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Plant responses to fertilization experiments in lowland, species-rich, tropical forests

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Abstract. We present a meta-analysis of plant responses to fertilization experiments conducted in lowland, species-rich, tropical forests. We also update a key result and present the first species-level analyses of tree growth rates for a 15-yr factorial nitrogen (N), phosphorus (P), and potassium (K) experiment conducted in central Panama. The update concerns community-level tree growth rates, which responded significantly to the addition of N and K together after 10 yr of fertilization but not after 15 yr. Our experimental soils are infertile for the region, and species whose regional distributions are strongly associated with low soil P availability dominate the local tree flora. Under these circumstances, we expect muted responses to fertilization, and we predicted species associated with low-P soils would respond most slowly. The data did not support this prediction, species-level tree growth responses to P addition were unrelated to species-level soil P associations. The meta-analysis demonstrated that nutrient limitation is widespread in lowland tropical forests and evaluated two directional hypotheses concerning plant responses to N addition and to P addition. The meta-analysis supported the hypothesis that tree (or biomass) growth rate responses to fertilization are weaker in old growth forests and stronger in secondary forests, where rapid biomass accumulation provides a nutrient sink. The meta-analysis found no support for the long-standing hypothesis that plant responses are stronger for P addition and weaker for N addition. We do not advocate discarding the latter hypothesis. There are only 14 fertilization experiments from lowland, species-rich, tropical forests, 13 of the 14 experiments added nutrients for five or fewer years, and responses vary widely among experiments. Potential fertilization responses should be muted when the species present are well adapted to nutrient-poor soils, as is the case in our experiment, and when pest pressure increases with fertilization, as it does in our experiment. The statistical power and especially the duration of fertilization experiments conducted in old growth, tropical forests might be insufficient to detect the slow, modest growth responses that are to be expected.

Key words: Barro Colorado Nature Monument; fertilization; fine litter production; foliar nutrient concentrations; meta-analysis; nitrogen; old growth forest; phosphorus; potassium; secondary forest; tree growth rates.

Introduction

Tropical forests cover just 7% of the Earth's land surface but store 25% of terrestrial carbon and account for 33% of terrestrial net primary productivity (Bonan 2008). The vast majority of these forests spread across the humid lowlands of tropical Africa, Asia, and the Americas and support tremendous numbers of species. How these lowland, species-rich, tropical forests respond to atmospheric and climate change will have profound implications for future global carbon and hydrological cycles (Bonan 2008), with the potential for nutrient supplies to limit future carbon sequestration being a crucial uncertainty (Wieder et al. 2015).

Comparative nutrient cycling studies generated the hypothesis that phosphorus (P) is limiting in many lowland tropical forests while nitrogen (N) is not. Briefly, leaf N:P ratios increase dramatically before abscission in many lowland tropical forests, suggesting more efficient reabsorption of P than N (McGroddy et al. 2004). Partly as a result, P tends to cycle more efficiently than N in fine litter in tropical lowland forests relative to temperate, boreal, and tropical montane forests (Vitousek 1984, Vitousek and Sanford 1986). In addition, gaseous and hydrological losses of N tend to be much larger in tropical lowland forests than in temperate and boreal forests, suggesting N supplies exceed plant demand in tropical lowland forests (Houlton et al. 2006, Hedin et al. 2009). Finally, foliar P concentrations correlate strongly with total soil P stocks (Cleveland et al. 2011), and fine litter production increases with litter P but not litter N concentration in lowland tropical forests (Vitousek 1984). These comparative studies are consistent with the hypothesis that P is limiting in many lowland tropical forests while N is not.

At least two mechanisms contribute to the nutrient cycling differences observed between tropical lowland forests vs.

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temperate, boreal, and tropical montane forests. Bedrock and biological fixation are the primary sources of P and N, respectively, and Walker and Syers (1976) showed that P availability declines as bedrock decomposes and P leaches away during pedogenesis and N availability increases as biological fixation develops. Rapid erosion keeps many montane soils in early stages of pedogenesis (Porder et al. 2007), and Quaternary glaciation exposed fresh bedrock and spread dust and till from ground bedrock over a large portion of temperate and boreal but not tropical latitudes (Vitousek 1984). In addition, warm, moist conditions enhance decomposition rates in the lowland tropics, preventing accumulation of unavailable organic N in an organic horizon. These regional differences in soil age and decomposition rates and the consistent results of comparative nutrient cycling studies motivate the hypothesis that lowland tropical forests growing on old, highly weathered Ultisols and Oxisols tend to be limited by P (or another rock derived nutrient) and not by N (Vitousek 1984, Vitousek and Sanford 1986, Vitousek et al. 2010). This hypothesis is now widely accepted (Elser et al. 2007), but experimental tests are few.

Operational definitions of nutrient limitation of biological processes include positive responses to experimental fertilization (Vitousek and Howarth 1991, Vitousek et al. 2010). Classic fertilization experiments confirmed the hypothesis that N and P limit Hawaiian forests growing on young vs. old soils, respectively (Harrington et al. 2001). Strong, positive responses to N and P fertilization indicate N and P both limit plants in most terrestrial biomes (Elser et al. 2007, LeBauer and Treseder 2008). These meta-analyses report reasonable numbers of experiments for tropical forests, but these mainly concern montane forests, Hawaiian forests dominated by a single tree species, species-poor mangrove and planted forests, and even potted seedlings (see *Discussion: Experimental evidence for nutrient limitation*). Just 14 fertilization experiments have been conducted in lowland, species-rich, tropical forests (LSRTF), with more than half published in the 10 yr since the two meta-analyses (Appendix S1: Tables S1 and S2). In a third global meta-analysis, temperate and boreal forest plants respond strongly to potassium (K) fertilization; however, the single tropical study concerned potted seedlings (Tripler et al. 2006). Experimental evidence of nutrient limitation of plants in LSRTF is scant and a systematic review is lacking.

Here, we update a key result from our own factorial NPK fertilization experiment conducted in central Panama and perform a meta-analysis of the 14 fertilization experiments conducted in LSRTF. In our experiment, each added nutrient increased plant tissue concentrations of that nutrient; K addition (henceforth +K) decreased fine root biomass and increased rates of seedling growth, fine root turnover, and decomposition; +P increased fine litter production and rates of photosynthesis, stomatal conductance, and decomposition; combined N and P addition (henceforth +NP) increased seedling growth rates; +PK further increased stomatal conductance; and +NK ameliorated declining tree growth rates (Kaspari et al. 2008, Wright et al. 2011, Yavitt et al. 2011, Pasquini and Santiago 2012, Santiago et al. 2012, Mayor et al. 2014, Pasquini et al. 2015). The key result that has changed as the fertilization treatments continue concerns tree growth rates, which are no longer responsive to +NK.

We also use newly available information on species-level responses to a natural gradient of P availability (Condit et al. 2013) to inform the first species-level analysis of tree growth rates for our experiment. We test the hypothesis that species whose regional distributions are associated with P-rich soils respond more strongly to P addition than do species associated with P-poor soils.

Our meta-analysis focuses on two hypotheses. The first hypothesis is that P limitation is stronger and N limitation is weaker in LSRTF. The second hypothesis is that nutrient limitation is stronger in secondary forests (and in high light tree-fall gaps) and weaker in old growth forests. The second hypothesis is motivated by the large nutrient sink imposed by rapid biomass accumulation in secondary forests and tree-fall gaps. The meta-analysis is limited to N and P because just two fertilization experiments have considered any other nutrient for LSRTF. The meta-analysis is also limited to four types of responses, foliar N and P concentrations, fine litter N and P concentrations, fine litter production, and tree or biomass growth rates, because too few experiments have considered other types of responses. The meta-analysis indicates that N and P are equally likely to be limiting in LSRTF and are more likely to limit tree/biomass growth rates in secondary forests than in old growth forests.

METHODS

Meta-analysis

We compiled 18 published articles from 14 fertilization experiments conducted in LSRTF (Appendix S1). For each experiment, we extracted a soil description, forest type (secondary or old growth), forest age for secondary forests, fertilizer type, number of years of fertilization, plot area and number, and any special circumstances. We tallied the number of significant responses to any type of fertilizer for four types of responses, foliar nutrient concentrations, fine litter nutrient concentrations, fine litter production, and tree or biomass growth rates. We are limited to these four response types because too few studies documented any other response.

We also conducted a formal meta-analysis for the subset of experiments that compared control vs. +N and/or +P treatments (or, in one case, −N and −P treatments vs. a complete fertilizer). We extracted community-level and/or species-level treatment means, standard deviations, and sample sizes for each response. We treated analyses for different species and for different tree size categories as separate tests. We excluded community-level analyses if analyses were also partitioned by species or size. Several studies did not report standard deviations for particular responses and these responses were excluded (tree growth [Mirmanto et al. 1999], species-level growth [Gehring et al. 1999], all responses [Newbery et al. 2002], foliar nutrient concentrations [Davidson et al. 2004]). Appendix S1, Metadata S1, and Data S1 present the articles and extracted data included in the meta-analysis.

We conducted the meta-analysis with the metafor package (version 2.0-0, Viechtbauer 2010) in R version 3.3.2 (R core team 2016). We used the escalc() function to calculate Hedge's *g* and random effect models to estimate 95% confidence intervals for each response. Plant performance improved significantly with fertilization when lower 95%

confidence intervals were positive. We added moderators to random effect models to test two directional hypotheses. Fertilization responses are (1) stronger for P addition than for N addition and (2) stronger for secondary forests than for old growth forests (see *Introduction* for rationale). Just two experiments conducted in secondary forests reported litter production and litter nutrient concentrations (Appendix S1: Table S2), so we could not isolate forest type for litter responses. We evaluated the first hypothesis with secondary and old growth forests pooled for all four types of response and for each forest type separately for foliar nutrient concentrations and tree/biomass growth. We also evaluated the second hypothesis for foliar nutrient concentrations and tree/biomass growth. We report Wald chi-square and one-tailed P values for directional hypotheses. We followed the recommendations of Jennions et al. (2013) to evaluate potential publication bias.

Study site

Our experiment is located on the mainland in the Barro Colorado Nature Monument in central Panama (9°06′31″ N, 79°50′37″ W). Tree species composition and stature (canopy heights up to 43 m) are characteristic of old growth (>200 yr) forest. Aerial photographs confirm the presence of tall forest in 1927 (S. J. Wright, *personal observation*). The soils developed on Miocene basalt and transition from Oxisols (Typic Hapludox in Soil Taxonomy; Soil Survey Staff 1999) in the upper northeast corner of the 38.4-ha experimental plot to poorly drained Inceptisols (Aeric Epiaquepts) in the low-lying, southwest corner (B. L. Turner, *unpublished data*). Although our experimental forest is fertile relative to many Amazonian forests (Wright et al. 2011), it is infertile for central Panama, with very low concentrations of exchangeable phosphate (<1 mg P/kg by resin extraction) and moderately low exchangeable K (Yavitt et al. 2009, Condit et al. 2013, Mirabello et al. 2013, Turner et al. 2013, 2015).

Experimental design

We replicated the eight treatments of a 2 × 2 × 2 factorial NPK experiment four times. Within each replicate, we blocked the N, P, K, and NPK treatments vs. the NP, NK, PK, and control treatments (see Wright et al. 2011: Fig. 1). This balanced, incomplete-block design minimizes uncontrolled error associated with spatial variation, enables evaluation of main effects and two-way interactions, but limits power to evaluate the three-way interaction (Winer 1971). The 32 experimental plots are each 40 × 40 m and are separated by a minimum distance of 40 m, with the exception of two plots separated by 20 m and a 2 m deep streambed.

Beginning in 1998, we added fertilizer by hand in four equal doses each wet season with 6–8 weeks between applications (approximate dates 15–30 May, 1–15 July, 1–15 September, and 15–30 October). Nitrogen was added as coated urea ($(NH_2)_2CO$), P as triple superphosphate ($Ca(H_2PO_4)_2 \square H_2O$), and K as potassium chloride (KCl). Annual doses were 125 kg $N·ha^{-1}·yr^{-1}$, 50 kg $P·ha^{-1}·yr^{-1}$ and 50 kg $K·ha^{-1}·yr^{-1}$, which equals 69%, 470%, and 88% of annual inputs from fine litter, respectively, at a site 3 km to the north (Yavitt et al. 2004). Similar large additions of P relative to annual litter inputs are standard practice in tropical nutrient addition experiments (see studies in Appendix S1: Tables S1 and S2) because tropical soils, including the soils at our site, tend to sequester large amounts of added P in forms believed to be inaccessible to plants (Mirabello et al. 2013).

We identified trees and measured diameter at breast height (DBH defined as 1.3 m) in 1997, 1998, 1999, 2000, 2001 (DBH ≥100 mm only), 2003, 2008, and 2013, using the methods of Condit (1998). We recorded measurement height if buttresses or deformities prevented measurement at 1.3 m. We censused all trees with DBH ≥ 100 mm and, for a central 20 × 30 m subset of each plot, all trees with DBH ≥ 10 mm. We used the 1998, 2003, 2008, and 2013 censuses to calculate relative growth rates (RGR) for three 5-yr census intervals as

$$\mathrm{RGR} = (\ln(\mathrm{DBH}_f) - \ln(\mathrm{DBH}_i))/(\mathrm{DOC}_f - \mathrm{DOC}_i)/365.25,$$

where DOC refers to day of century of the corresponding DBH measurement and the subscripts f and i refer to final and initial values, respectively. We excluded palms because diameter growth is absent or limited and dicots with broken main trunks, changes in measurement height, or multiple stems at the measurement height.

Analyses of community-level growth rates

We used repeated-measures ANOVA and a linear mixed effects analysis to analyze RGR. Repeated-measures ANOVA is the appropriate analysis for our designed experiment. The response variable was the average RGR value for each plot–census-interval combination, repeated measures were on census interval, and main effects were nutrient treatments, their two-way interactions, blocks within replicates, and all interactions with census interval. RGR tends to decline with DBH (r = –0.11, n = 17,824 in our data). To minimize this source of variation, we performed repeated-measures ANOVAs for five relatively narrow size classes as follows: shrubs and saplings (10 mm ≤ $\mathrm{DBH_i}$ < 25 mm), small poles (25 mm ≤ $\mathrm{DBH_i}$ < 50 mm), large poles (50 mm ≤ $\mathrm{DBH_i}$ < 100 mm), small trees (100 mm ≤ $\mathrm{DBH_i}$ < 250 mm), and large trees ($\mathrm{DBH_i}$ ≥250 mm). We performed repeated measures ANOVAs with the aov command in R 3.3.2. We repeated each analysis in SYSTAT 11 (SYSTAT, Richmond, California, USA) to evaluate the compound symmetry assumption, which was satisfied for all five size classes (Huynh-Feldt epsilon close to 1).

The repeated-measures ANOVAs partitioned by tree size suggested a possible fertilization–tree-size interaction (see *Results: Community-level growth rates*). We used a linear mixed effects analysis to evaluate this possibility, incorporating initial size ($\mathrm{DBH_i}$) as a covariate. The response variable was the RGR value for each individual-census interval combination. Fixed effects were the N, P, and K treatments, their two-way interactions, and their interactions with $\mathrm{DBH_i}$. Random effects were census interval, individual within species, and plot within block and replicate. We included species with 20 or more individuals. We compared Akaike information criterion (AIC) values for models that included all random effects and all possible combinations of fixed effects.

Analyses of species-level growth rates

We used the P effect sizes of Condit et al. (2013) to characterize species-level P affinities for the regional species pool and the experimental forest. Condit et al. (2013) evaluated relationships between occurrence and soil fertility for 550 tree species, using 72 tree and soil surveys conducted within 50 km of our site. Strong effect sizes, with absolute values >0.5, characterized relationships between occurrence probability and soil resin P availability for 57.6% of the 550 species (Condit et al. 2013). To describe P affinity for the regional species pool, we examined the distribution of the 550 central Panama species among P effect sizes. To describe P affinity for the experimental forest, we examined the distribution of individual trees among P effect sizes.

We used a linear mixed effects analysis to evaluate relationships between species-level RGR, P addition, and P affinity. We treated the P effect sizes of Condit et al. (2013) as a covariate to represent species-level P affinity, P addition as a fixed effect, and census interval, individual within species, and plot within block and replicate as random effects. We did not consider the N and K treatments because they were insignificant in the previous analysis (see *Results: Community-level growth rates*) and N and K effect sizes were consistently small in the analysis of Condit et al. (2013). We included species with four or more individuals in each P treatment. We compared AIC values for models that included all random effects and all combinations of P addition, P affinity, and the interaction between P addition and P affinity. To avoid the compounding number of interactions associated with a second covariate, we performed this analysis for the four smaller size classes described previously (see *Methods: Analyses of community-level growth rates*). We excluded the largest size class because too few species had four or more large individuals in each P treatment.

Power analysis

We conducted two simulations of our repeated measures ANOVA to evaluate statistical power. We used simulations because, to the best of our knowledge, a standard power analysis is not available for our incomplete block design (see *Methods: Experimental design*). The first simulation used a common overall plot mean RGR value and its standard deviation (SD). The second simulation used plot mean RGR and SD values observed for each block and census interval. To simulate positive responses to P addition, we increased means observed for no-P plots by 1%, 3%, 5%, . . . and 41% for +P plots. We then drew random values from normal distributions with the appropriate means and SDs for all 32 plots and performed the repeated-measures ANOVA. We repeated these steps 1,000 times for each percentage increase in +P means and tallied the number of times the main effect of P was significant.

RESULTS

Community-level growth rates

The number of RGR values ranged from 330 to 6,633 for the five tree size classes (Appendix S2: Table S1). The main effects of N, P, and K addition and their two-way interactions were insignificant for all five size classes in the repeated-measures ANOVAs, although the main effect of K addition was marginally insignificant ($P = 0.057$) for the largest trees (Appendix S2: Table S2). RGR varied significantly among census intervals for shrubs and saplings, with lower RGR in the second census interval (2003 to 2008), but did not vary significantly among census intervals for the four larger size classes (Appendix S2: Table S2). The repeated-measures ANOVAs provide little to no statistical evidence that fertilizers affected RGR.

The relative growth rates of shrubs, saplings, and small poles (<50 mm DBH) tended to be larger in the control treatment than in any of the nutrient addition treatments (Fig. 1). This insignificant tendency was absent for large poles and tended to be reversed for small and large trees (Fig. 1). This suggested a possible interaction between nutrient treatments and tree size. To evaluate this possibility, we performed a linear mixed-effects analysis of RGR that included trees of all sizes and treated initial size (DBH_i) as a covariate. This analysis included species represented by 20 or more individuals, 13,688 RGR measurements and 5,510 individual trees. The number of RGR values ranged from 73 to 208 (mean = 143) among plot-census interval combinations. The model that included DBH_i as a covariate minimized AIC, with $\Delta AIC = 12$ for the next best model and $\Delta AIC = 183$ for the null model that included just random effects (Appendix S2: Table S3). The linear mixed effects analysis provides no statistical evidence that fertilizers affected RGR.

Species-level growth rates

The 550 species for which Condit et al. (2013) determined P effect sizes include 93.1% of the species and 98.3% of the individuals in our experimental forest. Species with strong positive P effect sizes (>0.5) are associated with P-rich soils (high-P affinity) and comprised 20% of the species in the regional species pool (Fig. 2A), but just 6% of the individuals in the experimental forest (Fig. 2B). Species associated with P-rich soils are underrepresented in the experimental forest relative to the regional species pool.

The number of RGR values ranged from 747 to 5,851 for the four tree size classes for the linear mixed effects analysis that included P affinity (Appendix S2: Table S4). The main effects of P addition, P affinity and their interaction were insignificant for all size classes (Fig. 2C, Appendix S2: Table S5). As in the repeated-measures ANOVAs, RGR varied significantly among census intervals for shrubs and saplings, with lower RGR in the second census interval (2003 to 2008), but not for the three larger size classes (Appendix S2: Table S5).

Power analysis

Our repeated-measures ANOVA had a 46% chance of detecting a 20% increase in RGR (Appendix S2: Fig. S1). Relaxing control of spatial and temporal variation associated with blocks and census intervals had little effect on power (Appendix S2: Fig. S1). This is consistent with the uniformly insignificant effects of blocks and replicates in the repeated-measures ANOVAs (Appendix S2: Table S2).

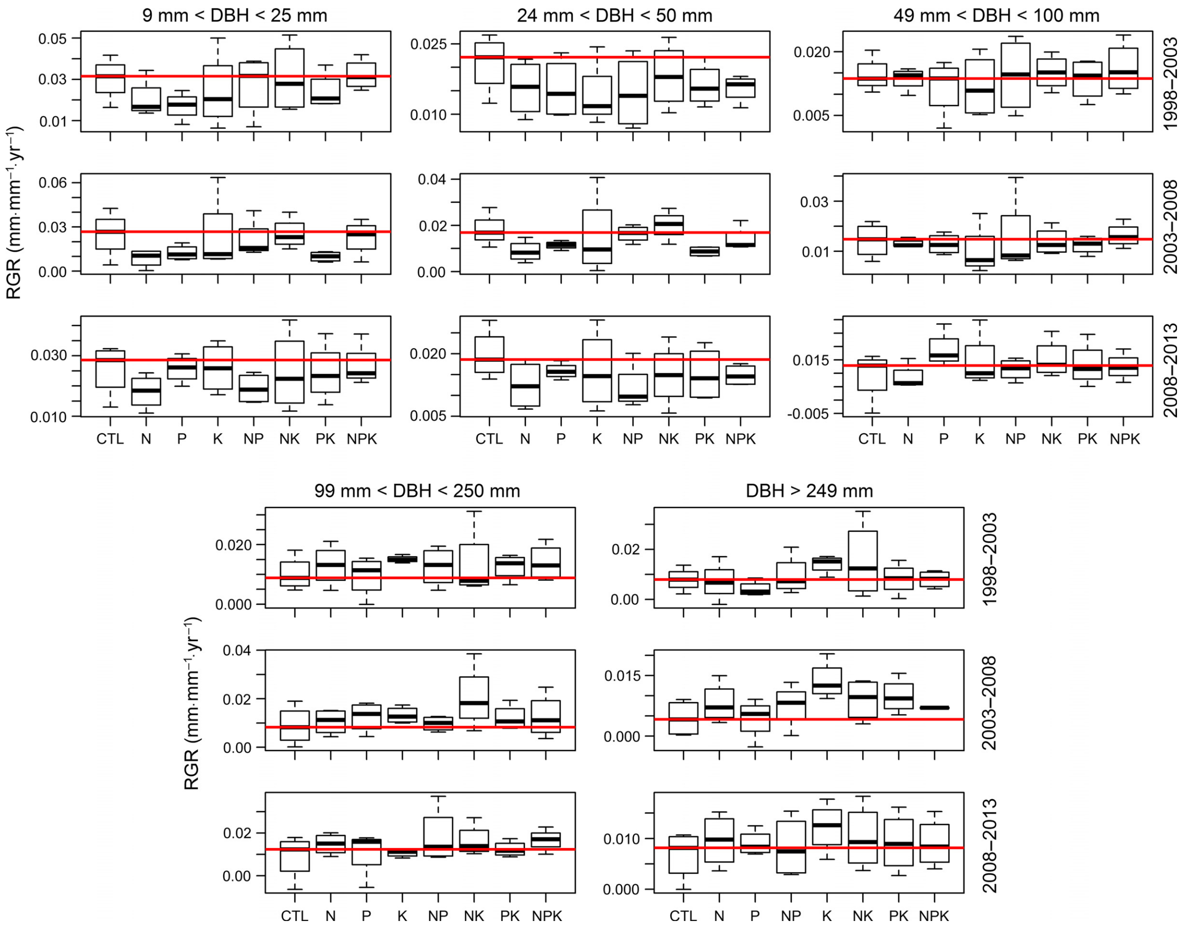

FIG. 1. Bar-and-whisker plots of mean relative growth rates (RGR) for five size classes and three census intervals. The solid red lines represent median RGR for the control treatment for each size class and census interval. The three census intervals are 1998–2003, 2003–2008, and 2008–2013. The five size classes are shrubs and saplings (10 mm ≤ DBH_i < 25 mm), small poles (25 mm ≤ DBH_i < 50 mm), large poles (50 mm ≤ DBH_i < 100 mm), small trees (100 mm ≤ DBH_i < 250 mm), and large trees (DBH_i ≥ 250 mm; where DBH_i is initial DBH). In the first four size classes, treatment order is control (CTL), one nutrient (+N, +P and +K), two nutrients (+NP, +NK and +PK), and three nutrients (+NPK). In the final size class, treatment order groups −K (control, +N, +P, and +NP) vs. +K (+K, +NK, +PK, and +NPK) treatments to illustrate the marginally significant effect of K addition (P = 0.057). Thick horizontal lines represent medians, boxes represent the interquartile range (25% to 75%) and whiskers represent extreme values.

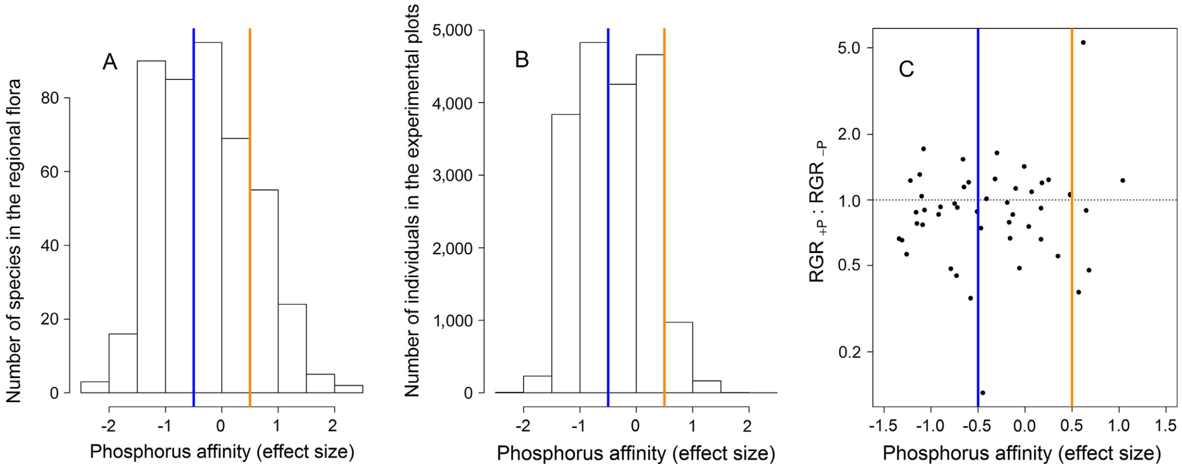

FIG. 2. Histograms of the distributions of (A) species in the regional species pool and (B) individuals in the 38.4-ha experimental plot with respect to species-level phosphorus affinity and (C) the relationship between species-level phosphorus affinity and the ratio of mean relative growth rates (RGR) of conspecifics with vs. without added phosphorus (RGR_{+P}: RGR_{-P}) for shrubs and saplings (10 mm ≤ DBH < 25 mm). In panel C, each symbol represents a species with four or more individuals in each phosphorus treatment, and the horizontal dashed line represents equal RGR values in both phosphorus treatments. The orange and blue vertical lines represent strong positive and negative phosphorus affinity thresholds, respectively.

Meta-analysis

Seven and nine of the 14 fertilization experiments enable isolation of N and/or P responses, respectively (Appendix S1: Tables S1 and S2). Sample sizes can be larger when single studies reported responses for multiple species or tree size classes. Sample sizes can also be smaller when only a subset of studies documented a particular response. There was no evidence for publication bias after accounting for heterogeneity between secondary and old growth forests (Appendix S1: Table S3).

All mean effect sizes were positive, indicating plants tend to be limited by N and by P in LSRTF (Fig. 3). Ten of the 16 mean effect sizes were individually significant ($P < 0.05$). Four of the six insignificant effect sizes concerned tree/biomass growth rates in old growth forests (Fig. 3F) and litter element concentrations (Fig. 3B).

We evaluated the interaction between forest type (secondary vs. old growth) and fertilizer type (+N vs. +P) and the directional hypothesis that responses are stronger in secondary forests and weaker in old growth forests for foliar nutrient concentrations and tree/biomass growth rates. Forest × fertilizer interactions were insignificant for foliar nutrient concentrations (Fig. 3E; $QM_1 = 0.287$, $P = 0.296$, where QM_1 is the Wald-type omnibus test of the null hypothesis that all model coefficients equal zero) and for tree/biomass growth rates (Fig. 3F; $QM_1 = 0.255$, $P = 0.307$). For foliar nutrient concentrations, the null hypothesis that fertilization responses were similar in secondary and old growth forests was accepted (Fig. 3E; $QM_1 = 1.64$, $P = 0.100$ for pooled responses; $QM_1 = 1.44$, $P = 0.116$ for N responses to +N; $QM_1 = 0.327$, $P = 0.284$ for P responses to +P). For tree/biomass growth rates, the null hypothesis that fertilization responses were similar in secondary and old growth forests was rejected (Fig. 3F; $QM_1 = 8.41$, $P = 0.0019$ for responses to pooled fertilizers; $QM_1 = 5.59$, $P = 0.0091$ for responses to +N; $QM_1 = 2.97$, $P = 0.0423$ for responses to +P). Tree/biomass growth responses were significantly stronger in secondary forests and weaker in old growth forests (Fig. 3F).

We evaluated the directional hypothesis that responses are stronger for P addition and weaker for N addition for all four responses with secondary and old growth forests pooled and for foliar nutrient concentrations and tree/biomass growth rates for each forest type. The null hypothesis that responses are similar for +P and +N could never be rejected. Figs. 3A–D present tests with secondary and old growth forests pooled (Fig. 3A, $QM_1 = 2.66$, $P = 0.051$ for foliar nutrient concentrations; Fig. 3B, $QM_1 = 0.153$, $P = 0.348$ for fine litter nutrient concentrations; Fig. 3C, $QM_1 = 0.111$, $P = 0.370$ for fine litter production; Fig. 3D, $QM_1 = 0.430$, $P = 0.256$ for tree/biomass growth rates). Fig. 3E presents foliar nutrient concentrations for each forest type ($QM_1 = 0.0957$, $P = 0.378$ for secondary and $QM_1 = 2.35$, $P = 0.063$ for old growth forests). Fig. 3F presents tree/biomass growth rates for each forest type ($QM_1 = 0.0253$, $P = 0.437$ for secondary and $QM_1 = 0.758$, $P = 0.192$ for old growth forests). The meta-analysis provides no evidence that plant responses differ for +P vs. +N treatments.

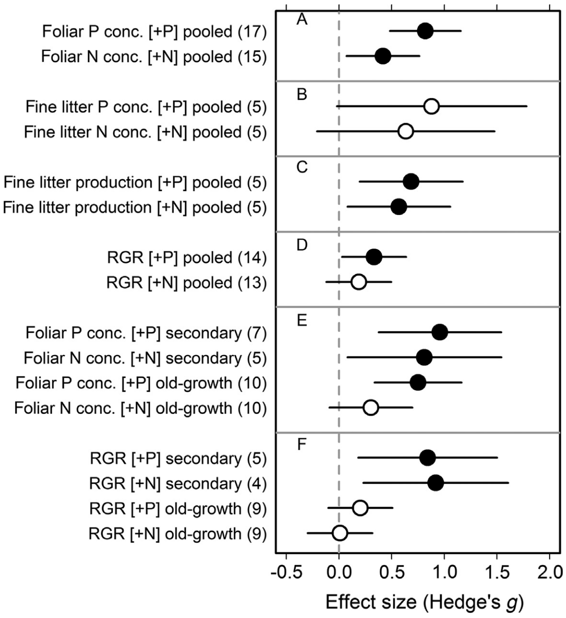

FIG. 3. Meta-analysis of nitrogen (N) and phosphorus (P) responses for fertilization experiments conducted in lowland, species-rich, tropical forests (see Data S1). Points are mean effect sizes, with 95% confidence intervals. Solid and open points identify significant (lower 95% CI > 0) and nonsignificant effect sizes, respectively. The y-axis label identifies the type of response (foliar or fine litter nutrient concentrations, fine litter production, or tree/biomass growth [RGR]), the added nutrient in square brackets (+N or +P), the type of forest (secondary, old growth, or pooled), and sample size in parentheses. The first three gray horizontal lines separate four tests of the directional hypothesis that responses are stronger for P addition and weaker for N addition, with secondary and old-growth forests pooled (sections A, B, C, and D). The final gray horizontal line separates tests for interactions between fertilizer type (+N or +P) and forest type (secondary or old growth) and for the directional hypothesis that responses are stronger for secondary forests and weaker for old growth forests for foliar nutrient concentrations (E) and tree/biomass growth rates (F).

DISCUSSION

When just two census intervals were available, our experiment included a significant interaction among census interval and the +N and +K treatments (henceforth, N*K*interval interactions) for growth for the three smaller tree size classes (Wright et al. 2011). Growth rates were larger in the first census interval, and +NK ameliorated the decline to the second census interval (see Fig. 1 in Wright et al. 2011). Now, with three census intervals available, all N*K*interval interactions are insignificant and the second census interval has significantly slower growth rates for the smallest size class only (Appendix S2: Table S2). Our new analysis includes 50% more RGR values and years of fertilization and must replace the earlier analysis. After 15 yr of chronic nutrient additions, our experiment provides virtually no evidence that nutrients limit tree growth (Fig. 1, Appendix S2: Tables S2 and S3).

Our treatments have significantly increased soil nutrient availability and many measures of plant performance. Phosphorus addition increased soil phosphate availability by 2800%; +K increased K availability by 91%; and +N increased nitrate availability by 120% (Yavitt et al. 2011, Mirabello et al. 2013, Turner et al. 2013). Species- and community-level plant responses, ranging from increases in metabolism (photosynthesis, stomatal conductance) to increases in production (fine litter), standing biomass, and tissue turnover rates (fine roots) were reviewed earlier (see *Introduction*). We now consider why these increases in soil nutrient availability and plant performance do not lead to increased tree growth. We begin with a meta-analysis of 14 fertilization experiments conducted in lowland, species-rich, tropical forests (LSRTF).

Experimental evidence for nutrient limitation

All 14 fertilization experiments address the hypothesis that some combination of nutrients limit plants in LSRTF, and a tally of statistically significant effects indicates that nutrient limitation is widespread (Appendix S1: Tables S1 and S2). Foliar and fine litter concentrations of at least one nutrient increased significantly in seven of eight and five of five experiments, respectively. Fine litter production increased significantly in five of seven experiments. Tree/biomass growth responses varied with forest environment. Tree/biomass growth rates increased significantly in seven of eight experiments conducted in secondary forests or with saplings in high light microsites in old growth forests. In contrast, six experiments conducted in old growth forests documented tree growth responses without finding significant responses for trees larger than 100-mm DBH and with a significant increase for smaller trees in just one study. The contrast between forest environments is significant (Fisher exact test, $P = 0.0256$ for trees < 100 mm DBH and $P = 0.00466$ for trees > 100 mm DBH). To summarize, fertilization is often associated with significant increases in tissue nutrient concentrations and fine litter production and, in secondary forests and tree-fall gaps, with significant increases in tree/biomass growth rates. There is, however, no experimental evidence for nutrient limitation of growth rates for trees larger than 100 mm DBH in old growth LSRTF.

Our formal meta-analysis of the subset of these experiments with +N or +P treatments produced broadly similar results. All 16 mean effect sizes were positive and 10 were strong (mean Hedge's $g > 0.5$), indicating widespread limitation by N and by P (Fig. 3). The directional hypothesis that N and P limitation of tree/biomass growth rates is stronger in secondary forests and weaker in old growth forests was also supported (Fig. 3F), and once again there was no evidence for N or P limitation of tree growth rates in old growth forests (open circles in Fig. 3F).

Our meta-analysis produced two related surprises. Nitrogen limits foliar N concentrations and fine litter production in LSRTF (Fig. 3A, C), and there is no evidence that P limitation is stronger than N limitation in LSRTF (all tests in Fig. 3). This is consistent with a meta-analysis of terrestrial N addition experiments in which "The degree of N limitation in the remainder of the tropical forest studies [when Hawaiian forests on recent lava flows were excluded]... was comparable to that of temperate forests..." (LeBauer and Treseder 2008). This conclusion of LeBauer and Treseder (2008) and our own meta-analysis are inconsistent with a second meta-analysis in which "... most fertilization experiments in forests were conducted in tropical latitudes, and this habitat type had a stronger response to added P than added N, suggesting support for the long-held belief that tropical ecosystems on old soils are predominantly P limited (Walker and Syers 1976)." (Elser et al. 2007). To reconcile these contrasting conclusions concerning N limitation, we examined the tropical forest studies in both earlier meta-analyses.

Both meta-analyses include experiments conducted in a wide range of tropical forest environments. Elser et al. (2007) include mangrove forests (three studies), montane forests (8), a monospecific *Eucalyptus* stand (1), and seedlings planted into pots (2), abandoned land (2), and forest understory (1). Several of these studies are of questionable relevance to their conclusion concerning P limitation on old soils because the experimental soils are artificial (pot experiments) or relatively young (many montane forests; Porder et al. 2007). These 17 studies are also irrelevant to our interest in LSRTF. LeBauer and Treseder (2008) also include seven studies conducted in montane forests. Just six and three experiments conducted in LSRTF remain in the compilations of Elser et al. (2007) and LeBauer and Treseder (2008), respectively. Our meta-analysis included these experiments plus eight additional experiments conducted in LSRTF, and we believe the conclusions of our meta-analysis stand for LSRTF.

To summarize those conclusions, both N and P addition are associated with strong increases in foliar nutrient concentrations (Fig. 3A, E), fine litter production (Fig. 3C) and fine litter nutrient concentrations (Fig. 3B) in LSRTF. The increases in fine litter nutrient concentrations are highly variable, however, suggesting variation in concentrations and/or resorption among tissues and studies (Fig. 3B, Schreeg et al. 2014, Alvarez-Clare and Mack 2015). Both N and P addition are also associated with strong increases in tree/biomass growth in secondary forests, where rapid biomass accumulation ensures a nutrient sink (solid circles in Fig. 3F). There is, however, no evidence for the long-standing hypothesis that P limitation is stronger and N limitation is weaker in lowland tropical forests (Fig. 3A–F) nor for nutrient limitation of tree growth rates in old growth forests (open circles in Fig. 3F).

Why is tree growth unresponsive to fertilization in old growth forests?

At least four mutually compatible mechanisms might contribute to the absence of tree growth responses to fertilization in old growth LSRTF (open circles in Fig. 3F). The first concerns local species composition and potential growth responses. Species adapted to low resource levels tend to have limited potential to increase growth rates in response to increased resource levels (Coley et al. 1985). This could limit fertilization responses until species adapted to high nutrient soils arrive changing species composition (Chapin et al. 1986). At our experimental forest, species whose regional distributions are strongly associated with P-poor and P-rich soils comprise 47% and just 6% of the individual trees, respectively (Fig. 2B). We should expect modest and slow responses to P addition when species associated with P-poor soils dominate local species composition (Chapin et al. 1986, Kitayama 2005, Dalling et al. 2016).

A second possible mechanism for muted growth responses to fertilization concerns plant enemies. Fertilization often increases tissue nutrient concentrations (Fig. 3A, B, E), making fertilized plants more attractive to herbivores and possibly other pests. Two fertilization experiments conducted in LSRTF considered herbivory. Herbivory increased with +P in 10-yr old forests in Mexico (Campo and Dirzo 2003) and with +K and +P in our experiment (Santiago et al. 2012). Potassium addition also reduced net adverse effects of foliar bacteria in our experiment (Griffin et al. 2016). Spatial scale becomes important if fertilized plants attract pests. Fertilizers applied to individual plants or small plots might create nutrient hotspots that recruit nearby pests. Most fertilization experiments are conducted at spatial scales of 10–50 m in LSRTF with measurements limited to a central core area (see plot sizes in Appendix S1: Tables S1 and S2). This might limit problems posed by immigration; however, enemy populations might still increase in large fertilized plots if their local demography changes. As an example, forest floor arthropod abundance increased with +K and +P in the central area of our 1,600-m^2 experimental plots (Kaspari et al. 2017, also see Bujan et al. 2016). If fertilization increases pest pressure, those pests might consume increased primary production, limiting potential tree growth responses (Andersen et al. 2010).

As an aside, pest pressure might also contribute to a striking difference between growth responses to +P in our experiment vs. a growing house experiment conducted with a subset of our species. In the growing house experiment, species-specific growth responses to +P increase steadily with the strength of species-level associations with P-rich soils (Zalamea et al. 2016). In our forest experiment, sapling growth responses were unrelated to these same species-level associations with P-rich soils (Fig. 2C). Species adapted to high resource levels tend to be poorly defended against herbivores and other pests (Coley et al. 1985). Pests that are absent from the growing house experiment might prevent species associated with P-rich soils from achieving their potential growth responses in the forest experiment. Of course, with so few individuals of species associated with P-rich soils present (Fig. 2B), our statistical power to evaluate their responses is also limited (Fig. 2C).

A third possible mechanism for muted growth responses to fertilization concerns time. Thirteen of the 14 fertilization experiments added nutrients for five or fewer years (Appendix S1: Tables S1 and S2) while tropical trees can live for centuries (Chambers et al. 1998, Worbes and Junk 1999). There is evidence for size-dependent responses to fertilization. Three studies fertilized in situ seedlings and seedling growth rates increased in all three studies (Hattenschwiler 2002, Yavitt and Wright 2008, Santiago et al. 2012). Four studies (in addition to ours) fertilized saplings only (Villagra et al. 2013, Chou et al. 2018) or partitioned growth analyses by tree size (Fisher et al. 2013, Alvarez-Clare et al. 2013), and growth rates of saplings or the smallest tree size class increased in three of the five studies (Alvarez-Clare et al. 2013, Villagra et al. 2013, Chou et al. 2018). In contrast, N and P fertilization had no effect on the growth rates of trees larger than 100 mm DBH in the six fertilization experiments that evaluated larger trees in old growth LSRTF (Appendix S1: Table S1). Large trees can accumulate large reserves of nutrients and carbohydrates, and many years might be required to capture their growth responses to nutrient addition.

The final reason for insignificant growth responses concerns statistical power. Our experiment has a reasonable chance of detecting a 20% increase in RGR (Appendix S2: Fig. S1). Sample sizes (see numbers of plots in Appendix S1: Tables S1 and S2) suggest power is likely to be similar or lower for 12 of the 13 remaining experiments conducted in LSRTF unless plot-to-plot variation is unexpectedly low. To summarize, the potential fertilization response of tropical forest trees will be limited if the species present are well adapted to nutrient-poor soils, as in our experiment (Fig. 2B), and if pest pressure increases with fertilization, as in our experiment (Santiago et al. 2012). The statistical power and especially the duration of fertilization experiments conducted in old growth, tropical forests might also be insufficient to detect the slow, modest growth responses that are to be expected.

Conclusions

Our review of 14 fertilization experiments conducted in LSRTF indicates that nutrient limitation is widespread (Appendix S1: Tables S1 and S2). Nutrient availability is already likely to be limiting the ability of these forests to sequester carbon despite rising atmospheric CO_2 concentrations (Wieder et al. 2015). Our formal meta-analysis of the subset of these experiments that include +N and/or +P treatments supports the hypothesis that nutrient limitation is stronger in secondary forest and weaker in old growth forest, but does not support the hypothesis that P limitation is stronger and N limitation is weaker. As an aside, evidence for P limitation is also suspect because every experiment that included a +P treatment used simple or triple super phosphate fertilizer. Super phosphate fertilizers supply calcium (Ca) and P at a 1:2 ratio of Ca to P. Bedrock is the primary source for Ca as well as P and Ca, like P, might limit tropical forests growing on highly weathered soils (Vitousek 1984, Vitousek and Sanford 1986, Baillie et al. 1987, Cuevas and Medina 1988). Nonetheless, we believe it would be premature to discard the hypothesis that P limitation is stronger than N limitation in lowland tropical forests for two reasons.

First, the number of fertilization experiments conducted in LSRTF remains small (Appendix S1: Tables S1 and S2) and most of the experiments share modest sample sizes and short durations (see *Discussion: Why is tree growth unresponsive to fertilization in old growth forests?*). Effect sizes tend to be larger for plant responses to P addition than to N addition; however, the difference is small and insignificant (Fig. 3). In contrast, a recent meta-analysis of microbial responses to fertilization experiments conducted in tropical forests found strong evidence for P limitation over all tropical forests and evidence for N limitation in montane but not lowland tropical forests (Camenzind et al., 2018). The contrasting generation times and fertilization responses of microbes and plants suggest that the responses of long-lived plants might strengthen as the duration of fertilization experiments increases.

The second reason we believe it would be premature to discard the hypothesis that plant limitation by P is stronger than limitation by N in lowland tropical forests concerns evidence from our own experiment after 15 yr of chronic nutrient additions. Soil Ca availability is extraordinarily high in our control plots (averaging 1,690 mg/kg; Yavitt et al. 2009), and the Ca added with the triple super phosphate fertilizer is not an issue. In contrast to the results of our meta-analysis, our own experiment provides much more evidence for P (and K) limitation than for N limitation. The evidence includes a wide range of bacterial, fungal, arthropod, and plant responses (summarized in Table S2 in Kaspari et al. 2017; additional responses in Schreeg et al. 2014, Pasquini et al. 2015, Wurzburger and Wright 2015, Griffin et al. 2016, 2017, Bujan et al. 2016, Sheldrake et al. 2017). Statistically significant plant responses are roughly equally divided between the +P and +K treatments, with just one significant response to the +N treatment (an increase in tissue N concentrations). We conclude that N rarely limits plant function at our site, and N addition is unlikely to affect tree growth in the future. We predict that the many significant plant responses to +P and +K will, with time, lead to significant increases in tree growth and net primary production. After 15 yr, a marginally insignificant trend ($P = 0.057$) suggests that growth responses might be developing first in response to K addition among trees larger than 249 mm DBH (Fig. 1, Appendix S2: Table S2). Lloyd et al. (2015) recently hypothesized that K availability plays a key role determining tropical forest structure. We are now in the 20th year of our chronic nutrient addition treatments, and we plan to continue indefinitely to test these and other predictions.

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Supporting Information

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