Tropical tree growth is correlated with soil phosphorus, potassium, and calcium, though not for legumes

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Abstract. Tropical forest productivity is widely assumed to be limited by soil phosphorus (P), but biogeochemical processes that deplete P also could deplete base cations, suggesting multiple resource limitation. Limitation by several resources could arise from species and functional diversity and from variation among groups in resource requirements, including ecophysiological strategies that minimize P limitation. We hypothesized that tree growth is positively related to soil base cation and P availability and negatively related to local competition; Fabaceae growth is weakly correlated with soil resources if fixed N is used indirectly to acquire other resources; growth of species with low wood density is more strongly related to soil resource availability than that of species with high wood density. Diameter growth and soil resource availability were measured in five mapped stands situated across natural soil resource gradients in lowland wet tropical forest (La Selva Biological Station, Costa Rica). Soil resource availability, and associated uncertainty, was estimated for each tree using a Bayesian multivariate spatial regression model, with individual tree growth being a function of diameter, local neighborhood, and soil resources. Separately, site-level mean tree growth and resource availability were modeled using linear regression. Individual diameter growth and site mean basal area increment correlated with soil base cations and P, but rarely with N; individual growth correlated negatively with neighborhood index for only three species. Growth of Fabaceae was unrelated to soil resources at both individual and site levels. When species were categorized by wood density, growth was related to soil P or base cation availability, with the strongest correlation between the lowest-density species and soil P. Several resources may limit tropical forest productivity, because tree growth was similarly correlated with soil P and base cations, but functional groups responded differently. Negligible growth relationships with soil resources in Fabaceae suggest that N fixation may alleviate mineral nutrient limitations. Correlations of soil P with growth of species of low wood density and base cations with species of higher density suggests variation in resource demands among functional groups. Thus, tropical tree growth may be limited by base cations and/or P, with degree and type of resource limitation dependent on functional or taxonomic group.

Key words: base cations; Fabaceae; functional groups; La Selva Biological Station, Costa Rica; legumes; neighborhood model; phosphorus limitation; plant–soil interactions; quantitative trait; resource limitation; tropical trees.

INTRODUCTION

Tropical forest productivity is a significant component of terrestrial carbon cycling (Luyssaert et al. 2007, Sitch et al. 2008), but accurately predicting tree growth in tropical forests is complicated by fine-scale biogeochemical heterogeneity (Townsend et al. 2008; E. K. Holste, R. K. Kobe, A. O. Finley, and T. W. Baribault, *unpublished manuscript*) and species diversity (Clark et al. 1999). Productivity in tropical forests may be limited by soil phosphorus (P) availability (Porder et al. 2007, Vitousek et al. 2010), nitrogen (N) (Vitousek and Farrington 1997, LeBauer and Treseder 2008), base cations (calcium (Ca), potassium (K), magnesium (Mg)) (Andersen et al. 2010, Wright et al. 2011), water

(Valdespino et al. 2009), or irradiance (Graham et al. 2003). In wet tropical forests in particular, studies often focus on whether soil P dynamics limit aboveground net primary productivity (Tanner et al. 1998), while the possibility that other soil resources influence growth has not been eliminated (Schuur and Matson 2001).

Evaluating a broad range of potentially limiting resources is important for understanding resource-based productivity constraints, particularly because macronutrients critical to plant physiology are all subject to loss from ecosystems (Asner et al. 2001, Wood et al. 2005, Corre et al. 2010). Soil weathering and high rates of nutrient leaching can deplete phosphate (PO_4) in some tropical forest soils (Hedin et al. 2003) and have similar effects on soil base cation and N content (Porder et al. 2006, Porder and Chadwick 2009). Physiologically, P participates in a wide variety of processes (Comas et al. 2002, Plassard and Dell 2010), but the base cations also perform indispensable functions (McLaughlin and

Wimmer 1999), as does N (Millard and Grelet 2010). Because all soil macronutrients are subject, to varying degrees, to leaching and immobilization, a comprehensive test for potential resource limitation of tree growth should investigate a broad array of resources, including mineral and organic forms of N.

Individual tree growth is influenced both by intrinsic factors—ontogeny (Peichl and Arain 2007) and genotype (Boyden et al. 2005, Boyden et al. 2008)—and by extrinsic factors such as climate (Clark et al. 2010), disturbance regime (Uriarte et al. 2004), resource availability (Gradowski and Thomas 2008), interactions with surrounding trees (Coates et al. 2009), and fungal (Hagerberg et al. 2003) or bacterial (Leblanc et al. 2005) mutualisms. Rarely, however, do individual growth models incorporate soil resource data measured at appropriate scales (Laubhann et al. 2009). A principal contribution of this study is to explicitly test how growth is related to several soil resources measured at a scale commensurate with individual trees. These estimates of individual-scale soil resource availability augment an established strategy for modeling ontogenetic and neighborhood effects on tree growth (Canham et al. 1999, 2006, Uriarte et al. 2004, Coates et al. 2009). Neighborhood effects characterize net local tree–tree interactions, including light competition (Canham et al. 2004), belowground competition (Coomes and Grubb 2000), plant–soil feedbacks (Fujinuma et al. 2005, McCarthy-Neumann and Kobe 2010), and other unmeasured size- and distance-dependent factors.

Soil resources are often measured at coarse spatial scales (Lundholm 2009), typically sacrificing high spatial resolution for expedited processing or improved temporal representation. Some recent work has attempted to measure resources at scales appropriate to individual trees (John et al. 2007, Gradowski and Thomas 2008, Holste 2010), but it is nonetheless a considerable logistical challenge to collect and analyze the thousands of soil samples required to properly assess individual-level resource availability across stands. Evolving geostatistical methods, however, facilitate prediction of resource availability at any scale from a relatively sparse sampling lattice (Banerjee et al. 2004). Using increased computational capacity and a Bayesian framework (Gelman 2006), it is possible to formulate models for multivariate and spatially dependent processes, such as resource availability, that provide prediction with associated uncertainty at any unobserved location within a study area (Finley et al. 2009).

If species respond similarly to resource availability and neighborhood interactions (i.e., ecological neutrality; Hubbell 2001), then strong relationships of growth to these variables should emerge when all species are analyzed together. The opposing view, that every species differs ecologically in measurable ways, motivates analysis of growth for individual species, as typically conducted for temperate (Canham et al. 2006) or relatively low-diversity tropical systems (Uriarte et al.

2004). Phylogeny (Swenson and Enquist 2009) or suites of functional traits (Swenson and Weiser 2010) also could define groupings of species that may grow similarly in response to environmental factors. Some important traits that define species functional groups include capacity for N fixation (Funk and Vitousek 2007), height at maturity (Falster and Westoby 2005), and wood density (Chave et al. 2009).

Nearly all species in Fabaceae develop symbioses with N-fixing bacteria, while endogenous N fixation is usually absent in other groups (Hedin et al. 2009). Nitrogen fixation capability may alleviate P limitation if N-fixing species can utilize N for rhizosphere phosphatase production that increases microscale PO_4 availability by dissociating recalcitrant forms of P (Treseder and Vitousek 2001). However, allocation of fixed N to phosphatase production could lead to limitation by base cations (Smethurst 2010). Nitrogen fixation also could increase photosynthetic rates and carbon available for diversion to mycorrhizal symbionts (Iversen and Norby 2008), which in turn increase plant access to PO_4 as well as base cations. These mechanisms would result in insensitivity of Fabaceae growth responses to mineral nutrients relative to other functional groups (Pearson and Vitousek 2002, Menge et al. 2008, Cusack et al. 2009).

Species differences in mature tree height also could influence responses to soil resources, so an additional functional grouping can be based on mature stature. Tree height governs physiological parameters such as transpiration (Sperry et al. 2008) and the amount of carbon dedicated to support structures (King 2005, Buckley and Roberts 2006, Cole and Ewel 2006), and consequently carbon requirements for respiration in non-photosynthetic tissues (MacFarlane and Kobe 2006, Elser et al. 2010). In addition, shorter-statured species experience lower irradiance and thus soil nutrients may have less measurable influence on growth under light limitation (Kobe 2006, Holste 2010).

From a theoretical perspective, species with high diameter growth rates should have either correspondingly high resource requirements (Holste et al. 2011) or low wood density (Chave et al. 2009). However, spatial heterogeneity in resource availability (Townsend et al. 2008), may weaken correlations between traits such as wood density (more precisely wood specific gravity) (Swenson and Enquist 2008), and growth rates (Ogle and Pacala 2009). In particular, species with low-density wood, faster growth rates, and higher leaf turnover might require more soil resources during rapid construction of foliar and other tissue (Oelmann et al. 2010). In contrast, species with higher density wood, which are often shade tolerant (Poorter et al. 2010) and exhibit slower growth rates (Fownes and Harrington 2004, Kelly et al. 2009), may tolerate lower nutrient concentrations over short timescales (Easdale et al. 2007) due to greater nutrient use efficiency (Hidaka and Kitayama 2009, Soolanayakanahally et al. 2009). Thus, growth of shade-tolerant species with high wood density could

appear unrelated to soil resource availability (Baltzer et al. 2009).

The major purposes of this study are to test for correlations between a broad suite of soil resources and individual and site-level tree growth. Furthermore, because shading by neighbors and other tree–tree interactions (e.g., McCarthy-Neumann and Kobe 2010) could strongly influence individual tree growth, we also tested for local neighborhood effects. In particular, we tested these hypotheses:

Hypothesis 1. Tree growth is positively related to soil P and base cations (Ca, K, and Mg).

Hypothesis 2. Individual growth is negatively related to local competitive pressure in neighborhoods defined by size- and distance-dependent functions of nearby trees.

Additionally, we expected variation in growth–resource relationships among functional groups, with specific hypotheses:

Hypothesis 3. Individual and stand-level growth of Fabaceae are unrelated to soil N and P. Effects of base cations depend on how fixed N is used to acquire other resources. Correlation of Fabaceae growth with base cations would be consistent with allocation of fixed N in phosphatase. A lack of growth correlation with base cations would be consistent with the provision of carbon to mycorrhizae.

Hypothesis 4. Across species, growth–soil resource relationships strengthen as wood density decreases.

Methods

Study location

This study was conducted in five wet tropical forest sites at La Selva Biological Station in northeastern Costa Rica (10°26′ N, 84°00′ W), an area that receives a mean annual rainfall of 4306 mm distributed relatively evenly across the year (*available online*).[2] Sites were established across a gradient in soil P (Appendix A), with sites 1–3 located on weathered volcanic ultisols and sites 4 and 5 located on entisols and inceptisols of recent alluvial deposition (McDade and Hartshorn 1994). The original intention was to position sites in undisturbed, primary forest (Vriesendorp 2003), but we later realized that 90% of one alluvial site (4) was ~60-year-old secondary forest. In this site, both mean growth and mortality rates in some taxa (e.g., Arecaceae) were slightly higher than at the other alluvial site, but standard deviations from this site were well within the range of standard deviations across all sites (Appendix A). In addition to representing a soil P gradient, the sites

also encompass a gradient in base cations and an opposing gradient in soil inorganic N availability (Appendix A). Each site included an area 240 × 41 m with the long dimension oriented at a randomly selected azimuth. In 2000, all woody stems larger than 5 cm diameter at 1.3 m height (excluding lianas) were measured (using diameter tapes) and their locations were mapped (Vriesendorp 2003). In 2009, each site was expanded to encompass an area 280 × 81 m, with the original sites occupying the center of the new areas.

Growth measurements

Growth was measured three times following the original 2000 census, in 2005, 2007, and 2009, with diameter increment calculated as the difference between the later and earlier measurements. Encroaching buttress growth compromised the reliability of the original measurement, so growth data used for this study were derived from the intervals between 2005–2009 or 2007–2009. For dicot species with no buttresses, diameter was measured at the same height in each census. Measurement height was 10 cm above a nail marker (or multiple nails for large-diameter trees), to avoid nail-associated scarring. When buttresses were >1.3 m height, measurements were taken above their termination (Metcalf et al. 2009). For 96 trees (1.8% of the total), buttresses had grown above the 2005 measurement point in later censuses, and it was necessary to infer the 2005 diameter. We measured diameter at two heights (separated by 1 m) above the buttresses to calculate taper, which was used to infer 2005 diameter at the new measurement height. For some Arecaceae species, stilt roots progressively lifted the measurement point; diameter was measured at the same stem location regardless of its distance to the ground. In 2009, trees that had been smaller than 5 cm diameter in 2005 (in-growth) were measured and mapped. For these in-growth trees, diameter growth was conservatively estimated by subtracting 5 cm (the minimum size of measured trees) from the measured diameter. Of the trees alive in 2005, 3.2% had died by 2009. Diameter increment was based on the 2005–2007 interval if the trees were alive in 2007; trees that died by 2007 (0.2%) were excluded from analysis.

Soil sampling and resource measurements

At each site in June 2008, soil samples were taken from 254 locations. Along a central transect, 200 samples were taken from consecutive 1-m² quadrats, with an additional grid of sampling points 10 m away from either side of the transect at 5-m intervals, and 14 locations randomly selected in each site. This is referred to as a lattice-plus-close-pairs design, optimal for estimating variance parameters in geostatistical models (Diggle and Lophaven 2006). Each composite sample consisted of three cores (2 cm diameter, 20 cm depth) arranged in an equilateral triangle of sides 33 cm centered on each sample point. Samples were air-dried for one week or until they achieved constant mass, and

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[2] http://www.ots.ac.cr/meteoro/default.php?pestacion=2

TABLE 1. Stand-level soil resource measurements (mean with SD in parentheses) for study sites at La Selva Biological Station, Costa Rica.

Site	Ca^{2+} (ppm)	K^+ (ppm)	Mg^{2+} (ppm)	Al^+ (ppm)	pH	P (ppm)	NH_4 (ppm)	NO_3 (ppm)	Total N (ppt)
1	106.82 (50.5)	82.17 (7.3)	54.08 (17.2)	1137.6 (47.3)	4.32 (0.59)	1.99 (0.3)	159.57 (23.7)	99.52 (21.8)	0.39 (0.15)
2	89.75 (40.3)	78.61 (8.0)	45.64 (48.0)	1201.6 (29.5)	4.33 (0.52)	1.84 (0.8)	180.30 (48.0)	110.60 (19.93)	3.62 (6.88)
3	58.90 (3.5)	67.56 (6.4)	35.53 (6.9)	892.5 (80.1)	3.90 (0.50)	1.71 (0.7)	120.93 (6.9)	100.17 (14.4)	0.49 (0.09)
4	153.61 (28.0)	116.71 (14.8)	66.00 (16.9)	1578.0 (219)	4.35 (0.52)	5.08 (1.2)	95.79 (16.9)	74.26 (3.76)	0.43 (0.10)
5	112.48 (2.1)	124.26 (1.6)	37.98 (3.0)	1191.0 (11.0)	4.02 (0.56)	3.32 (0.1)	112.51 (3.0)	61.65 (1.68)	0.32 (0.09)

then shipped from La Selva to Michigan State University for processing. The samples typically formed into solid clay masses that were coarsely ground so that roots, other biological debris, and pebbles could be removed. Samples were then finely pulverized in an electric grinder prior to resource measurements.

Ammonium (NH_4^+) and nitrate (NO_3^-) were measured from 10 g of soil in 50 mL of a 2-mol/L potassium chloride solution. Colorimetric measurement of NH_4 (Sinsabaugh et al. 2000) and NO_3 (Doane and Horwath 2003) was achieved with an absorbance spectrometer (ELx808 Absorbance Microplate Reader, BioTek Instruments, Winooski, Vermont, USA). Due to concerns that altered microbial processes in air-dried soils might not reflect field availability of NH_4 and NO_3, total soil N was also measured. Although not all forms of N are directly available to plants, organic N may be absorbed by plant roots and mycorrhizae, so total N may adequately reflect plant-available N. Total soil N content was measured using soil samples that were ground into powder using a ball-bearing mill (Kleco, Visalia, California, USA). Subsamples (0.1–0.2 mg) were used to measure total N content (Table 1). These samples were analyzed by combustion and gas chromatography (Costech, ECS 4010 CHNSO analyzer, Valencia, California, USA).

Base cations [calcium (Ca^{2+}), potassium (K^+), magnesium (Mg^{2+}), aluminum (Al^+), phosphorus (P), and phosphate (PO_4^-)] (Table 1), were measured in a Melich III extract (Mehlich 1984, Carter 1993, Loide et al. 2005) consisting of 6 g soil in 42 mL of solution. Subsamples (15 mL) of the extract were used to measure Ca, K, Mg, Al, and P with an Optima 2100DV ICP (inductively coupled plasma) Optical Emission Spectrometer (Perkin-Elmer, Shelton, Connecticut, USA). A separate colorimetric assay was used to measure PO_4 (Frank et al. 1998). Although P (as measured using ICP spectrometry) and PO_4 (colorimetric assessment) were highly correlated (r = 0.920), only the former was used in the analysis because the soil PO_4 pool is extremely labile in these soils (Vincent et al. 2010); extractable P measured with the ICP thus captures both PO_4 and organic P that will become available to plants. Soil pH was measured in solution of 2 mol/L KCl (Table 1).

Local-scale soil resource estimation

Using the soil data, resource values were predicted at each tree location using a Bayesian multivariate spatial

regression model. This model accounts for variability in resource response variables through a multivariate linear mean function that comprised topographic predictor variables and resource-specific regression coefficients. Spatially dependent model residuals were accommodated using a multivariate Gaussian process, with the resources' spatial cross-covariance following a linear model of co-regionalization (Gelfand et al. 2004, Finley et al. 2009). Topographic predictor variables included elevation, slope, aspect, curvature (concavity), flow length (length over which flow velocity remains constant), and flow direction (azimuth), and were derived from a high-resolution lidar digital elevation map of La Selva (Kellner and Asner 2009).

The multivariate resource models were estimated for each of the five sites. These computations were done using the spMvLM routine within the spBayes R package (Finley et al. 2007). For all models, there were three chains of 75 000 Markov chain Monte Carlo (MCMC) iterations. Convergence was diagnosed within 50 000 MCMC iterations and parameter inference and model fit were assessed using the 25 000 post-convergence MCMC samples. These post-convergence samples were further subset and used to generate, via composition sampling, 1000 samples from the resources' posterior predictive distributions at each tree location (for details, see Finley et al. 2009). Together, these posterior predictive samples (PPS) approximate the resources' posterior predicted distributions and comprise an ensemble data set used to propagate uncertainty in resource availability through the individual tree-based models detailed in the subsequent section.

Individual growth analysis

Data were analyzed at several levels, including all species together (representing ecological neutrality), species with at least 50 focal trees (15 species), five wood density classes as fifths of the wood density range (Zanne et al. 2009), and three taxonomic divisions further categorized by adult stature (Fabaceae, canopy and smaller; Arecaceae, subcanopy and smaller; nonlegume dicots, canopy and smaller). For each of these divisions, we evaluated individual diameter growth (G_d) as a function of (1) tree diameter, (2) a neighborhood index, and (3) each of the soil resources (Ca, K, Mg, P, NH_4, NO_3), and a species- or category-specific coefficient P_{gr}:

$$G_d = P_{gr} \times \text{Diameter effect} \times \text{Neighborhood effect}$$
$$\times \text{Soil resource effect} \quad (1)$$

where P_{gr} was a scalar value representing theoretical maximum growth for each species or group (Canham et al. 2006), and each remaining term was an exponential decay function constrained between 0 and 1 that could either reduce or have no effect upon P_{gr}. Effect of diameter on tree growth was modeled as a lognormal function:

$$G_d = P_{gr} \times \exp(-0.5[\ln(\text{dbh}/\delta)/\sigma]^2) \quad (2)$$

where δ represents the diameter at which maximum growth occurs (consistent with the data), and σ controls the rate at which the function achieves the maximum. Neighborhood effect was calculated as a size- and distance-dependent function (Wimberly and Bare 1996, Vettenranta 1999, Berger and Hildenbrandt 2000, Canham and Uriarte 2006) of the number of neighbors:

$$\text{Neighborhood effect} = \exp\left(B \sum_{i=1}^{n} \text{dbh}_i^\alpha \exp^{(-\beta/\text{dist}_i)}\right) \quad (3)$$

where B is a coefficient to control the relative contribution of the neighborhood overall, α is an estimated exponent controlling the influence of neighbor diameter, and β is an estimated exponent controlling the influence of distance to the focal tree. The sum was calculated for $i = 1 \ldots n$ neighbors within either a set radius of 20 m or within an estimated radius ($\leq$20 m) determined by the data.

The soil resource effect was modeled as

$$\text{Soil resource effect} = 1 - \exp(C \times \text{resource}) \quad (4)$$

where the exponential decay is subtracted from 1 so that lowest resource availability results in the lowest growth. In addition to the full model (Eq. 1), we tested a variety of simpler models, including each of the effects (i.e., diameter, soil resources, and neighborhood) alone, and every possible pair of effects (Appendix B). The uncertainty in the resource was quantified for individual-level growth using the PPS ensemble data set, calculating the range of parameter values and predicted growth for the most parsimonious model formulation for each category.

Parameter estimation and model comparison

Growth models were fit to all species, individual species with >50 focal trees, six functional groups, and five wood density classes. Model parameters were estimated with maximum likelihood using a simulated annealing algorithm (Metropolis sampler) implemented in Delphi (Version 3.0, Borland Corporation, Austin, Texas, USA), running each model for 50 000 steps. Growth was treated as a normal random variable in the likelihood function, with mean growth specified by Eq. 1 and variance estimated as a parameter from the data. Residuals were normally distributed, justifying the

normal probability density function. The 95% confidence interval for each parameter was calculated by likelihood profiling; the square of the Pearson correlation coefficient (r^2) of model-predicted vs. observed growth was used to assess goodness of fit. The models for each analysis group were compared using Akaike's Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002); we report only models that have $\Delta\text{AIC}_c < 2$.

Site mean growth analysis

We also tested relationships of site-level mean basal area increment (BAI) to mean resource availability for the same functional groupings as before. In addition to the resources tested for the individual-based models (Ca, K, Mg, P, NH_4, NO_3), we also tested correlations of site-level growth with total soil N, Al, and pH. Because growth of the Fabaceae was not correlated with soil resources, they were excluded from the wood density analyses. We used simple linear regressions because small sample size ($n = 5$ sites) precluded fitting more complex functions. To account for differences in tree size among sites, site mean growth was calculated as the average BAI of all individuals at each site (Appendix A). Similarly, site mean resource values were calculated as an average across all trees within the defined functional group. Calculating site-level mean growth and soil resource values for each functional group was necessary because each tree was associated with different soil resource levels; thus, different functional groups could experience different mean resource levels even within a single site. For several instances in which estimated intercepts were not significantly different from zero, data were presented on the original scales, as opposed to centered (Chatterjee and Hadi 2006), to facilitate comparison to other species or groups. To propagate the uncertainty in predicted resource availability, we calculated regression models of BAI as a function of site-mean resource values using all 1000 PPS for each resource.

Results

Overview

For many functional group categories, site mean BAI and individual tree growth were positively related to soil P and base cations, results that generally supported our first, third, and fourth hypotheses (Tables 2 and 3, Figs. 1–3). Individual growth was rarely correlated with local neighborhood, however, providing negligible support (Appendix D) for our second hypothesis that growth should be negatively correlated with neighborhood. At both the individual tree and site levels, growth of Fabaceae was not related to resources (except for a very weak relationship for one species), consistent with our third hypothesis. Among wood density classes, growth for only the lowest-density species was related to soil P, in accordance with our fourth hypothesis (Table 2; Appendix C); for higher wood density classes, growth

TABLE 2. Summary of results (goodness-of-fit R^2 values) for stem growth as a function of soil resources for all species together, for functional groups, and for wood density categories; strongest relationships occurred at the site level.

Analysis category	Ca	K	Mg	P
All species		0.790		0.985
FC				
F < C				
AS				0.868
A < S	0.843			0.961
NLDC		0.864		
NLD < C	0.816	0.822		
Wood density class (g/cm^3)				
0.2–0.4		0.815		0.912
0.4–0.55			0.851	
0.55–0.7				
0.7–1.2	0.799			
Unknown				0.780

Notes: All values presented are from linear regressions for site-level analyses. Site-level mean tree growth was not significantly correlated with either NH_4 or NO_3 for any functional group, so these elements are not included in the table. Functional group and size class abbreviations are: FC, Fabaceae, canopy size; F < C, Fabaceae, smaller than canopy size; AS, Arecaceae, subcanopy; A < S, Arecaceae, smaller than subcanopy; NLDC, nonlegume dicot species, canopy size; NLD < C, nonlegume dicot species, smaller than canopy.

generally was correlated with base cations (K or Mg). Although site-level growth was occasionally correlated with NH_4 or NO_3 for some taxonomic groups, growth was never correlated with total soil N. Focal tree diameter was a relatively weak predictor of tree growth, and accounted for ≤19.3% of the total variance (Appendices C–E).

For many functional groupings, P and base cation availability were correlated. Thus, in the absence of resource manipulations, and even with resource additions in some cases (Gleason et al. 2009), it is difficult to

judge which element constrained growth. However, strengths of correlations often differed among elements and, in many cases, not all elements were significantly correlated with tree growth. In addition, soil Al content ($0.47 < R^2 < 0.61$, $0.12 < P < 0.19$) and pH ($0.09 < R^2 < 0.33$, $0.31 < P < 0.62$) were never significant predictors of tree growth at the site level.

Stand-level growth correlated positively to soil P, Ca, and K

Grouping all species together, relationships of mean BAI to soil resources across sites supported our first hypothesis, with growth related to P ($R^2 = 0.958$, R^2 95% credible interval (CI$_{95\%}$): 0.314–0.979), K ($R^2 = 0.790$, CI$_{95\%}$: 0.528–0.925), and marginally related to Ca ($R^2 = 0.744$, CI$_{95\%}$: 0.218–0.914) (Fig. 1; Appendix F). Sites located on the older volcanic soil types had lower growth rates and considerably lower levels of P; the difference in Ca and K between volcanic and alluvial sites was less pronounced (Appendix A). When considering all species together, base cations and P availability covaried (Appendix G).

Refining the site-level analysis into functional groupings, results were consistent with P, K, and/or Ca limitation, with P most important for the Arecaceae, but base cations for the nonlegume dicot species. Mean BAI of subcanopy Arecaceae was related to extractable P ($R^2 = 0.868$, CI$_{95\%}$: 0.023–0.978), with growth expected to vary from 2 to 12 cm^2/yr across the range of soil P. Mean BAI of smaller palms was related to both P ($R^2 = 0.961$, CI$_{95\%}$: 0.001–0.979) and to Ca ($R^2 = 0.843$, CI$_{95\%}$: 0.138–0.925; Fig. 2; Appendix H), which themselves were strongly correlated ($r = 0.975$; Appendix G). BAI of nonlegume dicot canopy species was related to K ($R^2 = 0.864$, CI$_{95\%}$: 0.558–0.968), and was expected to increase

TABLE 3. Summary of results (goodness-of-fit R^2 values) for stem growth as a function of soil resources for single species.

Analysis category	Ca	K	Mg	P	NH$_4$	NO$_3$
Welfia regia						
Pentaclethra macroloba						
Socratea exorrhiza					0.916	0.873
Rinorea deflexiflora				0.980		
Iriartea deltoidea		0.871		0.839	0.876	
Capparis pittieri						
Faramea parvibractea	0.963	0.997	0.953	0.981		
Euterpe precatoria						
Cryosophila warscewiczii	0.820			0.960		
Dendropanax arboreus						
Casearia arborea						
Prestoea decurrens						0.997
Coussarea hondensis						
Warszewiczia coccinea		0.949				
Goethalsia meiantha						
Other						

Notes: All of the strongest relationships again occurred at the site level (with goodness of fit presented as the R^2 value). For three species (*Welfia regia*, *Cryosophila warscewiczii*, *Coussarea hondensis*), neighborhood effects (defined only at the individual level) were significantly correlated with growth (Appendix D); neighborhood index and soil resource levels did not demonstrate significant covariance (Appendix D).

from 12 to 21 cm^2/yr across the K gradient. For subcanopy and smaller species, growth was related to K ($R^2 = 0.822$, CI$_{95\%}$: 0.676–0.984) and Ca ($R^2 = 0.816$, CI$_{95\%}$: 0.523–0.971; Appendix G), which themselves were correlated ($r = 0.795$; Appendix G); BAI was expected to vary from 3.5 to 7.5 cm^2/yr (Fig. 2; Appendix H). However, BAI of nonlegume dicots was not significantly correlated with P.

Site-level mean BAI for single species was generally aligned with functional group results. Among the Arecaceae, mean BAI in four species (*S. exorrhiza*, *I. deltoidea*, *C. warscewiczii*, *P. decurrens*) was positively related to at least one resource, including N, P, and base cations (Appendices H–J). For the nonlegume dicot species, mean BAI for three species (*R. deflexiflora*, *F. parvibractea*, *W. coccinea*) was related to the base cations and P, but not to N (Appendices I and J).

Growth of Fabaceae was unrelated to soil resources

Supporting our third hypothesis, site mean BAI of the Fabaceae was unrelated to soil resources, either for canopy or smaller species (Fig. 2; Appendix H). Site mean BAI for the single legume species with sufficient sample size to warrant species-level analysis, *Pentaclethra macroloba*, was not related to any soil resource (Appendix J).

Similarly, individual diameter growth for the Fabaceae was unrelated to P or inorganic N, and only very weakly related to K. For canopy Fabaceae, K was significantly correlated with growth but explained only 2.1% more variance than diameter alone (Appendix E). For subcanopy and smaller-statured species, diameter alone was correlated with growth (Appendix E). For *P. macroloba*, despite having the largest sample size of any species ($n = 368$), growth was only nominally correlated with Ca ($r^2 = 0.026$; Appendix D).

Individual growth correlated positively but weakly to soil P, base cations, and N

Treating all species together, individual diameter growth was related only to initial diameter and soil K (Appendices E and K; second lowest $\Delta AIC_c = 18.5$, for Ca), and the model explained little variance in growth ($r^2 = 0.081$). Examining growth by functional group, individual growth of the Arecaceae was correlated with soil P ($r^2 = 0.105$), whereas nonlegume dicot growth was correlated with K ($r^2 = 0.044$). For subcanopy palm species, P explained 10.5% of the total variance (Appendix E). Growth of treelet and understory palms demonstrated a similarly robust correlation with P (Appendix E). For all other species, growth was weakly related to resources, with a maximum of 4.4% additional total variance explained by soil K for species that could attain canopy stature (Appendices E and K). For single species, individual diameter growth was related to base cations, P, or NH$_4$, but relationships were generally weak (Appendices D and L). Contrary to the prediction of hypothesis 2, neighborhood index was not correlated
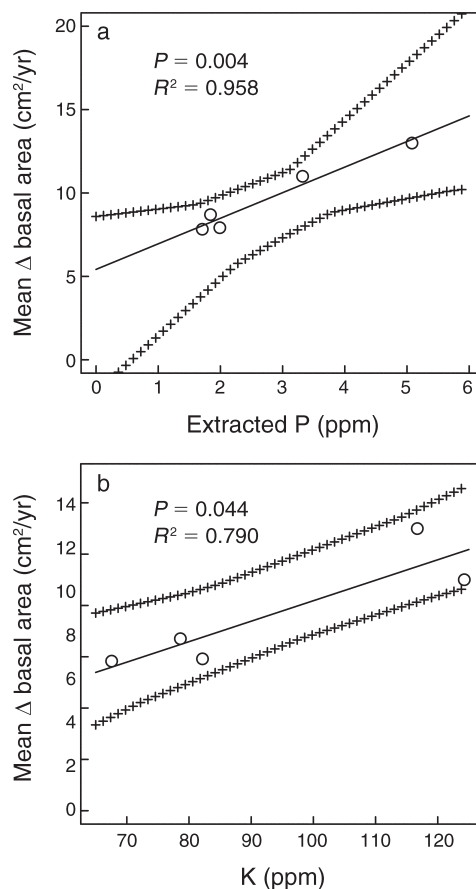

FIG. 1. Site mean basal area increment for all tree species present in the mapped stands as functions of soil resources. Basal area increment was significantly related to soil (a) P and (b) K. Solid lines represent simple linear regression of growth as a function of mean soil resource with an estimated intercept, presented with associated R^2 and P values. Cross symbols represent the envelope of predicted growth based on 1000 resource data sets subsampled from the posterior predictive distribution of each resource.

with growth across all species or for any functional groups, and was only rarely correlated with growth of single species. For two palm species and one nonlegume dicot species, growth was negatively related to neighborhood index, although the structure of this index varied among these three species (Appendices D and L).

Growth of species with low-density wood correlated more strongly with soil P

Among wood density categories, the base cations and P were positively correlated with BAI. Extractable P ($R^2 = 0.912$, CI$_{95\%}$: 0.780–0.984) and K ($R^2 = 0.815$, CI$_{95\%}$: 0.775–0.936) were correlated with BAI of species constituting the minimum wood density class, with growth expected to increase from 5.5 to 13.5 cm^2/yr across the resource gradient (Fig. 3). Consistent with our fourth hypothesis, these relationships were slightly stronger (assessed by goodness of fit for simple linear
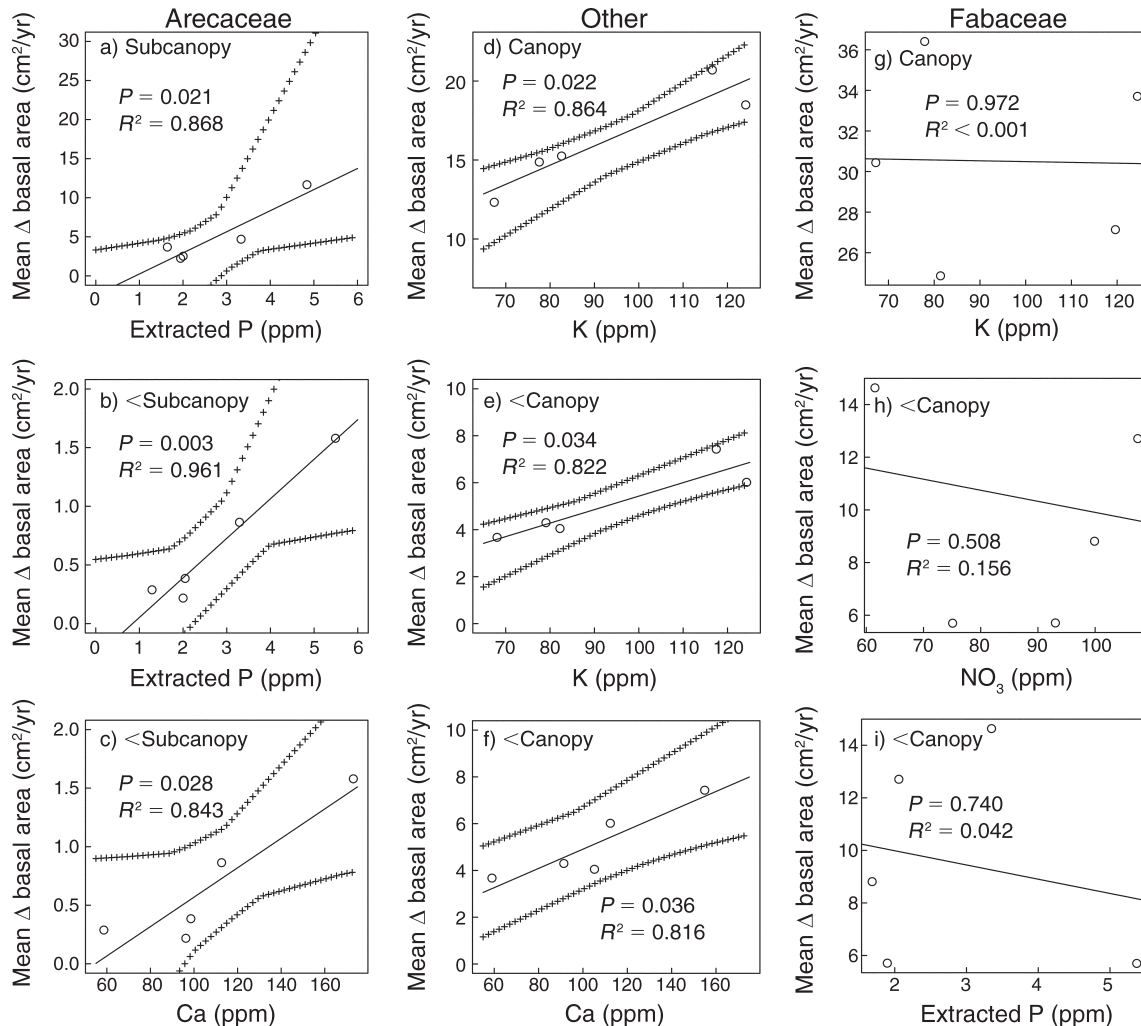
FIG. 2. Site mean basal area increment for six taxonomic groups as functions of soil resources. Lines represent simple linear regression of growth as a function of soil resource, with associated P and R^2 values. (a) Growth of subcanopy palm species (Arecaceae) was related to P, while (b, c) growth of treelet and understory (<subcanopy) palms was related to (b) Ca and/or (c) P. (d–f) Among nonlegume dicot species (Other), (d) mean diameter growth of canopy species was related to K, and diameter growth of subcanopy, treelet, and understory (<canopy) species was related to (e) Ca or (f) K. Notably, growth of Fabaceae was unrelated to resources regardless of size class (g–i), shown here as functions of the soil resources most strongly correlated (none significantly) with individual growth. Cross symbols represent the envelope of predicted growth based on 1000 resource data sets subsampled from the posterior predictive distribution of each resource. Envelopes were not calculated for Fabaceae because regressions were not significant.

regression) for the lowest density class than for other categories (Appendix M). For the higher-density classes, site-mean BAI was related to Mg ($R^2 = 0.851$, $CI_{95\%}$: 0.775–0.951) and Ca ($R^2 = 0.799$), whereas for species of unknown wood density (probably representing many low-density species, based on taxonomic groupings) BAI was again related to P ($R^2 = 0.780$, $CI_{95\%}$: 0.774–0.921; Fig. 3).

Considering individual diameter growth, the group of species with lowest wood density showed considerably stronger correlation of diameter growth with P than species with higher-density wood (supporting hypothesis 4), but in all cases, resources explained little variation in growth (Appendices E and N).

Use of the resources' PPS allowed us to acknowledge and propagate prediction uncertainty through subsequent models that explored individuals' growth–resource response (Appendix P). At the site level, the envelope of possible predicted growth was typically limited to a narrow range around the mean predictions (Figs. 1 and 3). Within functional groups or wood density categories, the uncertainty resulting from estimating values of P was often larger than that of base cations (Figs. 1–3), although the R^2 values were often higher for P correlations.
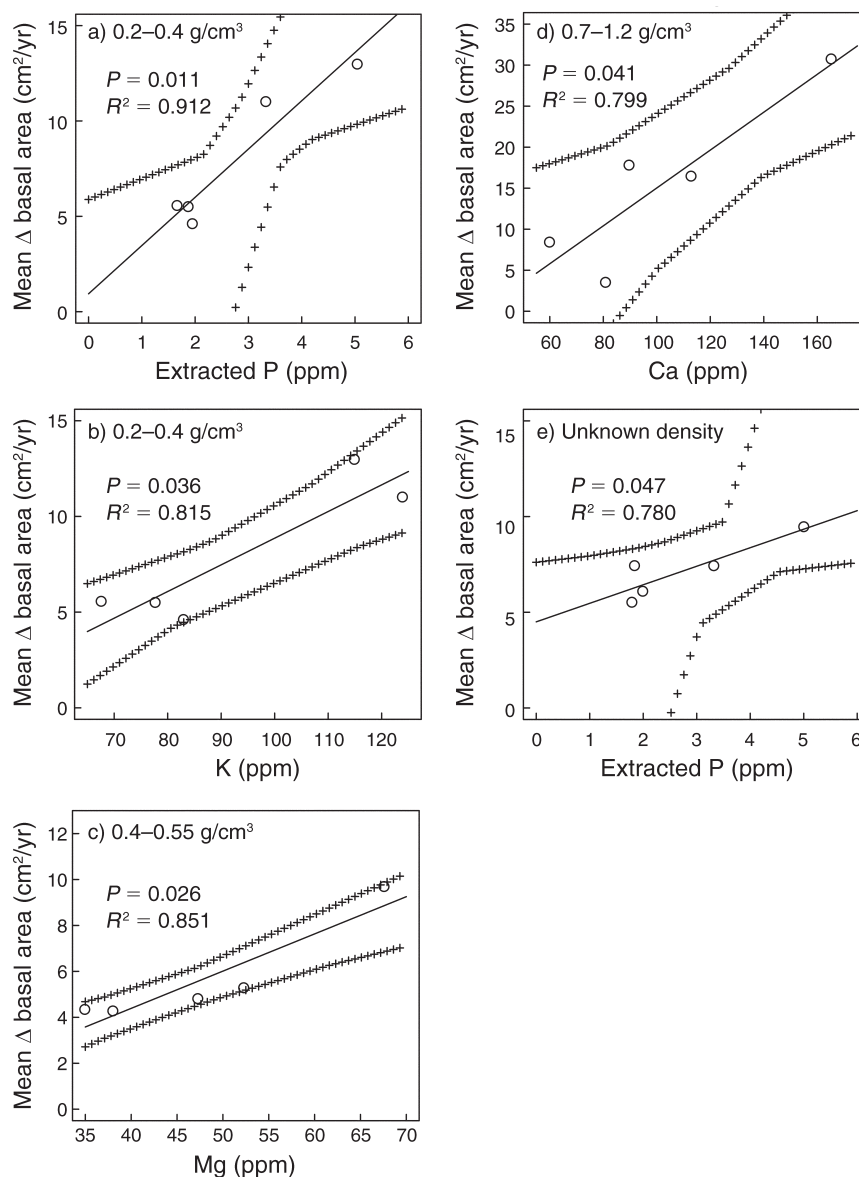
Fig. 3. Site mean stem area growth for wood density categories, excluding legume species, plotted vs. soil resources. Lines represent simple linear regression of growth as a function of soil resource, with associated P and R^2 values. For the two lightest density groups (a, b, c), P, K, and Mg were correlated with growth. In the second-highest density group (d, e), growth was related to K and Ca. Mean basal area increment (BAI) was not significantly correlated with soil nutrients for species in the 0.55–0.7 g/cm^3 density class. Cross symbols represent the envelope of predicted growth based on 1000 resource data sets subsampled from the posterior predictive distribution of each resource.

DISCUSSION

Growth and productivity in wet tropical forests are typically considered to be limited by P availability (Vitousek et al. 2010), yet results were consistent with limitation not only by P, but also by base cations, supporting our first hypothesis. There were very strong relationships between site-level mean growth and soil P, K, and Ca, even though individual tree growth was weakly related to soil resources and neighborhood. Growth of some functional groups, including the most common group of nonlegume dicots, was correlated

only with base cations and not P. Deficiencies in P or the base cations are common on older soils subject to high rates of leaching (Vitousek and Farrington 1997, Porder et al. 2007), so our results were consistent with expected resource limitations on these types of soils.

Local neighborhood was negatively correlated with growth for only three species and explained between 10% and 15% of the total growth variance, suggesting, contrary to our second hypothesis, that competition was relatively unimportant (Uriarte et al. 2004). In addition, it is unlikely that neighborhood and soil resource effects

were confounded because neighborhood index and soil resource availability did not appear concurrently in any empirically supported models (Appendix D), and covariance has not been demonstrated in similar analyses (Baribault and Kobe 2011). However, competition and neighborhood interactions probably exert much greater influence on growth (Guariguata and Ostertag 2001, Hood et al. 2004, Canham et al. 2006) than these data were able to detect. In these forests of minimal disturbance, growth of all trees, especially those in the subcanopy, is likely to be heavily suppressed by neighbors (Coates et al. 2009). Thus, lack of variation in neighborhood conditions (Coates et al. 2009) may have precluded detection of neighborhood effects.

However, it also is possible that weak individual-level effects (both phenomenological neighborhood and measured soil resource availability) are a real feature of this wet tropical forest because common mycorrhizal networks (Simard 2009) homogenize carbon and soil resource availability among individuals within a site. Stronger relationships between growth and soil resources could emerge at the site level because resource homogenization via common mycorrhizal networks would not extend between sites.

Individual diameter growth and site mean BAI were related to soil resources for palm and nonlegume dicot species but not for legumes. We offer two potential explanations for this apparent legume escape from mineral nutrient limitations. An alleviation of P limitation could originate from the diversion of fixed N_2 to production of rhizosphere phosphatase (Olander and Vitousek 2000, Wang et al. 2007) that dissociates plant-available PO_4 from recalcitrant sources (Adams et al. 2010). The extensive N fixation that occurs in tropical forests appears paradoxical because N_2 fixation should be down-regulated under conditions of excess N availability (Hedin et al. 2009, Menge et al. 2010). Measurement of NH_4 and NO_3 in air-dried soils may not reflect availability under field conditions, but growth was also unrelated to total N, which, given uptake of organic forms of N by plants and mycorrhizae (Leduc and Rothstein 2010), could also be a good index of plant available N. Although this lack of relationship of growth to soil N may be due to excess N, we cannot eliminate the possibility that our soil analysis did not properly capture plant-available N. Our results suggest that legume stem growth was limited by neither N nor P, and that growth was correlated with soil P only for nonlegume species and functional groups. However, the lack of correlative evidence for N limitation across other taxonomic groups suggests that nonlegumes could acquire sufficient N from the environment to also exploit the rhizosphere phosphatase strategy. Furthermore, P is itself required for N fixation in legumes (Cassman et al. 1980). In addition, from a resource balance perspective, increased inorganic soil N content and plant-available P (facilitated by legume N_2 fixation and phosphatase production) could induce growth

limitation by base cations (Treseder and Vitousek 2001), particularly for legumes (Høgh-Jensen 2003). But site mean legume growth was unrelated to base cations, so allocation of N to phosphatase is unlikely to be a complete explanation for the patterns that we observed.

Increased N availability from N_2 fixation could lead to higher foliar N concentrations and concomitantly higher maximum photosynthetic rates (Wright et al. 2004). The fixed carbon from greater photosynthetic rates might be used to support mycorrhizae, which in turn increase access to mineral nutrients (Phillips and Fahey 2007), including P and based cations. Our results are most consistent with this idea that N_2 fixation increased carbon fixation that is allocated to mycorrhizae and nutrient uptake, which also alleviated base cation limitation (Smethurst 2010).

In contrast to the legumes, we found two lines of evidence consistent with base cation or P limitation for other functional groups. The primary support for base cation or P limitation was the positive correlations of BAI to these resources for the Arecaceae and nonlegume dicots, and for single species within these functional groups. Second, negative correlations of soil N to soil P and base cations (e.g., Appendix O) are consistent with N accumulation and P and base cation depletion over time (Vitousek and Farrington 1997, LeBauer and Treseder 2008). Negative covariance between soil N (NH_4 and NO_3) and base cations or P (Appendix O) may also explain that for three individual species (*S. exorrhiza*, *I. deltoidea*, and *P. decurrens*) the strongest growth–resource relationships were negative correlations with NH_4 and NO_3 (Appendix J), indirectly suggesting soil base cations or extractable P (Appendix O) limitations.

Evidence consistent with P and K limitation was strongest for species with lowest wood density, in accordance with our fourth hypothesis, which predicted that faster-growing species should be more resource-limited (Finzi 2009). Contrary to prediction, we also found strong correlations between growth and base cation availability for species with higher wood density. Evidence consistent with P limitation at the site level existed only for potentially faster-growing species of low wood density (Oelmann et al. 2010) whereas results for slower-growing species with higher wood density (Kelly et al. 2009) were consistent with base cation limitation. However, species with low wood density and fast diameter growth rates do not necessarily have high rates of mass growth, which would more strongly influence demand for mineral nutrients (Easdale and Healey 2009, Smethurst 2010), assuming that wood tissue stoichiometry is consistent across wood density classes. Thus, we calculated a proxy for mass increment as the product of mean BAI and mean wood density for a 1-cm high cross-section of annual growth at the point of diameter measurement. Based on this index, the fastest mass growth (10.79 g/yr) occurred in the highest wood density class (0.7–1.2 g/cm^3), followed by the 0.4–

0.55 g/cm^3 class (2.28 g/yr). Slowest mass growth (1.59 g/yr) occurred in the lowest wood density (0.2–0.4 g/cm^3) class. We do not, however, have the information necessary to calculate whole-tree mass increment, which may differ from stem cross section mass increment due to variation in tree height and branching patterns (Chave et al. 2005) and within-tree variation in wood density. Nevertheless, a shift from P limitation in early-succession, low-density species to base cation limitation in late-succession, shade-tolerant species with high wood density could indicate differences in either stoichiometric resource limitation or resource use efficiency between early- and late-succession species (Gleeson and Tilman 1994, van Kuijk and Anten 2009).

We identified strong correlations of site mean growth (BAI) to soil P and base cations, particularly among the Arecaceae and nonlegume dicot species and for several wood density categories, but generally not for legume species. Although P has often been implicated in limiting productivity of tropical forests, soil K was correlated with growth for more species and functional groups, both at the site and individual levels (Wright et al. 2011) (H_1). In addition, competition appeared to have limited influence on individual tree growth (H_2), although data from a variety of disturbance regimes could provide a different conclusion. For the legumes, both individual diameter growth and site mean BAI were unrelated to soil resources (H_3), consistent with alleviation of resource limitation (e.g., by diverting extra photosynthate, gained by N_2 fixation, to mycorrhizae). We emphasize that our results were based on natural variation in soil resources and that resource limitation must ultimately be resolved using fertilizer addition experiments, although even such experiments may fail to induce a growth response to fertilizer addition if species characteristic of low-resource environments have evolved high resource-use efficiency (Gleason et al. 2009). At this point, we also cannot exclude the possibility that positive growth correlations with base cations reflect negative effects of aluminum (Al), but this possibility is not supported by the data, because we observed positive covariance between extracted Al and base cations. Although our results identify P as a possible limiting resource, our strong correlative support for limitation by the base cations, particularly K, suggests that base cations also should be more rigorously examined for their potential in limiting tree growth and wood production in wet tropical forests (e.g., P × base cation fertilization experiments). Although we stress the potential importance of base cations, our results also suggest that P is the most probable limiting resource for growth of species with low wood density (H_4), which tend to be early-succession species. Thus, P availability may determine the rate of early-successional dynamics on tropical soils. Overall, our results support that hypothesis that tropical tree growth may be limited by base cations and/or P; furthermore, the degree and type of resource limitation may depend on functional group differences in wood density and potential for N fixation.

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SUPPLEMENTAL MATERIAL

Appendix A

Site-level inventory data and growth rate data, including basal area and diameter, with density and mortality (*Ecological Archives* M082-007-A1).

Appendix B

Parameter definitions and effects for the neighborhood-influenced growth models (*Ecological Archives* M082-007-A2).

Appendix C

Goodness of neighborhood model fit and AIC results for wood density groups (*Ecological Archives* M082-007-A3).

Appendix D

Goodness of neighborhood model fit and AIC results for selected individual species (*Ecological Archives* M082-007-A4).

Appendix E

Goodness of neighborhood model fit and AIC results for functional groups (*Ecological Archives* M082-007-A5).

Appendix F

Regression parameters for significant site-level models of growth across all species as a function of single soil resources (*Ecological Archives* M082-007-A6).

Appendix G

Covariance of soil resources estimated at the locations of individual trees (*Ecological Archives* M082-007-A7).

Appendix H

Regression parameters for significant site-level models of growth for functional groups as a function of single soil resources (*Ecological Archives* M082-007-A8).

Appendix I

Mean basal area increment at the site level for individual species (*Ecological Archives* M082-007-A9).

Appendix J

Regression parameters for significant site-level models of growth for selected individual species as a function of single soil resources (*Ecological Archives* M082-007-A10).

Appendix K

Parameter values for empirically supported neighborhood models of functional groups (*Ecological Archives* M082-007-A11).

Appendix L

Parameter values for empirically supported neighborhood models of single species (*Ecological Archives* M082-007-A12).

Appendix M

Regression parameters for significant site-level models of growth for wood density classes and for functional groups as a function of single soil resources (*Ecological Archives* M082-007-A13).

Appendix N

Parameter values for empirically supported neighborhood models of wood density groups (*Ecological Archives* M082-007-A14).

Appendix O

Soil resource correlations and sample sizes by functional group (*Ecological Archives* M082-007-A15).

Appendix P

Soil resource uncertainty effects on envelopes of parameter estimates (*Ecological Archives* M082-007-A16).

Appendix Q

Soil resource uncertainty effects on predicted diameter growth expressed as minimum, mean, and maximum growth (*Ecological Archives* M082-007-A17).

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.r9p70