

Nutrient Availability in Tropical Rain Forests: The Paradigm of Phosphorus Limitation

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Abstract A long-standing paradigm in tropical ecology is that phosphorus (P) availability limits the productivity of most lowland forests, with the largest pool of plant-available P resident in biomass. Evidence that P limits components of productivity is particularly strong for sites in Panama and the Amazon basin. Analyses of forest communities in Panama also show that tree species distributions are strongly affected by P availability at the regional scale, but that their local distributions in a single site on Barro Colorado Island (BCI) are as frequently correlated with base cations as with P. Traits associated with species sensitivity to P availability require more detailed exploration, but appear to show little similarity with those associated with N limitation in temperate forests. Recent research indicates that a large fraction of P in tropical forests exists as organic and microbial

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P in the soil; plant adaptations to access organic P, including the synthesis of phosphatase enzymes, likely represent critical adaptations to low P environments. Plants also cope with low P availability through increases in P use-efficiency resulting from increased retention time of P in biomass and decreased tissue P concentration. Although foliar P responds strongly to P addition, we show here that foliar P and N:P are highly variable within communities, and at BCI correlate with regional species distributional affinity for P. An improved understanding of P limitation, and in particular the plasticity of responses to P availability, will be critical to predicting community and ecosystem responses of tropical forests to climate change.

Keywords Ecosystem nutrient budget · Fertilization experiments · Nutrient uptake · Physiological traits · Soil nutrients

Introduction

Humid low elevation tropical forests support among the highest above-ground biomass and net primary productivity of any ecosystem (Scurlock and Olson 2002; Houghton 2005). Yet, many tropical forests that have been cleared for agriculture fail to support crop yields for more than a few years without large fertilizer inputs (Nye and Greenland 1960; Sanchez et al. 1983; Lal 1986). This apparent paradox suggested that much of the nutrient reserve of tropical forests is stored in plant tissue, resulting in critical nutrient limitation once biomass is removed. A synthesis of datasets on nutrient concentrations in leaves and senescent tissue returning to the ecosystem as litterfall highlighted phosphorus (P) as the nutrient that most clearly distinguishes the stoichiometry of tropical from temperate forests, leading to the paradigm that P availability constrains the productivity of most lowland tropical forests (Vitousek 1984). Here we review the evidence for this paradigm, highlighting the insights gained over the past three decades on the distribution of P in tropical ecosystems, its availability to plants, adaptations of plants for P acquisition and use, and evidence that plant growth and forest diversity reflects not only P supply, but also co-limitation by nitrogen (N) and base cations.

Nutrient Limitation in Tropical Forests

Many tropical soils are strongly weathered, reflecting warm, moist conditions acting on stable land surfaces that were not directly affected by Quaternary glaciations (Baillie 1996). These older, well-weathered ‘Oxisol’ (Soil Taxonomy system; Soil

Survey Staff 1999) or ‘Ferralsol’ soils (IUSS Working Group WRB 2014) are characterized by a moderately organically enriched surface horizon, and deep, relatively uniform yellow-red subsoils, reflecting weathering of clay minerals into ferric sesquioxides (Baillie 1996). Chemically, these soils are acidic, highly leached, with a low cation exchange capacity and high aluminum saturation. Beyond this broad generalization, however, lies a diversity of soil physical properties (notably influencing drainage patterns and water-holding capacity) and chemical properties reflecting heterogeneous parent materials, substrate age, and topographic effects on soil development. Nonetheless, a feature of many soil orders associated with tropical forests is limited P availability and low total P, resulting from long periods of leaching and strong adsorption or occlusion of P with iron and aluminum oxides (summarized in Table 10.12 in Baillie 1996).

The central importance of P limitation to the productivity of lowland forests reached prominence after comparisons of litterfall in temperate and tropical forests (Vitousek 1984). If P is a key limiting nutrient, then plants might be expected either to function with less of it (reflected in lower tissue P concentrations), or to cycle it more efficiently (reflected in part in higher resorption efficiency of P as tissues senesce). Analysis of nutrient concentrations and nutrient ratios in leaf litter is consistent with both mechanisms. Litterfall from lowland tropical forests, particularly those on older, more weathered soils of the Amazon basin, had low P concentrations, whereas tissue N and Ca concentrations were mostly comparable to temperate forests (Vitousek 1984). This study also highlighted differences in nutrient limitation between lowland and montane tropical forests. In montane forests, P availability can be low, and foliar P generally declines with elevation (Tanner et al. 1998; Benner et al. 2010). However, N limitation appears to be much more important in the mountains than in the lowlands, probably due to temperature and moisture effects on rates of mineralization (e.g. Grubb 1977; Vitousek et al. 1994; reviewed in Benner et al. 2010).

Fertilization experiments have generally supported the view of P limitation in lowland forests, and N or N and P limitation in montane forests (reviewed by Sayer and Banin, this volume, Dalling et al. 2015). However, insights from fertilization experiments are incomplete with regard to the scale and generality of nutrient limitation. This is because factorial fertilization experiments are expensive to establish and therefore restricted in the number of nutrient addition treatments that can be included, and may take many years to yield clear treatment effects (Sullivan et al. 2014). Fertilization experiments may therefore miss co-limitation scenarios that could arise either because productivity in different plant size classes or tissue types have different and distinct nutrient requirements (as seen in responses to growth vs. litterfall responses to N, P and K in the Gigante fertilization experiment; Wright et al. 2011), or because the limited scale and replication of fertilization experiments precludes analyses of the individual species responses that contribute to heterogeneous nutrient limitation (Alvarez-Clare et al. 2013; Dalling et al. 2015).

Mixed Evidence of Phosphorus Limitation at the Local Scale

If P availability alone governs forest growth and productivity then we would predict that, at the community level, N:P would be relatively tightly constrained, with ratios >16 (the Redfield ratio; Koerselman and Mueleman 1996) reflecting selection for efficient P use. However, evidence from community-wide analyses of foliar N:P do not support this prediction, with very wide variation in N:P in lowland forests, but declining N:P with elevation (Fig. 1). In an analysis compiling published datasets of foliar nutrients from neotropical sites, Townsend et al. (2007) found limited evidence for environmental control over N:P. Instead, they found large interspecific variation in N:P among species in lowland forests, suggesting coexisting tree species are likely to differ widely in their nutrient requirements (see also Hättenschwiler et al. 2008; Hedin et al. 2009).

Similarly, analyses of species distributions within large forest dynamics plots show correlations with a multitude of soil nutrients, with no clear preference for P (John et al. 2007). For example, at Barro Colorado Island (BCI), Panama, 40 % of

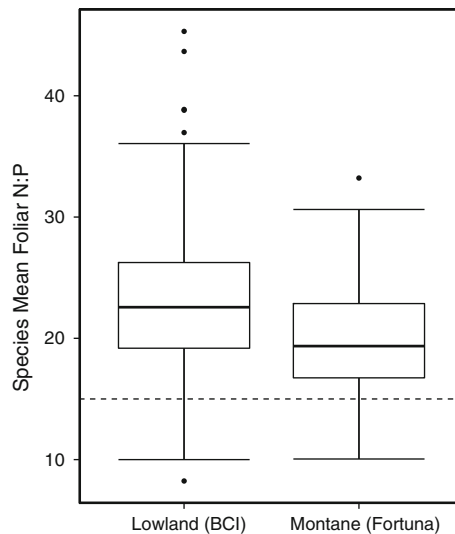


Fig. 1 The distribution of species mean foliar N:P ratios for 281 lowland tree species sampled on Barro Colorado Island (BCI) in the Panama Canal and 91 montane tree species sampled at Fortuna Forest Reserve in western Panama (800–1300 m a.s.l.). The hinges of the boxplot represent the interquartile range (IQR), and the whiskers extend to the largest and smallest values within $1.5 \times$ IQR. Community mean N:P ratio was significantly higher on BCI (NP = 22.8) than Fortuna (NP = 19.5; $t = 5.65$, $df = 179.3$, $P < 0.001$). However, variance did not differ significantly between sites (levene test, $F = 2.8$; $df = 1,370$; $P = 0.093$). The line at N:P = 15 represents the Redfield Ratio, which is the empirically derived threshold between N and P limitation in terrestrial ecosystems

the 258 most common tree species in the 50 ha forest dynamics plot show a significant association in their local distribution patterns with at least one principal component axis representing variation in soil chemical variables (John et al. 2007). Analysis of individual soil variables shows a relatively even distribution in the frequency of associations across soil variables (Fig. 2), with as many species showing significant distributional associations with boron (B), calcium (Ca), potassium (K), and zinc (Zn) as with P.

The lack of a clear pattern of association between tree species distributions and soil P could reflect insufficient variability in P availability at the plot level, strong spatial autocorrelation among soil nutrients, or strong similarity among species in P requirements. Despite its location on a relatively flat andesite plateau, nutrient availability within the BCI plot is quite variable. Soil P, extracted using Mehlich III and analyzed using ICP, ranged from 0.45 to 6.8 mg/kg (10th–90th percentiles). Although as a group base cations were strongly positively correlated at BCI (defining the first principal component of soil chemical variation), P concentration was only weakly correlated with base cations and instead loaded most strongly on a second principal component axis. Although it might therefore be tempting to conclude that demographic rates, and therefore distributions of species on BCI are not primarily differentiated by P requirements, species distributions across the Panama Canal area forests suggest otherwise.

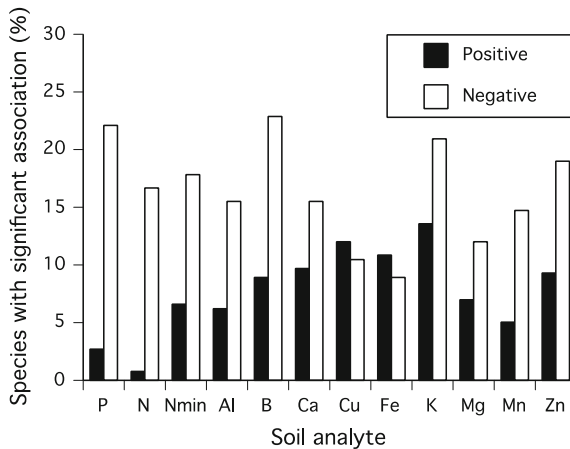


Fig. 2 Frequency of association of 258 tree species with 12 soils variables measured at 300 locations in the 50 ha forest dynamics plot on Barro Colorado Island, Panama. Positive and negative associations indicate that species occurred at sites with higher and lower than expected concentrations ($p < 0.05$) of that variable based on assessment using the Poisson Cluster Method (John et al. 2007)

Evidence for Phosphorus Limitation at Landscape and Regional Scales

Analysis of tree communities in 72 forest plots distributed across the 66 km-wide Isthmus of Panama surrounding BCI has revealed a much stronger imprint of soil P on species distributions. Condit et al. (2013) examined whether the distribution of 550 tree species in this regional species pool showed distributional associations with seven environmental variables measured at each plot, and with dry season moisture availability estimated from a network of rain gauges. This analysis confirmed that dry season rainfall was the strongest environmental predictor of tree distributions, with strong effects on 66 % of species, reflecting a steep gradient in dry season intensity from the Caribbean to Pacific coasts of Panama. More of a surprise, however, was that P availability affected nearly as many species (58 %), revealing a previously unrecognized environmental filter acting on the composition of these forests. Furthermore, species partitioned a gradient of P availability relatively evenly, with 23 % of species showing affinity for high P and 35 % for low P soils.

Phosphorus effects on tree community composition may be particularly strong in central Panama because of the remarkable variation in P availability (resin extractable P varies from <0.1 to 22.8 mg P kg⁻¹; Condit et al. 2013); comparable in magnitude to that of the entire lowland tropics (Condit et al. 2013 and references therein). However, other soil nutrients, notably calcium, were associated with the distribution of 35 % of tree species, raising the possibility that observed associations are at least in part driven by other correlated resources. To test whether species associations reflect differences in growth response to P availability, we have begun measuring seedling growth rates in a pot experiment manipulating P availability. Seedlings of fifteen species with contrasting distributions across the Isthmus were transplanted to a low P soil (0.13 mg kg⁻¹ resin extractable P) and fertilized weekly with a full nutrient solution either with or without added P. The magnitude of species growth increase in the P addition treatment was significantly positively correlated with the degree to which species distributions were skewed towards high P soils (determined from the Condit et al. (2013) dataset).

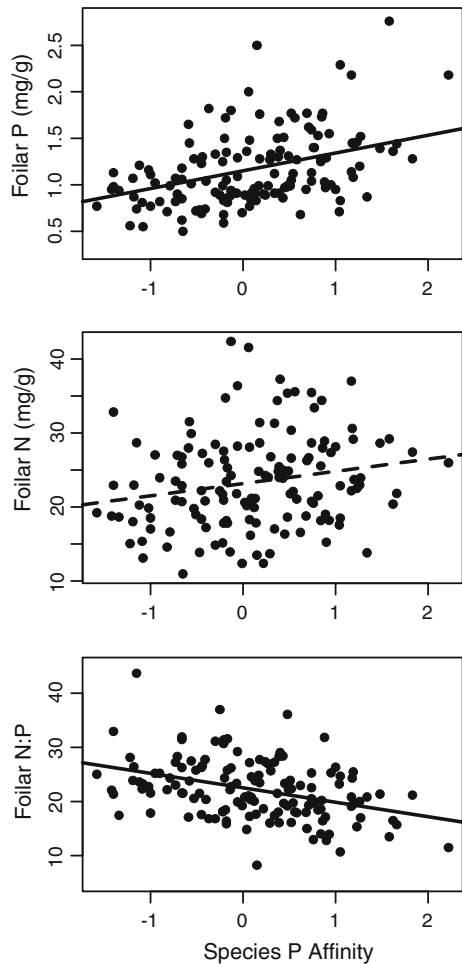
Phosphorus Limitation: Links to Functional and Physiological Traits

Species distributional affinity for P is also likely to be correlated with plant functional traits that potentially impact ecosystem processes. In another pot experiment exploring how Panamanian tree species respond to P availability, Vargas and Lopez (unpublished data), found that *Hura crepitans*, a species with affinity for high P soils, showed significantly higher leaf specific hydraulic conductance (K_L) when grown under high P conditions, suggesting the potential for P availability to

influence ecosystem water balance. Higher K_L under high P might be the result of increased xylem vessel diameter or a by-product of shifts in allocation patterns, and reduction in wood density (Goldstein et al. 2013).

More broadly, soil P availability is often correlated with foliar P concentration (Vitousek and Sanford 1983), with effects on decomposition rates and therefore nutrient cycling (reviewed in Cornwell et al. 2008). While foliar P concentration is a plastic trait that responds to P fertilization (e.g., Santiago et al. 2012; Mayor et al. 2014), community wide foliar P values may also reflect the wider distribution patterns of constituent species. We compared foliar N and P concentrations measured in shade leaves of three individuals of each of 137 species collected on BCI (Wright and Turner, unpublished data) with species distributional affinity for P from Condit et al. (2013). Foliar P was significantly positively correlated with distributional affinity for P (Fig. 3; $r = 0.45$, $p < 0.001$), and foliar N:P was significantly

Fig. 3 Relationship between foliar N, P, and N:P of shade leaves of 137 tree species collected on Barro Colorado Island, Panama, and the index score of species affinity for P, based on the distribution of the same species across 72 sites across the Isthmus of Panama varying in resin-extractable P. Positive P affinity index scores indicate that species were associated with sites with high resin-extractable P



negatively correlated ($r = -0.38$, $p < 0.001$). Foliar N was not significantly correlated with P affinity ($r = 0.17$). Interspecific variation in foliar nutrient concentration may, in turn, be expected to correlate with juvenile and adult growth rates, however no significant relationships were found between foliar N, P and N:P with sapling (>1 cm DBH) or juvenile and adult (>10 cm DBH) growth rates of the same 137 species in the BCI 50 ha plot.

Elsewhere, an affinity for low P soils has been found to correlate with a high P use-efficiency (PUE; a measure of biomass increment per unit P). In Queensland, Australia, Gleason et al. (2009) found that tree species that were specialists on P-poor schist-derived soils had twice the PUE of generalist species. High PUE in turn was related to lower wood P concentrations and to higher retention time of P in the canopy, but was unrelated to above-ground net primary productivity (sum of radial growth and litter production). In contrast, along a steeper gradient of soil P availability spanning the eastern slope of the Andes to the highly weathered and P impoverished soils of the Guiana Shield, total soil P correlates positively with foliar P concentration (Fyllas et al. 2009) and wood production, and inversely with wood density (Mercado et al. 2011; Quesada et al. 2012).

Phosphorus Pools in Soil and Biomass

Much of our understanding of the chemistry of P limitation is based on temperate chronosequences (Walker and Syers 1976). These studies generally show that given sufficient time for pedogenesis, a decline in the total P pool size occurs, and is accompanied by a decline in primary mineral P, and a corresponding increase in the proportion of the total P occurring in occluded and organic forms. Similar shifts between inorganic and organic P pools have been observed in the Hawaiian island chronosequence (Crews et al. 1995), and are likely to be more generally reflected in wet tropical forests (although no long-term chronosequence has been identified in species-rich lowland tropical rain forest).

Nonetheless, a traditional view of P cycling in tropical forests holds that the biological uptake of P is tightly coupled with the deposition of labile P via canopy litterfall and relies very little on soil organic and inorganic P pools. According to this hypothesis, nearly all the biologically available P in tropical forests should be sequestered in plant biomass. This view is supported by the observation that while intact tropical forests are highly productive, forested land cleared and converted to pasture is often P-impoverished and frequently abandoned within a few years of conversion (Serrao et al. 1996). Furthermore, Stark and Jordan (1978) provided evidence for “direct-cycling” of P by demonstrating that only 0.1 % of isotopically-labeled P and calcium applied directly soil surface was lost beyond the root mat in a Venezuelan rainforest, indicating that there should be little chance that organic P is leached from the ecosystem, or sequestered to iron or aluminum oxides in the soil.

Recent studies, however, provide increasing evidence that soil organic P pools, which constitute about 25 % of total soil P in tropical forests (Turner and Engelbrecht 2011), are more dynamic and chemically variable than previously thought. For example, total soil organic P concentrations decline markedly (up to 25 %) during the dry season (Turner et al. 2015), while Vincent et al. (2010) showed that organic P contained in DNA and phosphate monoesters declined in response to experimental litter removal and increased in response to litter addition. These studies indicate that there are more persistent pools of accessible organic P in the soil beyond those directly re-assimilated from litter into plant biomass. In broad terms, the pool of organic P available to plants can be considered to constitute three groups: (1) recently senesced plant or microbial material, (2) P sequestered in live microbial biomass and (3) “stable” organic P bound to iron or aluminum oxides. Soil microbial biomass, characterized by low C:P ratios relative to plant biomass, is an important P sink in forested ecosystems, and can represent a large fraction of the total biomass-associated P (Turner et al. 2013). In a lowland tropical forest in Panama, microbial P was estimated to account for approximately two thirds of the total soil organic P (Turner et al. 2015). While microbes may compete with vascular plants for P, microbial sequestration of P prevents the loss of ecosystem P to more permanent geochemical sinks (Oberson et al. 1997), and facilitates the mineralization of organic P to plant available phosphate (Richardson and Simpson 2011). A recent detailed ecosystem P budget for sites representing a five-fold range in total P storage in a Panamanian montane forest reveals that the amount of available P contained in soil microbial and non microbial pools greatly exceeds the amount of P sequestered in foliar and woody plant tissues at all sites (Heineman unpublished data), contrary to the paradigm that labile P is sequestered primarily in plant biomass.

Acquisition of Organic Phosphorus in Tropical Forests

Adaptations of plants to low P environments may reflect alterations both in P use efficiency and in the ability to acquire P from less readily available sources. Turner (2008) suggested that a gradient of biological availability of soil organic P exists, which is determined by the investment cost to plants of producing an array of enzymes required to catalyze the hydrolysis and release of phosphate. At one extreme, plants can take up dissolved phosphate directly from the soil solution or via mycorrhizas. Simple phosphate monoesters, such as glucose 6-phosphate however require hydrolysis using phosphomonoesterase enzymes. Phosphate diesters, including phospholipids and nucleic acids, require both phosphomonoesterase and phosphodiesterase enzymes to release phosphate. Finally, inositol hexakisphosphates require both solubilization from organic matter or clay minerals and hydrolysis by phytase enzymes. Turner (2008) further suggested that differences in the enzymatic capacity of plants confronted with an array of potential P sources could represent an axis of resource partitioning among plant species.

Consistent with the hypothesis that species partition P sources, pools of organic P differ in composition across a gradient in total soil P (Turner and Engelbrecht 2011) with a higher ratio of phosphomonoesters to phosphodiesteres in sites with higher total P. Nonetheless, to date, little evidence has emerged to suggest that plants from P impoverished tropical forests differ in their capacity to produce phosphatase enzymes when compared to those from more P-rich sites. In lower montane forest at Fortuna, Panama, Steidinger et al. (2015) measured the production of phosphomonoesterase and phosphodiesterase of excised roots of arbuscular mycorrhizal (AM), ectomycorrhizal (EM) and non-mycorrhizal (NM) plant species. They found only weak evidence for differences in enzymatic activity among these groups, with no difference in activity between AM and EM taxa but significantly higher phosphodiesterase activity in the NM taxon. A second experiment with the same taxa compared growth rates of seedlings infected with mycorrhizas and grown in acid-washed sand fertilized with inorganic phosphate, glucose phosphate, RNA and phytate as the sole P source. Again, AM and EM species did not differ in their response to organic sources of P, but the NM taxon, *Roupala montana* (Proteaceae) was the only species capable of exploiting phytate as a P source. At Fortuna EM and AM taxa, as well as *Roupala* occur in multiple sites that differ in P availability (as determined by resin-extractable P and total P). Although the difference in P source use between *Roupala* and other taxa suggests P source partitioning could occur, its ecological significance in tropical forests requires further exploration, including greater species replication of mycorrhizal groups.

Investment in phosphatase enzymes, however, may explain the abundance of N fixing legumes, which can account for a large fraction of stems and basal area in lowland tropical forests (Losos and Leigh 2004) and on occasions form monodominant stands (Connell and Lowman 1989). The dominance of nitrogen fixers in ecosystems where P is considered to limit forest productivity suggests that increasing N availability may indirectly impact P acquisition. Houlton et al. (2008) pointed out that phosphatase production is nitrogen-intensive (up to 15 % N by mass), and that N₂ fixing plants might therefore be able to increase allocation to phosphatase relative to non-fixers. Evidence generally supports the Houlton hypothesis, with higher phosphatase activity in soil beneath N₂ fixing plants (Houlton et al. 2008), higher root phosphatase activity (and AM infection) in N₂ fixing lowland tropical trees (Nasto et al. 2014), and an increase in the phosphomonoesterase activity of N₂ fixing legumes relative non-fixers with declining soil P along a chronosequence in Western Australia (Png et al. 2014).

Conclusions and Future Directions

The consequences of P limitation from the individual to the whole community-level remains a relatively poorly studied aspect of tropical plant ecophysiology and forest ecology. Just as N availability can limit the productivity of temperate plants under elevated CO₂ (e.g., Long et al. 2004; Norby et al. 2010; but see Drake et al. 2011),

chronic P limitation has the potential to constrain the response of tropical forest plants to rising CO₂, particularly if reduced transpiration rates also reduce P uptake (Cernusak et al. 2011). Despite this, experimental data to explore how CO₂ and P interact to influence the growth of tropical plants remains extremely scarce (Cernusak et al. 2013). Likewise, an understanding of how tropical forest plants have adapted to low P environments, either through increases in P-use efficiency or phosphate-acquisition efficiency, can provide insights into how to manage P inputs more efficiently in agricultural settings to maximize crop yields while minimizing P exports from the system (Veneklaas et al. 2012).

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