances plant fitness through population progression) and species-specific variation in those adaptations play a fundamental role in shaping the long-term capacity of the biosphere to persist under abiotic change (Steffen and others 2015; Aoyagi and others 2023). Despite this, there remains little consideration of the extent to which plant adaptation and associated strategies can modify growth rate under environmental stress, nor the conditions in which plant adaptation is unable to mitigate against environmental stress.

To address how inherently acquired adaptive mechanisms modify the response of plants to environmental stress, we examined relationships among tree species adaptation, growth, and soil phosphorus (P) in hyper-diverse tropical rain forests as a model system. The growth of tropical trees is often presumed to be limited by P availability, because tropical soils are strongly weathered and low in bioavailable P (Vitousek and others 2010). This hypothesis is supported by variations in plant and soil N:P stoichiometry along latitudinal (for example, Vitousek 1984; Reich and Oleksyn 2004; Reed and others 2012) and soil-age gradients (Vitousek and others 1995; Richardson and others 2004; Hayes and others 2014), experimental manipulations of tropical tree seedlings (Zalamea and others 2016), species-specific measurements of tree trunk growth along natural P gradients in tropical forests (Turner and others 2018), and by a nutrient addition experiment in the Hawaiian Islands (Harrington and others 2001). However, the process of retrogression—a decline in tree biomass and productivity in forests growing on strongly weathered soils where P has been depleted (Peltzer and others 2010)—does not appear to occur in

species-rich tropical forests (Kitayama 2005), and a growing number of nutrient addition experiments have found that community-level tree growth rates in species-rich tropical forests do not respond strongly to an increase in the P availability (for example, Wright and others 2011; Alvarez-Clare and others 2013; Fisher and others 2013). Given the widespread low-P availability on strongly weathered tropical soils, why does the growth of tropical trees rarely respond to changes in P availability?

Wright and others (2018) suggested that plant adaptation underpins the lack of strong growth responses to P addition in tropical forests. Tropical trees might not respond to P addition because many species are adapted to low-P soils and their growth is, therefore, limited by other resources such as nitrogen (N), moisture, or light (that is, carbon, C). Adaptation to low P is conferred by several physiological mechanisms related to the ability to increase P-use and uptake efficiency (Veneklaas and others 2012; Aoyagi and others 2022); hereafter, we describe these physiological mechanisms as plant strategies to cope with P limitation. Efficient P uptake mechanisms include the synthesis of phosphatase enzymes in roots to acquire P from soil organic matter (Turner 2008; Yokoyama and others 2017), association with mycorrhizal fungi that are efficient at acquiring P (Treseder 2004), and secretion of organic anions from roots to mobilize sorbed forms of P in the soil (Lambers and others 2015). Efficient use of P in the plant can also be achieved through a variety of mechanisms, including the synthesis of galactolipids rather than phospholipids (associated with greater C fixation rate per leaf P; Lambers and others 2012; Garnier and others 1995), preferential P allocation to leaves by decreasing P stored in wood (Aoyagi and Kitayama 2016; Heineman and others 2016), efficient P resorption from wood and leaves (Freschet and others 2010; Hidaka and Kitayama 2011) and greater tissue longevity (Aerts 1990). Efficient P resorption and tissue longevity both reduce P loss from the plant in litterfall.

Although there are many potential strategies for plants to improve P-use and uptake efficiency, the effects of these strategies on the growth of tropical trees have not been examined quantitatively. As a result, the role of plant strategies in muting the growth response of old-growth tropical forests to P addition remains unknown. Interestingly, responses to experimental P addition seem to be greater in tropical secondary forests (Wright and others 2018), small-sized trees within a tree community (Alvarez-Clare and others 2013; Li and

others 2018), and seedlings (Lawrence 2003; Santiago and others 2012), suggesting that the effects of plant strategies might change in relation to tree size (that is, tree diameter, height, or ontogenetic stages); inherent strategies *de facto* do not function well in small plants compared with large trees (the interactive effect of P and light availability is discussed later). Clarification of the mechanisms underlying these size-dependent differences in P limitation are therefore critical for the development of a general understanding of the relationships between P availability, ecosystem productivity, and plant adaptation (or strategy), and for efforts to predict the response of tropical forests to future environmental change.

There is some evidence for size-dependent changes in traits related to P-use and uptake efficiency. Larger trees in Chinese tropical and subtropical forests exhibit higher resorption efficiency (Li and others 2018) and higher photosynthetic P-use efficiency (maximum photosynthetic rate per foliar P concentration) at a given specific leaf area (Liu and others 2010). Furthermore, theoretical (Falster and others 2011) and empirical (Hérault and others 2011; Rüger and others 2012; Gibert and others 2016) studies have shown that some functional traits (for example, leaf mass per area and wood density) are correlated strongly with growth rate and that trait–growth relationships change with tree size, possibly because resource allocation among organs varies considerably with tree size. Together, these findings suggest that rapidly growing small-sized forests or trees and slowly growing large-sized forests or trees might have different P economies. However, the physiological mechanisms by which tree size affects the pattern of P limitation remain unclear.

In this study, we aimed to elucidate the significance of tree strategies (that is, physiological mechanisms to improve P-use and uptake efficiency) on plant growth in low-P environments by examining patterns and mechanisms of size-dependent P limitation in tropical forests. To understand the relationship between adaptive traits and growth, we first developed a theoretical framework to predict how low-P strategies affect the growth rate of trees under P limitation, and how this varies in relation to tree size. Second, we quantitatively examined size-related variation in traits and their effects on growth in Bornean tropical forests with contrasting fertility. Finally, we conducted a meta-analysis of nutrient addition experiments conducted across the tropics, to understand the general patterns of nutrient limitation in relation to tree size and stand age.

MATERIALS AND METHODS

Background: How do Functional Traits Related to P-Use and Uptake Efficiency Affect Plant Growth and the Patterns of P Limitation?

Plant growth under limiting resources can be described mathematically using Liebig's Law of the Minimum, in which the realized plant growth rate equals the potential growth rate under limiting resource(s) as follows:

$$\text{Realized growth rate} = \text{minimum} (G_{\text{potential}}(\text{P}), G_{\text{potential}}(\text{N}), G_{\text{potential}}(\text{C}) \dots) \quad (1)$$

where $G_{\text{potential}}(X)$ is the potential growth rate when growth is limited only by resource X ($\text{g g}^{-1} \text{ year}^{-1}$). In this study, we used relative growth rate to compare growth rate among plants with different size classes. Growth rate at a limited P supply is indicated as $G_{\text{potential}}(\text{P})$. When $G_{\text{potential}}(\text{P})$ is the lowest among $G_{\text{potential}}(X)$, supplementation with P increases the realized growth rate (that is, P limitation). However, in low-P environments where $G_{\text{potential}}(\text{P})$ is improved by plant adaptation related to P-use and uptake efficiency, $G_{\text{potential}}(\text{P})$ is no longer the lowest among $G_{\text{potential}}(X)$. In such cases, the addition of P does not significantly affect the realized growth rate. Thus, the influence of plant traits on $G_{\text{potential}}(\text{P})$ must be examined to understand the quantitative relationship between plant traits and growth. These formulas can be applied to other nutrients such as N.

Theoretical Prediction: Size-Dependent Relationship Between Potential Growth Rate and Functional Traits

The muted growth response of old-growth tropical forests to P addition, and stronger P limitation in small trees and young forests in the tropics (Lawrence 2003; Alvarez-Clare and others 2013; Li and others 2018; Wright and others 2018), suggest that the effects of functional traits on $G_{\text{potential}}(\text{P})$ are weaker for small plants than for large trees. There are two possible mechanisms to explain size-dependent P limitation, which are not mutually exclusive: (i) larger trees have traits that are better adapted to low-P availability, such as higher nutrient resorption (mechanism 1, Figure 1a); and (ii) the effects of functional traits associated with high P-use and uptake efficiency on $G_{\text{potential}}(\text{P})$ are greater for larger trees; that is, there are greater

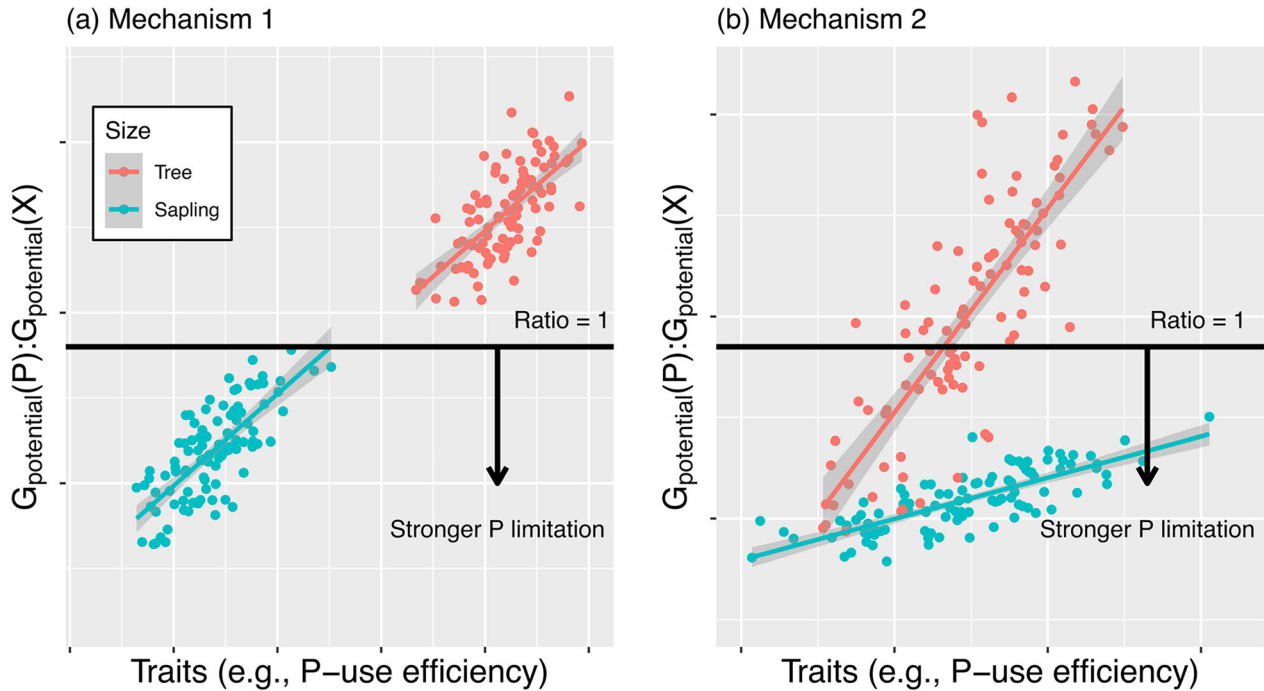


Figure 1. Hypothesized mechanisms for the size dependence of P limitation for plants growing in a low-P environment but having different traits. Each dot indicates an individual or species, and blue and red colors indicate small saplings and large trees, respectively. Both figures show hypothesized relationships between the values of traits related to the adaptation to P environments (for example, foliar resorption efficiency) and the ratio of potential growth rate under P limitation ($G_{\text{potential}}(P)$) to potential growth rate under the limitation of another resource ($G_{\text{potential}}(X)$). Whether growth of each plant is limited by P or not can be understood as follows. When $G_{\text{potential}}(P)$ is greater than $G_{\text{potential}}(X)$ (that is, $G_{\text{potential}}(P):G_{\text{potential}}(X)$ is greater than 1), the individual or species grows under the limitation of resource X (Eq. 1). Conversely, when $G_{\text{potential}}(P)$ is smaller than $G_{\text{potential}}(X)$ (that is, $G_{\text{potential}}(P):G_{\text{potential}}(X)$ is smaller than 1), the individual or species grows under P limitation. Generally, $G_{\text{potential}}(P)$ and $G_{\text{potential}}(P):G_{\text{potential}}(X)$ increase when the plant has a trait more adaptive to low-P environments, and thus, growth of plants in severely low-P environments can be limited by other resources. There are two possible mechanisms for the size dependence of P limitation that are not mutually exclusive: large trees have traits more adaptive to low-P environments than small saplings (mechanism 1), and $G_{\text{potential}}(P)$ and $G_{\text{potential}}(P):G_{\text{potential}}(X)$ increase more rapidly with increasing trait values for larger trees than for smaller saplings (mechanism 2). Both cases result in stronger P limitation for small saplings.

effects of changes in a trait on $G_{\text{potential}}(P)$ (mechanism 2, Figure 1b).

We examined whether larger trees have traits related to more efficient P use and uptake (mechanism 1) using data on the size-dependent variation in functional traits in Bornean tropical forests (see below). To examine the relationship between traits and $G_{\text{potential}}(P)$ (that is, mechanism 2), we developed a theoretical framework to predict how different types of traits linked to low P, that is, increasing P uptake, decreasing P loss, increasing P productivity (growth rate per canopy P content) or decreasing wood P concentration, change $G_{\text{potential}}(P)$, and how the effects of functional traits on $G_{\text{potential}}(P)$ vary in relation to tree size (Figure 2). We began by describing the relationship between $G_{\text{potential}}(P)$, P uptake, and plant functional traits related to P limitation (Eq. 2), formularized the

response of $G_{\text{potential}}(P)$ to a change in the four functional traits (Eq. 3–8), and discussed how tree size affects the relationship between $G_{\text{potential}}(P)$ and traits by determining factors affecting the relationship.

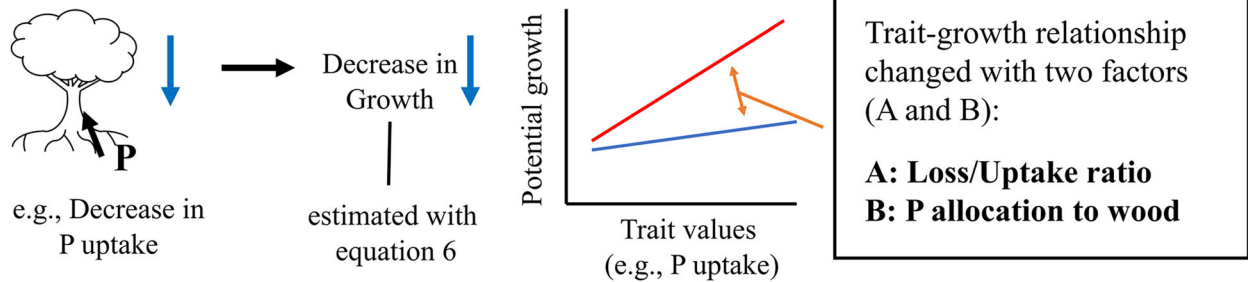
Phosphorus uptake rate ($\text{g P g}^{-1} \text{ year}^{-1}$) is decomposed into two factors: P accumulation in plant tissue ($\text{g P g}^{-1} \text{ year}^{-1}$) and nutrient loss ($\text{g P g}^{-1} \text{ year}^{-1}$) (Paoli and others 2005):

$$\begin{aligned} \text{P uptake} &= \text{P accumulation} + \text{P loss} \\ \text{P accumulation} &= P_w \times \text{RGR} \\ \text{P loss} &= \sum [P_i \times B_i \times 1/L_i \times (1 - R_i)] \end{aligned} \quad (2)$$

where P_w is the whole-plant P concentration (g P g^{-1}) calculated as the total amount of nutrients in the plant body divided by the whole-plant biomass (Aoyagi and Kitayama 2016); RGR is the relative growth rate ($\text{g g}^{-1} \text{ year}^{-1}$); P_i is the nutrient con-

Theoretical prediction: Size dependence of the trait-growth relationship

Step 1: Determine the relationship between traits and $G_{\text{potential}}(P)$ & key factors for the relationship.



Step 2: Discuss how size-related changes in tree properties affect the key factors

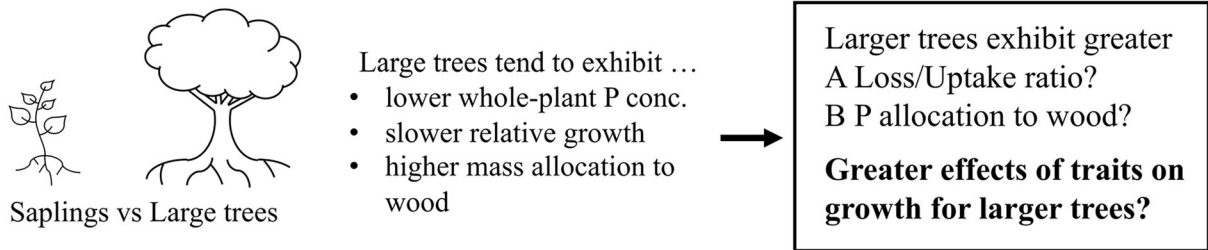


Figure 2. Overview of the theoretical prediction for how tree size affects the relationship between functional traits and potential relative growth rate under P limitation, $G_{\text{potential}}(P)$. We discussed if large trees show steeper trait-growth relationship than saplings (mechanism 2, Figure 1b). First, we determined how functional traits and $G_{\text{potential}}(P)$ are related to each other (Eqs. 4–8), and what are key factors for the relationship. The ratio of P loss to uptake and P allocation ratio to wood were two important factors (Figure 3). We then discuss how size-related changes in tree property such as biomass P concentration and biomass allocation affect the key factors. Overall, our framework suggested that effects of traits on growth were greater for larger trees than saplings.

centration of organ i , i = leaf, outer wood (we define outer wood as woody organs other than heartwood, which includes sapwood and inner and outer bark), and fine roots (g P g^{-1}); and B_i , L_i , and R_i are, respectively, the biomass allocation ratio (decimal), lifespan (year), and resorption efficiency before senescence (decimal) of each organ. Resorption efficiency is calculated as the ratio of the amount of resorbed nutrient to the nutrient content in the living organ (for example, live leaves, wood and fine roots) (Supporting Information S1.2).

Equation 2 describes implications of the effects of functional traits on $G_{\text{potential}}(P)$, and how these effects vary in relation to tree size. To examine the significance of functional traits on $G_{\text{potential}}(P)$, we assume that RGR is limited by P (that is, $\text{RGR} = G_{\text{potential}}(P)$) and show how $G_{\text{potential}}(P)$ responds to changes in functional traits with an α value: when $\alpha = 1.1$, the value is multiplied by 1.1. For example, an increase in P loss ($\alpha > 1$) results in

a decrease in $G_{\text{potential}}(P)$, because plants accumulate less P at a given P uptake (Eq. 2). The effects of functional traits on $G_{\text{potential}}(P)$ are expressed as the ratio of RGR at a trait value multiplied by α ($\text{RGR}_{\text{changed}(\alpha)}$) to base RGR (RGR_{base}) (Eq. 3).

$$\alpha(\text{decimal}) = \text{Trait value}_{\text{changed}} / \text{Trait value}_{\text{base}}$$

Effects of functional traits on $G_{\text{potential}}(P)$

$$= \text{RGR}_{\text{changed}(\alpha)} / \text{RGR}_{\text{base}}$$

(3)

We examined four types of tree strategies to cope with P limitation: increasing P uptake, decreasing P loss, increasing P productivity, and decreasing wood nutrient concentration. Phosphorus productivity was calculated as $\text{RGR} / \text{P}_{\text{leaf}}$. From Eqs. 2 and 3, the responses of $G_{\text{potential}}(P)$ to changes in different types of plant strategies can be expressed as:

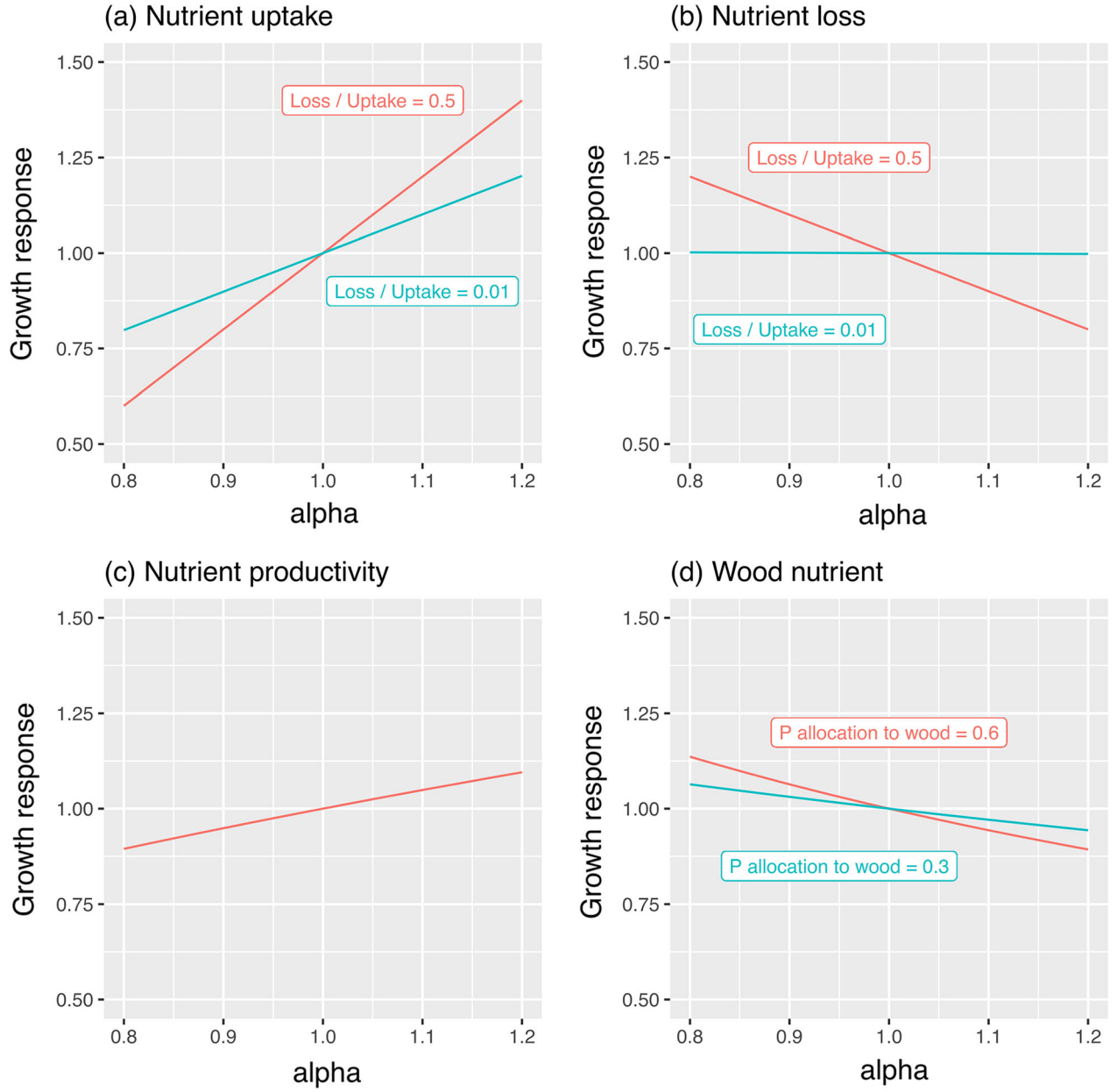


Figure 3. Model predictions for effects of changes in nutrient uptake **(a)**, nutrient loss **(b)**, foliar nutrient productivity (growth rate per foliar nutrient) **(c)**, and wood nutrient concentration **(d)** on potential growth rates under nutrient limitation. The alpha value represents the relative change in a quantitative functional trait; when alpha = 1.1, the value was multiplied by 1.1. Effects of nutrient uptake and loss (a and b) on growth varied with the balance between nutrient loss relative to nutrient accumulation or uptake (Loss/Uptake ratio, Eq. 2) whereas effects of wood nutrient (d) varied with the nutrient allocation to wood relative to nutrient allocation to leaves.

Effects of changes in P uptake on $G_{\text{potential}}$ (P)
(Figure 3a)

$$\begin{aligned} \text{RGR}_{\text{changed}(z)} &= (\text{Uptake} \times \alpha - \text{Loss})/P_w \\ \text{RGR}_{\text{base}} &= (\text{Uptake} - \text{Loss})/P_w \\ \text{RGR}_{\text{changed}(z)}/\text{RGR}_{\text{base}} &= (\alpha - \text{Loss}/\text{Uptake})/(1 - \text{Loss}/\text{Uptake}) \end{aligned} \quad (4)$$

Effects of changes in P loss on $G_{\text{potential}}$ (P) (Figure 3b)

$$\begin{aligned} \text{RGR}_{\text{changed}(z)} &= -1/P_w \times \text{Loss} \times \alpha + \text{Uptake}/P_w \\ \text{RGR}_{\text{base}} &= -1/P_w \times \text{Loss} + \text{Uptake}/P_w \\ \text{RGR}_{\text{changed}(z)}/\text{RGR}_{\text{base}} &= (-\alpha + \text{Uptake}/\text{Loss})/(-1 + \text{Uptake}/\text{Loss}) \end{aligned} \quad (5)$$

Effects of changes in foliar P productivity on $G_{\text{potential}} (P)$ (Figure 3c)

$$\begin{aligned} \text{RGR} &= (\text{Uptake} - \text{Loss})/P_w \\ (\text{RGR})^2 &= (\text{Uptake} - \text{Loss}) \times \text{RGR}/P_{\text{leaf}} \times P_{\text{leaf}}/P_w \end{aligned} \quad (6)$$

*Foliar P productivity (growth rate per canopy P content, $\text{g g}^{-1} \text{P year}^{-1}$) = $\text{RGR}/P_{\text{leaf}}$

$$\begin{aligned} \text{RGR}_{\text{changed}(\alpha)} &= [(\text{Uptake} - \text{Loss}) \times \text{RGR}/P_{\text{leaf}} \times \alpha \times P_{\text{leaf}}/P_w]^{0.5} \\ \text{RGR}_{\text{base}} &= [(\text{Uptake} - \text{Loss}) \times \text{RGR}/P_{\text{leaf}} \times P_{\text{leaf}}/P_w]^{0.5} \\ \text{RGR}_{\text{changed}(\alpha)}/\text{RGR}_{\text{base}} &= \alpha^{0.5} \end{aligned} \quad (7)$$

Effect of changes in wood P concentration on $G_{\text{potential}} (P)$ (Figure 3d)

$$\begin{aligned} \text{RGR}_{\text{changed}(\alpha)} &= (\text{Uptake} - \text{Loss})/ \\ & (P_{\text{leaf}} \times B_{\text{leaf}} + P_{\text{outer wood}} \times B_{\text{outer wood}} \times \alpha + P_{\text{Fine-root}} \times B_{\text{Fine-root}}) \\ \text{RGR}_{\text{base}} &= (\text{Uptake} - \text{Loss})/P_w \\ P_w &= P_{\text{leaf}} \times B_{\text{leaf}} + P_{\text{outer wood}} \times B_{\text{outer wood}} + P_{\text{Fine-root}} \times B_{\text{Fine-root}} \\ \text{RGR}_{\text{changed}(\alpha)}/\text{RGR}_{\text{base}} &= \\ & 1/[1 + (P_{\text{outer wood}} \times B_{\text{outer wood}})/P_w \times (\alpha - 1)] \end{aligned} \quad (8)$$

Note that we assume that a small change in a functional trait value does not influence other traits (discussed below). The four types of tree strategies affect $G_{\text{potential}} (P)$ differently and the effects of functional traits on growth vary considerably depending on two factors: loss:uptake ratio and P allocation to wood, $P_{\text{outer wood}} \times B_{\text{outer wood}}/P_w$ (Figure 3). In our model, $G_{\text{potential}} (P)$ decreases linearly with decreasing nutrient uptake and increasing nutrient loss (lower leaf lifespan and resorption efficiency), and the slope of the relationship is determined by the ratio of P loss to P uptake, that is, the balance between nutrient accumulation and loss (Figure 3a, b). In contrast, the relationship between wood P and $G_{\text{potential}} (P)$ varies with relative P allocation to sapwood (Figure 3d). Phosphorus productivity, that is, photosynthetic P-use efficiency, affects growth rate irrespective of the initial plant conditions (Figure 3c).

These equations indicate how the effects of functional traits on $G_{\text{potential}} (P)$ vary with tree size. The effects of functional traits on $G_{\text{potential}} (P)$ are much smaller for “effectively” growing plants with a low P loss:uptake ratio (that is, efficient P accumulation, Eq. 2) and lower P allocation to wood (that is, high P allocation to leaves). Plant individuals continue growing (P accumulation > 0) but the balance between accumulation and loss can

change with plant size. In general, a considerable decline in RGR and whole-plant P concentration with increasing tree size (West and others 1997; Elser and others 2000) can reduce P accumulation relative to P loss and possibly increase the loss:uptake ratio (Eq. 2). This yields a steeper relationship between traits and $G_{\text{potential}} (P)$ for larger trees. Furthermore, greater biomass allocation to wood in larger trees can be associated with high relative P allocation to wood, which is also associated with greater effects of traits on $G_{\text{potential}} (P)$. Consequently, we hypothesize that the effects of tree functional traits on $G_{\text{potential}} (P)$ increase with increasing tree size (Figure 1b).

Testing Theoretical Predictions Using Data from Bornean Tree Species

We investigated whether (i) larger trees have traits that are better adapted to low-P environments compared to small trees (mechanism 1, Figure 1a), and (ii) the effects of functional traits associated with P-use and uptake efficiency on $G_{\text{potential}} (P)$ are greater for large trees compared to small trees (mechanism 2, Figure 1b). To test these hypotheses, we quantitatively examined size-dependent changes in functional traits and their effects on $G_{\text{potential}} (P)$ using data for three different size classes (saplings and trees with a diameter at breast height, DBH of 10 and 30 cm) of canopy tree species in the Dipterocarpaceae in two Bornean tropical rain forests with contrasting soil nutrient availability (Table 1). We also examined the difference between the effects of traits on $G_{\text{potential}} (P)$ and $G_{\text{potential}} (N)$, because co-limitation by P and N is widely observed in tropical forests (Wright and others 2018), suggesting that the effects of traits are relatively small for $G_{\text{potential}} (N)$ compared to $G_{\text{potential}} (P)$.

Growth and Trait Measurements

Trait values and growth rates were determined on trees in and around 2-ha plots in the Tawau Hills Park (fertile site) and the Deramakot Forest Reserve (infertile site), Sabah, Malaysia (Borneo) (Table 1). These two forests differ in the availability of soil P and N, which reflects differences in soil parent materials (andesitic volcanic ashes and Tertiary sedimentary rocks, respectively). For three different size classes of each species (saplings and trees with 10-cm and 30-cm DBH), the relative growth rate (RGR) of living biomass (leaves, sapwood, and roots), biomass allocation, nutrient concentrations in each organ, and tissue turnover rate were mea-

Table 1. Climatic and Soil Characteristics of the 2-ha Vegetation Plot in the Tawau Hills Park and Deramakot Forest Reserve, Borneo

	Tawau Hills Park (fertile) (4° 24' N, 117° 53'E)	Deramakot Forest Reserve (Infertile) (5° 22' N, 117° 25' E),
<i>Climate factors</i> (Aoyagi and others 2016)		
Mean annual precipitation (mm)	2200	2500
Mean annual temperature (°C)	27	27
<i>Soil Factors</i> (Imai and others 2010; Aoyagi and others 2016)		
Parent materials	Andesitic volcanic ash	Tertiary sedimentary rocks
Soil pH in water	4.8	3.4
KCl extracted NH ₄ -N (µg g ⁻¹)	73.6	16.8
KCl extracted NO ₃ -N (µg g ⁻¹)	69.8	19.9
NaHCO ₃ -extracted inorganic P (µg g ⁻¹)	5.2	3.2
NaOH-extracted inorganic P, (µg g ⁻¹)	41.7	5.6
Total organic P (µg g ⁻¹)	158	50.3
Total P (µg g ⁻¹)	512	268

Soil inorganic N concentrations of both sites were very high, which might be a consequence of the storage time before extraction (Turner and Romero 2009). However, the apparent difference in leaf N concentrations between the sites (Table 2) indicates the significant among-site difference in soil N availability.

sured or estimated (Eqs. 2 and 4; see Supporting Information S1 for details of the procedures used to derive growth and trait values). The RGR, biomass allocation, nutrient concentrations in green leaves, stems, and roots, and leaf dynamics for the sapling stage were obtained from previous studies (Aoyagi and Kitayama 2015, 2016). Briefly, tree growth and leaf dynamics of saplings were monitored for ca. 17 months, and RGR and leaf loss rate at 3 mm diameter at ground height (DGH) and a high light condition (15% global site factors derived from hemispherical photographs) were estimated by linear regression. Leaf lifespan was calculated as the inverse of the annual foliar loss rate. To examine biomass allocation, more than 20 saplings (range 21–31) were harvested from each study species after DGH and light conditions were measured. Subsequently, biomass allocation to leaves at 3 mm DGH and under high light conditions was estimated for each species by linear regression. We further measured biomass allocation to fine roots (≤ 2 mm diameter) and resorption efficiency of saplings (Supporting Information S1.2. Table S1.4). We adopted the value for root lifespan (1 year) used in a previous simulation study (Falster and others 2011).

The detailed procedure to derive RGR of living biomass (heartwood is not included) at DBH = 10 and 30 cm is described in Supporting Information S1.1. Tree growth rates were calculated using data from the 2-ha census plots (Aoyagi and others 2016). To calculate the sapwood ratio required for the calculation of RGR of living biomass, we ob-

tained data on sapwood width for each species (Soerianegara and Lemmens 1993). The data were provided as a range, so we conducted analyses for both extremes. Leaf biomass allocation was estimated using allometric equations for Bornean tree species (Yamakura and others 1986; Niiyama and others 2010) (Supporting Information S1.2). Biomass allocation to fine roots of larger trees was estimated using the assumption of the pipe model that expects a fixed leaf area: fine-root mass ratio among/within species (that is, fine-root mass (kg) = $0.07 \times$ leaf area (m²)) (Falster and others 2011). Because fine-root allocation can change the pattern of nutrient loss, we also estimated the effects of functional traits on potential growth using an alternate assumption, that the leaf area: fine-root mass ratio of larger trees is the same as that of saplings. We measured the leaf area: fine-root mass ratio for each species using data from saplings (Table S1.5) and used these values to estimate fine-root allocation for larger trees. The estimated leaf area: fine-root mass ratios were much smaller than the values reported in a previous study (Falster and others 2011). Thus, the second assumption (leaf area: fine-root mass ratios are derived from the data of saplings and estimated for each species) leads to smaller nutrient loss than the first assumption (fixed leaf area: fine-root mass ratios for all species). See Supporting Information S2 for the results of the assumptions for sapwood width and fine-root allocation.

Canopy leaf and wood samples were collected from individuals with varying DBH (4–10 individu-

als for each tree species). We chose individuals with at least partly exposed crowns to minimize the potential effects of light availability on nutrient concentrations in the plant organs. We collected senescent leaves on the ground around three different large individuals at least 50 m apart and used the mean values of nutrient concentrations to calculate foliar resorption efficiency, as we did for saplings (Supporting Information S1.2). Only fresh senescent leaves with green to yellow cross-sections of the petiole were used for the analysis. We determined C, N, and P concentrations in the plant samples by the same method used for the senescent leaves of saplings (Supplementary S1.2). Leaf lifespans at 10-cm and 30-cm DBH were estimated from the global patterns for the relationship between leaf N concentration and leaf lifespan (Wright and others 2004) (Table S1.8). Leaf and wood nutrient concentrations were regressed against DBH, and nutrient concentrations at 10-cm and 30-cm DBH were estimated using the *lm* function in R for the subsequent analyses (Table S1.6, Table S1.7).

We estimated the nutrient (N and P) uptake, accumulation, and loss using Eq. 2 and trait data. Nutrient loss via heartwood formation was calculated as the nutrient concentration in outer wood (Eq. 2) multiplied by the heartwood formation rate (Supporting Information S1.3).

Testing the Hypothesis

First, differences in tree functional traits (leaf N and P concentrations, foliar resorption efficiency, and wood N and P concentrations) and estimated P-use and uptake characteristics (growth, leaf lifespan, leaf P productivity, uptake: loss ratio, and P allocation to wood) among size classes (saplings and trees at 10-cm DBH, and 30-cm DBH and soil types) were examined with the *lm* function in R (mechanism 1, Figure 1a). Models with the lowest Akaike information criterion (AIC) were considered to be the best-fit models. To examine the possible trade-off among traits related to adaptation to low-P environments, we tested the relationship between leaf P concentration (as an index of tree P status) and leaf lifespan, P resorption, P productivity, and wood P concentration using the *lm* function in R.

Subsequently, responses of $G_{\text{potential}}$ (P) to changes in four fundamental strategies related to P uptake, P loss, foliar P productivity, and wood P were estimated using two approaches based on Eqs. 4–8 (mechanism 2, Figure 1b). First, we simulated 10% changes in these functional traits (that is, $\alpha = 1.1$ or 0.9) and estimated the growth responses with Eqs. 4–8 using the data for infertile

sites. Second, we calculated trait differences between the fertile and infertile sites and estimated the growth responses to the hypothetical changes in trait values of species in the infertile site to the level of the species in the fertile site. Growth response to P uptake was not estimated for this category because P uptake is affected not only by species characteristics but also by soil P availability.

Patterns of Nutrient Limitation: A Meta-Analysis of Fertilization Experiments

Our hypotheses and theoretical predictions suggest that saplings and/or young forests respond to supplementation with P more markedly than do old-growth forests. To test this, we quantified the effects of P and N supplements on tree growth by conducting a meta-analysis of nutrient addition experiments for old-growth forests (five studies), young forests (six studies), and saplings (27 studies) in lowland tropical forests worldwide. We used the Thompson Reuters Web of Science database to search for “tropical forests” and either “fertilization”, “N addition”, “P addition”, or “nutrient addition” and similar search terms. All studies listed in Wright and others (2018) and Laurence and others (2003) were included. All forests with evidence of disturbance were classified as young. Wright and others (2018) conducted a meta-analysis of old and young forests. We added three recently published datasets on these size classes (Tian and others 2017; Li and others 2018; Cunha and others 2022). We extracted data on growth indicators (achieved biomass or relative and absolute growth rates in terms of height, diameter, and biomass), standard errors, sample size, study site, vegetation, species, light conditions, and soils. Based on the description of the study site and species in each study, we included experiments conducted in lowland and hill tropical forests (< 1100 m a.s.l.) and species from those regions only, and excluded savannas, plantations, mangroves, and montane forests. Only the growth responses of all size classes were used in the analyses of stand-level experiments. The literature lists and extracted data are provided in Supporting Information S4 and S5.

The effect size of nutrient supplements on tree growth in each study was calculated as a standardized mean difference (Hedge’s *g*) using the *escalc* function in the *metafor* package in R (Viechtbauer 2010), whereby the mean difference in plant growth between the treated and control groups was divided by the mean standard deviation. To estimate possible publication bias, we inspected funnel plots con-

Table 2. Trait Values Related to Nitrogen (N) or Phosphorus (P)-Use Efficiency in Relation to Soil Nutrient Availability and Size for Bornean Tree Species (Leaf N and P Concentrations, Wood N and P Concentrations, and N and P Resorption Rate Before Leaf Senescence)

	Leaf N (mg N g ⁻¹)	Leaf P (mg P g ⁻¹)	Wood N (mg N g ⁻¹)	Wood P (mg P g ⁻¹)	Resorption N (decimal)	Resorption P (decimal)
<i>Infertile</i>						
Sapling	18.8 ± 2.6	0.71 ± 0.09	8.29 ± 0.85	0.26 ± 0.06	0.33 ± 0.24	0.35 ± 0.16
10-cm DBH	15.3 ± 3.4	0.64 ± 0.13	0.79 ± 0.30	0.026 ± 0.012	0.42 ± 0.02	0.56 ± 0.1
30-cm DBH	16.4 ± 2.1	0.64 ± 0.13	0.95 ± 0.19	0.031 ± 0.007	-	-
<i>Fertile site</i>						
Sapling	20.4 ± 2.8	0.94 ± 0.19	8.76 ± 0.77	0.44 ± 0.11	0.30 ± 0.02	0.55 ± 0.05
10-cm DBH	17.7 ± 2.2	0.90 ± 0.16	0.91 ± 0.22	0.040 ± 0.027	0.50 ± 0.03	0.58 ± 0.06
30-cm DBH	18.7 ± 2.3	0.90 ± 0.16	0.91 ± 0.22	0.048 ± 0.020	-	-
<i>Statistics</i>						
Site Infertile	(-)*	(-)*		(-)**		(-)**
Size 10-cm DBH	(-)*		(-)**	(-)**	(+)	(+)
Size 30-cm DBH	(-)		(-)**	(-)**		
Infertile:10-cm DBH				(+)**		(+)
Infertile:30-cm DBH				(+)**		
<i>p</i>	***	***	***	***	0.12	*

The results of the linear regression analysis are also shown. (+) and (-) indicate that positive and negative coefficients in the best-fit model based on Akaike information criterion, respectively. The degrees of significance are described as follows: **p* < 0.05, ***p* < 0.01, and ****p* < 0.001.

Table 3. Relative Growth Rate of Living Biomass (RGR) and Estimated Characteristics Related to Phosphorus (P)-Use and Uptake Efficiency in Relation to Soil Nutrient Availability and Size for Bornean Tree Species

	RGR (g g ⁻¹ year ⁻¹)	Leaf lifespan (year)	P productivity (g mg ⁻¹ P year ⁻¹)	P uptake per unit fine-root mass (mg P g ⁻¹ year ⁻¹)	P loss/ uptake (decimal)	P allocation to wood (decimal)
<i>Infertile site</i>						
Sapling	2.37 ± 0.28	2.86 ± 0.59	3.41 ± 0.73	53.8 ± 61.1	0.08 ± 0.03	0.31 ± 0.01
10-cm DBH	0.09 ± 0.00	1.28 ± 0.52	4.94 ± 1.06	0.79 ± 0.09	0.70 ± 0.11	0.56 ± 0.17
30-cm DBH	0.07 ± 0.02	1.07 ± 0.23	4.97 ± 0.83	0.88 ± 0.18	0.77 ± 0.05	0.68 ± 0.06
<i>Fertile site</i>						
Sapling	3.17 ± 0.89	2.24 ± 1.02	3.32 ± 0.43	662 ± 791	0.09 ± 0.08	0.45 ± 0.06
10-cm DBH	0.14 ± 0.05	0.94 ± 0.20	5.77 ± 2.63	1.21 ± 0.32	0.63 ± 0.19	0.56 ± 0.19
30-cm DBH	0.09 ± 0.02	0.85 ± 0.20	4.85 ± 2.33	1.28 ± 0.28	0.72 ± 0.14	0.69 ± 0.13
<i>Statistics</i>						
Site Infertile	(-)**	(+)		(-)**		
Size 10-cm DBH	(-)**	(-)**	(+)*	(-)**	(+)**	(+)**
Size 30-cm DBH	(-)**	(-)**	(+)*	(-)**	(+)**	(+)**
Infertile:10-cm DBH	(+)			(+)**		
Infertile:30-cm DBH	(+)*			(+)**		
<i>p</i>	***	***	*	***	***	***

The results of the linear regression analysis are also shown. (+) and (-) indicate that positive and negative coefficients in the best-fit model based on Akaike information criterion, respectively. The degrees of significance are described as follows: **p* < 0.05, ***p* < 0.01, and ****p* < 0.001.

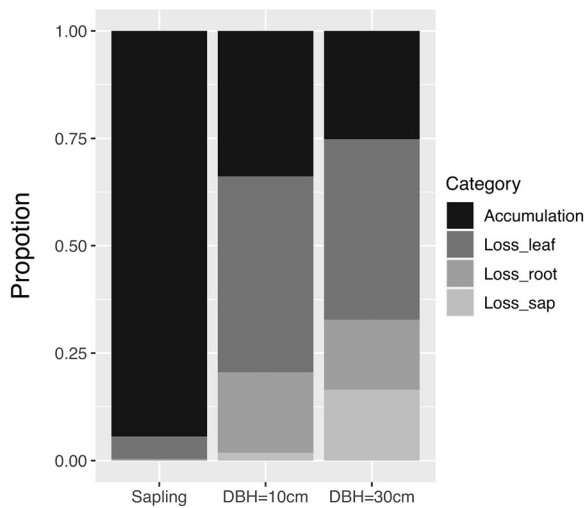


Figure 4. Proportions of phosphorus accumulation (black color) and loss via leaf, sapwood (or outer wood), and fine-root turnover (gray colors; Loss_leaf, Loss_sap, and Loss_root, respectively) for Bornean tropical tree species on the infertile soils (species in the Deramakot Forest Reserve, Malaysia). Values were estimated using empirical data and Eq. 2 with the minimum sapwood and fixed fine-root assumptions (see Materials and methods). Results based on other assumptions are shown in Supporting Information S2.

structured using the metabias function in the package of meta (Balduzzi and others 2019), which showed non-significant slopes for old-growth and young forests ($p > 0.05$). We conducted the analysis on both the full dataset of sapling data, and the dataset excluding studies with a high effect size (≥ 2.5), because a significant publication bias was detected for the full dataset ($p < 0.05$), but not for the dataset with exclusions ($p > 0.05$). All excluded data (Khurana and Singh 2004; Hashim and Hughes 2010; Gleason and others 2011; Cárate-Tandalla and others 2015) were from studies that applied P or P + N supplements.

We estimated the effect sizes of N, P, and complete nutrient (including N and P) supplements for different size classes (old-growth forests, young forests, and saplings) separately, with random-effect models (the restricted maximum-likelihood estimator) using the rma function in the metaphor package. For saplings, when growth responses of multiple species and soil types to nutrient supplements were reported, we first calculated the mean effect of all observations of the study and then used the rma function to combine the results of all studies, across multiple species and multiple soil types, weighting by the number of observations.

For saplings, light conditions can influence plant responses to nutrient supplements, so experiments under high and low light conditions (defined by ‘sun exposure or $\geq 15\%$ canopy openness’, and ‘under forest canopy or $< 15\%$ canopy openness’, respectively) were analyzed separately. The effect of nutrient supplementation was considered to be positive if the lower bound of the 95% confidence interval did not include zero. All statistical analyses were performed using the R software version 3.6.3 (R Core Team 2021).

RESULTS

Traits and Tree Performances in Relation To Size Classes in Borneo

Functional traits related to low nutrient availability varied in relation to site (soil type) and tree size. Leaf N and P concentrations and wood P concentrations were lower at the infertile site than the fertile site, whereas wood N concentration did not differ between sites (Table 2). Leaf N concentrations and wood N and P concentrations were lower for larger trees than for saplings, whereas leaf P concentrations did not vary among the size classes (Table 2). The efficiency of P resorption from senescent leaves was unexpectedly higher for the fertile site, whereas N resorption did not differ between the sites, possibly due to the high N availability at both sites (Table 2). Size class was not significant for nutrient resorption efficiency, suggesting that size exhibited limited effects (Table 2).

The RGR was lower at the infertile site (Table 3). We show the results of the minimum sapwood and fixed leaf area: fine-root ratio assumptions here (the pattern of effects of functional traits on $G_{\text{potential}}$ (P) did not change among the assumptions for sapwood width and fine-root allocation, Supporting Information S2). Estimated P productivity was greater for larger trees than for saplings, whereas leaf lifespan and P uptake per fine-root biomass were lower for larger trees (Table 3). Larger trees exhibited a higher nutrient loss: uptake ratio and higher P allocation to wood (Table 3, Figure 4), indicating that larger trees have a less efficient P economy.

As demonstrated in many previous studies, leaf lifespan increased and wood P concentration decreased with decreasing leaf P concentration (Figure 5). In contrast, P productivity (growth rate per canopy P content) and P resorption efficiency were not related to leaf P concentration (Figure 5).

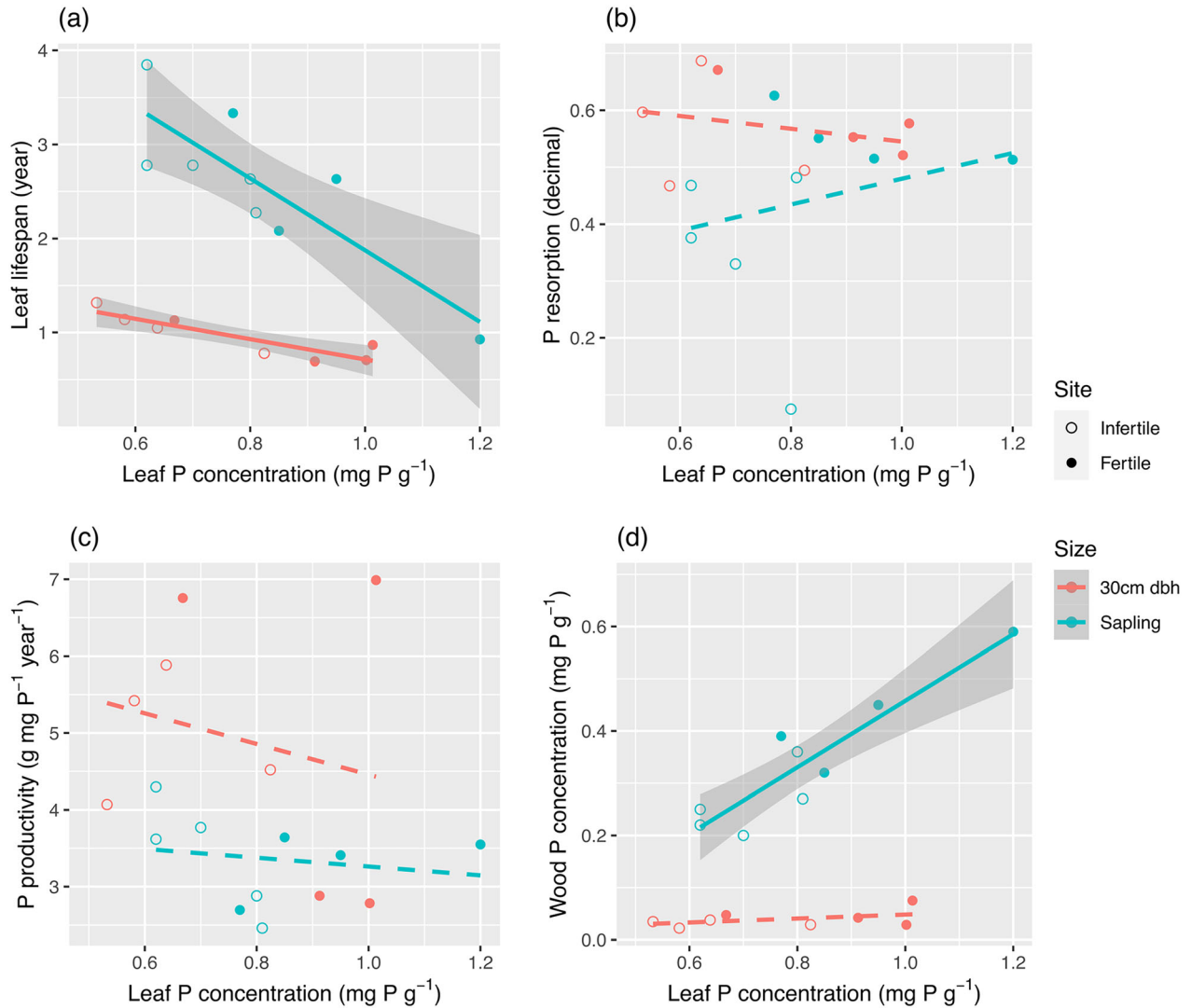


Figure 5. Relationships between leaf phosphorus (P) concentrations and traits associated with plant adaptation to low-P environments: leaf lifespan (a), P resorption (b), P productivity (c) and wood P concentration (d) for Bornean tree species. Linear regression analyses were performed separately for saplings (blue color) and trees with 30-cm diameter at breast height (DBH) (red color). Solid and dashed lines indicate significant ($p < 0.05$) and non-significant relationships, respectively. Shaded areas indicate confidence intervals. Each symbol indicates a species growing on either fertile (filled symbols) or infertile soils (open symbols). P productivity and leaf lifespan of large trees was estimated with Eqs. 6 and 7 with the minimum sapwood and fixed fine-root assumptions, and with leaf N concentration (Wright and others 2004), respectively (see Materials and methods).

The Effects of Functional Traits on Potential Growth Rate Under P Limitation

Effects of 10% changes in functional traits on $G_{\text{potential}}(\text{P})$ were greater for larger trees than for saplings; the effect size was 0.7–10.7%, 5.1–38.4% and 5.1–45.9% for saplings, small trees (10-cm DBH), and large trees (30-cm DBH), respectively

(Figure 6). When the values of functional traits of species at the infertile site changed to the levels observed in species at the fertile site, $G_{\text{potential}}(\text{P})$ decreased by 0–14.4%, 4.7–61.7% and 0–67.9% (for saplings and trees with 10-cm and 30-cm DBH, respectively; Supporting Information S2.9). The effects of changes in functional traits on $G_{\text{potential}}(\text{N})$ to the levels observed in species at the fertile site also increased with increasing tree size (Sup-

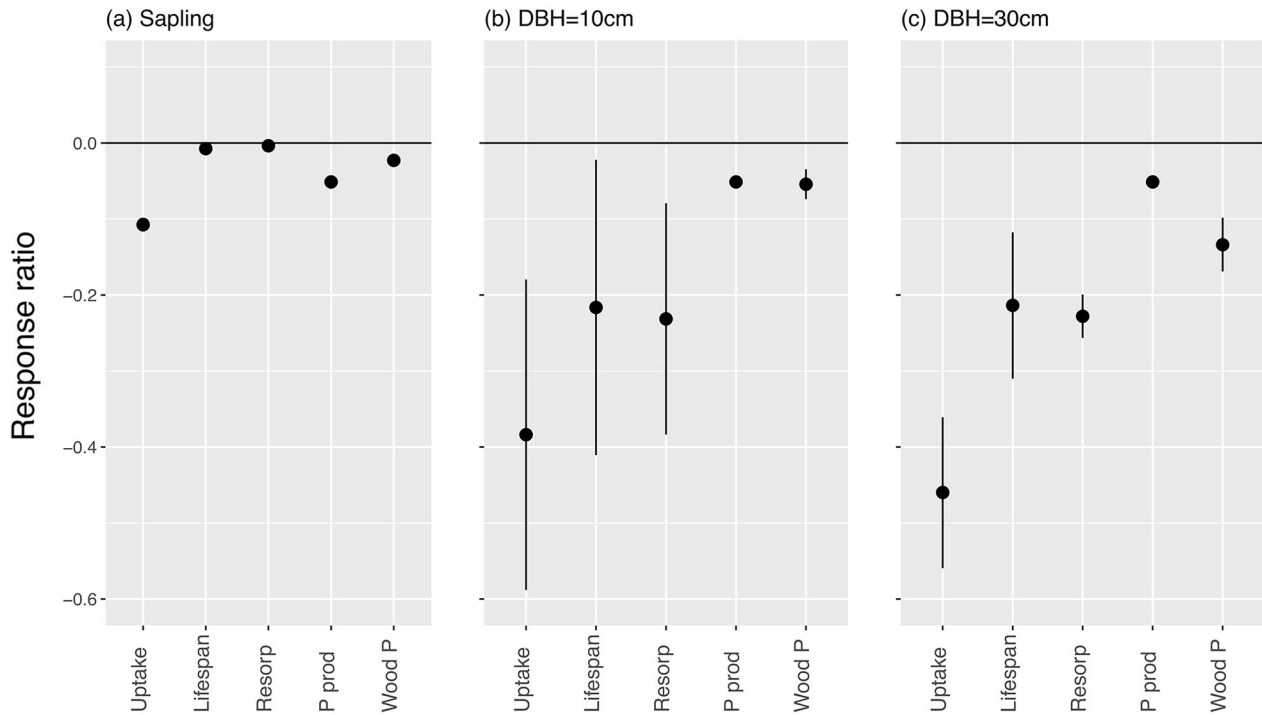


Figure 6. Effects of 10% changes (that is, $\alpha = 1.1$ or 0.9) in plant traits associated with adaptation to low-phosphorus (P) environments on potential growth rate under P limitation, that is, $G_{\text{potential}}(\text{P})$ for sapling (a) and trees with 10-cm (b) and 30-cm (c) diameter at breast height (DBH) at the infertile site in Borneo. Impacts of P uptake (Uptake), leaf lifespan (Lifespan), P resorption from senescent leaves (P resorp), P productivity (biomass production rate per P allocated to canopy, denoted as P prod) are shown as a reduction of potential growth rate (with \pm standard deviation). More negative values indicate greater effects of functional traits on $G_{\text{potential}}(\text{P})$. The response ratio was calculated based on empirical data and Eqs. 4–8 with the assumptions that (i) plant growth, P uptake and functional traits are related to each other following Eq. 2 and (ii) a minute change in functional traits value does not influence other traits (see Materials and methods).

Table 4. Results of the Meta-analysis

	Element	<i>n</i>	Effect size	Lower CI	Higher CI	<i>p</i>
Old growth	N	6	0.14	−0.29	0.58	0.51
	P	5	0.16	−0.29	0.61	0.49
	N + P	4	0.98	0.36	1.60	**
Secondary forest	N	4	0.51	0.25	0.76	***
	P	5	0.54	0.21	0.87	**
	N + P	4	1.23	0.96	1.50	***
Sapling (Light)	N	7	0.56	−0.15	1.27	0.12
	P	9 (13)	0.44 (1.30)	0.02 (0.21)	0.86 (2.39)	* (*)
	N + P	15 (16)	1.20 (1.38)	0.78 (0.94)	1.62 (1.83)	*** (***)
Sapling (Shade)	N	6	0.37	−0.23	0.97	0.23
	P	6	0.14	−0.30	0.58	0.53
	N + P	8	0.37	−0.15	0.89	0.17

The number of references (N), effect size (Hedge's *g*; effects of nutrient addition on biomass, diameter, or height growth), lower and higher confidence intervals (CI), and *p* values are shown. Numbers in parentheses indicate the results, including studies with large (> 2.5) effect sizes.

porting Information S2.9), but did not for wood N concentration, which did not differ between sites (Table 2). Differences between $G_{\text{potential}}(\text{P})$ and

$G_{\text{potential}}(\text{N})$ are discussed further in Supporting Information S2.

Meta-Analysis

The meta-analysis demonstrated that effect sizes of N and/or P supplementation experiments were always positive, irrespective of tree size (age) (Table 4), indicating the overall positive effects of nutrient supplements on tree growth in tropical forests. However, effect sizes differed among size classes. Old-growth tropical forests did not respond significantly to P or N addition, whereas secondary (young) forests responded significantly to both P and N addition (Table 4). Phosphorus addition significantly affected young forests and saplings under high-light conditions (Table 4). When studies with a high effect size (> 2.50) were excluded, the effect size was still associated with the pattern of P addition (Table 4). Combined P and N addition generally yielded greater impacts on growth than N or P alone for old-growth forests, young forests, and saplings under high light (Table 4).

DISCUSSION

We assessed the influence of tree adaptation on plant growth under environmental stress by examining patterns and mechanisms of size-dependent P limitation in tropical forests. We hypothesized that plant P acquisition and use strategies and their effects on growth explains size-dependent P limitation of tropical tree species by the following two mechanisms: (i) larger trees have traits that are more adaptive to low-P environments, and (ii) the effects of functional traits associated with P-use and uptake efficiency on $G_{\text{potential}}$ (P) are greater for larger trees. We find that larger trees have functional traits related to high P-use efficiency, including considerably lower wood P concentration and greater P productivity (but shorter leaf lifespan). Although leaf lifespan and P productivity of larger trees were estimated with some assumptions, P-use efficiency (the ratio of growth to P uptake) of saplings was 2.14 ± 0.32 and 1.68 ± 0.32 ($\text{mg g}^{-1} \text{ P} \pm \text{SD}$) in the infertile and fertile sites, respectively, which was far less than for trees with 30-cm DBH; 4.72 ± 0.66 and 3.84 ± 1.63 ($\text{mg g}^{-1} \text{ P} \pm \text{SD}$) in the infertile and fertile sites, respectively (Supporting Information S3). Given that the nutrient concentration of wood was considerably lower and the relative biomass allocation to wood was generally greater for larger trees than for saplings, increasing P-use efficiency with size (saplings vs. larger trees) may be a common characteristic of tropical tree species. However, P uptake per fine-root mass, which is related to the other component of $G_{\text{potential}}$ (P) (that is, P

uptake), declined considerably with increasing tree size. Thus, our data did not fully support mechanism 1, that larger trees have strategies that are better adapted to low-P environments.

On the other hand, our theoretical analysis and empirical data from Borneo support mechanism 2: the effects of functional traits on $G_{\text{potential}}$ (P) are greater for larger trees. Canopy tree species in Borneo demonstrated that a 10% change in individual functional traits had impacts on $G_{\text{potential}}$ (P) of 5.1–45.9% for large trees and only 0.7–10.7% for saplings. When the values of individual functional traits of species in the infertile site were changed to the levels observed for species in the fertile site, the impacts of the traits on $G_{\text{potential}}$ (P) were 0–67.9% for large trees and 0–14.4% for saplings. These values correspond to the effects of P limitation on growth shown by nutrient addition experiments (30–70%; Lawrence, 2003), suggesting that even a single functional trait has the potential to mask the impact of P limitation on large trees.

Another important finding is that the effects of functional traits on $G_{\text{potential}}$ (P) vary in relation to the loss:uptake ratio or P allocation to wood, except for P productivity. While plant functional traits such as longer leaf lifespan and enhanced foliar nutrient resorption are considered important strategies in low-nutrient environments (Silla and Escudero 2004; Hirose 2012), these traits had almost no impact on the growth rate of saplings that exhibited low loss:uptake ratios under high light. It is reasonable that a low loss:uptake ratio reduces the impact of traits related to P loss on $G_{\text{potential}}$ (P), because a decrease in P loss has a relatively small impact on the whole-plant P budget if P loss is considerably smaller relative to P accumulation (that is, P demand for building new biomass) (Eq. 2). Thus, an increase in leaf lifespan or resorption (that is, decreases in P loss) cannot effectively increase $G_{\text{potential}}$ (P) in rapidly growing plants and stands (that is, high nutrient accumulation and low loss:uptake ratio). This finding implies that smaller plants with high growth rates are inherently susceptible to nutrient depletion because of a lack of strategies to maintain their growth. The effects of functional traits related to wood nutrients and uptake also increased as trees grew larger, suggesting that larger trees can maintain growth more efficiently than saplings. In this study, the nutrient resorption in wood and fine roots was not considered, but is probably important given that nutrient loss via wood and fine-root senescence is greater for larger trees (Freschet and others 2010; Heineman and others 2016).

On the other hand, mechanisms related to nutrient uptake, efficiently improve $G_{\text{potential}}$ (P) in small-sized trees with high growth rate. This raises the hypothesis that traits related to nutrient uptake determine sapling performances and the significance of traits varies by tree size. Although above-ground traits for plants adapted to infertile environments are relatively well studied, it remains unclear how below-ground traits vary in relation to tree adaptation to infertile environments (Mommer and Weemstra 2012; Aoyagi and others 2022). Our results provide a theoretical explanation for the significance of traits related to nutrient uptake for saplings and young forests (that is, rapidly growing systems).

We assumed that changes in functional trait are unrelated (that is, no among-trait trade-offs exist). One of the best-known among-trait trade-offs is between leaf N productivity (or photosynthetic N-use efficiency) and leaf toughness (that is, leaf lifespan) (Hikosaka and Shigeno 2009). To increase leaf lifespan, more N is allocated to structural fractions such as cell wall proteins, which decreases relative N allocation to proteins in the photosynthetic machinery and, therefore, decreases leaf N productivity (Hikosaka and Shigeno 2009). If this is also the case for P, our estimation of the effects of leaf lifespan and P productivity on $G_{\text{potential}}$ (P) is inflated, because increases in leaf lifespan or P productivity reduce the effects of other traits on $G_{\text{potential}}$ (P). However, leaf lifespan increased with decreasing leaf P concentration, yet P productivity did not decrease, suggesting that there was no tradeoff between leaf lifespan and P productivity (see also Hidaka & Kitayama 2009). Physiological studies also support a difference in the response of N and P productivity to leaf nutrient concentrations (photosynthetic N or P-use efficiency) (Hidaka and Kitayama 2011; Aoyagi and others 2022). These observations indicate that we did not overestimate the impacts of traits, because a longer leaf lifespan does not reduce P productivity. However, an increase in leaf lifespan (that is, a decrease in nutrient loss) generally leads to a lower maximum photosynthetic rate (Wright and others 2004; Onoda and others 2017), which decreases potential growth under C limitation, $G_{\text{potential}}$ (C). Thus, species adapted to low-P environments can be limited by C (that is, light), even for canopy tree species (Graham and others 2003).

The results of our meta-analysis provide additional evidence for the size dependency of the effects of functional traits on $G_{\text{potential}}$ (P) in the tropics, because saplings and secondary forests responded to supplementation with P more strongly

than did old-growth forests (Lawrence 2003; Wright and others 2018). Higher light availability elevates $G_{\text{potential}}$ (C) in secondary forests and saplings, which is associated with greater nutrient demand and stronger P limitation. However, high light intensity does not explain why saplings and tree species in secondary forests cannot increase $G_{\text{potential}}$ (P) with increasing $G_{\text{potential}}$ (C). Our study suggests that this occurs because plants with high growth rate (and therefore low P loss:uptake ratio) inherently cannot improve $G_{\text{potential}}$ (P) by modifying functional traits (see Figure 3). In fact, nutrient addition experiments have demonstrated stronger nutrient limitation in small-sized trees compared to larger trees with exposed canopy in Costa Rica (Alvarez-Clare and others 2013) and sub-tropical China (Li and others 2018) (although not in Panama, Wright and others 2018). On the other hand, Turner and others (2018) reported that species-level growth rates along a natural soil P gradient in Panama increased with increasing soil P availability for most species regardless of size. This suggests that responses of species-level growth to natural variations in soil P, which reflect long-term plant responses, differ from responses to a substantial but short-term change in nutrient availability (typically ≤ 10 years). Plants can adjust nutrient demands (that is, $G_{\text{potential}}$) to maximize their growth rate by substituting a limiting element in biochemical processes (for example, by replacing phospholipids with galactolipids and sulfolipids in cell membranes) and increasing the uptake of a limiting element (Saito and others 2008; Ågren and Weih 2012; Lambers and others 2012). These biochemical adjustments in the potential growth rate may explain the differences among growth responses to natural P gradients and nutrient addition experiments.

The difference in species characteristics between young and old-growth forests might partly explain the stronger growth response of secondary forests. We do not have whole-plant trait data for pioneer tree species and our empirical data are based on late-successional tree species (Dipterocarpaceae). Therefore, the conclusion of our theoretical framework (that is, the size dependency of the effects of functional traits on $G_{\text{potential}}$ (P)) might not apply to pioneer tree species. However, biomass allocation to leaves and relative growth rate generally decrease with increasing tree size irrespective of species characteristics, suggesting that the size-dependent changes in the impacts of tree strategies that we have identified are general for both pioneers and later-successional tree species.

Another possible explanation for stronger P limitation in young forests than in old-growth forests is that soil nutrient availability is lower in young forests. Although this possibility cannot be excluded, the availability of soil nutrients in secondary forests varies depending on prior land use. For example, nutrient enrichment following prior agricultural land use is common in tropical secondary forests (Howarth and others 2005), whereas soil disturbance through logging or erosion reduces nutrient availability by removing nutrients from the system (Griscom and Ashton 2011; Aoyagi and others 2013). On the other hand, a study included in the meta-analysis reported similar concentrations of soil nutrients (total N, P, and exchangeable cations) in forests abandoned after slash-and-burn agriculture and a nearby undisturbed forest (Uhl 1987). In addition, the difference between secondary and old-growth forests in nutrient availability cannot explain why smaller individuals within forests tend to experience stronger nutrient limitation. The relative importance of endogenous (plant strategy and size) and exogenous (nutrient and light availability) factors for the pattern of nutrient limitation requires further exploration.

Understanding why species-rich tropical forests respond weakly to supplementation with P is important for understanding the relationship between global and regional gradients of soil P availability and ecosystem functioning. Based on theory and literature synthesis, we suggest that “efficiently” growing plants, represented by small plants (that is, high relative growth, low loss:uptake ratio, and low nutrient allocation to wood), cannot greatly improve $G_{\text{potential}}(\text{P})$ by modifying functional traits. Small-sized plants can therefore be more strongly constrained by P availability. Conversely, larger trees can modify $G_{\text{potential}}(\text{P})$ more efficiently, which may explain why their growth is unresponsive to P addition. These findings provide new insight into the relationships among resource constraints, plant adaptation, and growth performance, and conditions under which tropical forest ecosystems respond to environmental change. Successional ecosystems and early life stages of tree species are more susceptible to anthropogenic perturbations of environmental P availability caused by agriculture and forestry.

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DATA AVAILABILITY

Data are available in article supplementary materials and the Dryad data repository: Aoyagi, Ryota; Imai, Nobuo; Kitayama, Kanehiro (Forthcoming 2023). Allocation and functional traits of trees and saplings of Bornean tree species growing under contrasting soil nutrient availabilities [Dataset]. Dryad. <https://doi.org/https://doi.org/10.5061/dryad.66t1g1k55>.

Declarations

Conflict of interest There are no conflicts of interest to declare.

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