Ecology, 102(10), 2021, e03469
© 2021 by the Ecological Society of America

Nutrient limitation of plant reproduction in a tropical moist forest

Riley Fortier[1,2,3] and S. Joseph Wright[1]

[1]*Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Panama*
[2]*Department of Biology, University of Miami, Coral Gables, Florida 33146 USA*

Citation: Fortier, R., and S. J. Wright. 2021. Nutrient limitation of plant reproduction in a tropical moist forest. Ecology 102(10):e03469. 10.1002/ecy.3469

Abstract. Nutrient addition experiments indicate that nitrogen and phosphorus limit plant processes in many tropical forests. However, the long-term consequences for forest structure and species composition remain unexplored. We are positioned to evaluate potential long-term consequences of nutrient addition in central Panama where we have maintained a factorial nitrogen–phosphorus–potassium fertilization experiment for 21 yr and an independent study quantified the species-specific nutrient requirements of 550 local tree species. Here, we ask whether nutrients limit reproduction at the species and community levels. We also ask whether species-specific reproductive responses to nutrient addition are stronger among species associated with naturally fertile soils, which could contribute to a shift in species composition. We quantified species-level reproductive responses for 38 focal species in the 21st year of the experiment and community-level reproductive litter production for the first 20 yr. Species-level reproductive responses to nitrogen and potassium addition were weak, inconsistent across species, and insignificant across the 38 focal species. In contrast, species-level responses to phosphorus addition were consistently and significantly positive across the 38 focal species but were unrelated to species-specific phosphorus requirements documented independently for the same species. Community-level reproductive litter production was unaffected by nutrient addition, possibly because spatial and temporal variation is large. We conclude that phosphorus limits reproduction by trees in our experiment but find no evidence that reproductive responses to phosphorus addition favor species associated with naturally phosphorus-rich soils.

Key words: fertilization; nitrogen; nutrient augmentation; nutrient limitation; phosphorus; plant reproduction; potassium; reproductive litter production; tropical forests.

Introduction

Plant reproduction is fundamental to most agriculture and to the fitness of natural plant populations. Nutrients often limit reproductive yield in crop plants, giving rise to the fertilizer industry. Nutrients can also limit reproduction in natural plant populations; however, unlike crops, natural plant populations are adapted to local environmental conditions. Species adapted to low nutrient supplies can maintain high levels of productivity despite infertile soils (Turner et al. 2018), and often have limited responses to improved soil fertility (Chapin et al. 1986, Zalamea et al. 2016). The potential for nutrients to limit reproduction in natural plant populations adapted to infertile soils is therefore uncertain and is largely unexplored (DiManno and Ostertag 2016).

Most lowland tropical forests grow on highly weathered Oxisols and Ultisols. Low soil pH, low soil cation and phosphorus (P) availability, high levels of biological fixation of atmospheric dinitrogen, and high soil nitrogen (N) availability characterize these soils (Sanchez 1976, Vitousek and Sanford 1986). Vitousek and Sanford (1986) hypothesized that plants are likely to be limited by P or a cation but not by N in these forests. Multiple resource limitation characterizes many plant populations, with individual plants adjusting their physiology and morphology to acquire the shifting mixture of resources demanded by growth, maintenance, and reproduction (Bloom et al. 1985, Field et al. 1992, Farrior et al. 2013). Given multiple resource limitation, it is perhaps unsurprising that N and P both limit plant function in meta-analyses of nutrient addition experiments conducted in tropical forests (LeBauer and Treseder 2008, Ostertag and DiManno 2016, Wright 2019). The possibility remains that N, P, and/or cations are proximate limiting resources, and P and possibly cations are also ultimate limiting resources.

Vitousek et al. (2010) “. . . define a proximate limiting nutrient as one for which additions stimulate biological processes or pools directly, while an ultimate limiting nutrient is one capable of transforming ecosystems, typically by driving a substantial and persistent change in ecosystem structure and/or species composition as well as increasing the rates of biological processes.” Comparative studies across soil fertility gradients suggest proximate limitation of reproduction by soil nutrients in tropical forests. For example, seed production increases

Manuscript received 9 November 2020; revised 11 April 2021; accepted 14 May 2021; final version received 8 July 2021. Corresponding Editor: Richard T. Corlett.

[3] E-mail: fortier.riley@gmail.com

with stand-level soil fertility in a dominant tree in a Costa Rican forest (Tully et al. 2013) and the proportional contribution of reproductive litter to total fine litter production increases with soil fertility across the Neotropics (Chave et al. 2010). Comparative studies across soil fertility gradients also suggest ultimate limitation of ecosystem properties including aboveground biomass and productivity by soil fertility in tropical forests (reviewed by Muller-Landau et al. 2020). Nutrient addition experiments readily identify proximate limitation of plant processes and could help to identify ultimate limitation of species composition if interspecific variation in demographic responses to nutrient addition differed systematically among species. Altered growth, survival and/or reproductive rates could herald a shift in species composition, with species adapted to fertile soils predicted to respond more strongly to nutrient addition than species adapted to infertile soils (Chapin et al. 1986, Zalamea et al. 2016).

To evaluate this last possibility, species-specific resource requirements must be known. Condit et al. (2013) evaluated relationships between occurrence and soil N, P, and cation availability for 550 tree species across 72 sites spanning strong soil fertility gradients within 40 km of our study site. Condit et al. (2013) quantified species-specific responses to each nutrient as effect sizes defined as the first-order parameter of a Gaussian logistic regression model relating occurrence probability to standardized nutrient availability. Strong negative and positive effect sizes identify species strongly associated with low and high soil nutrient availabilities, respectively. A positive correlation between these effect sizes for a particular nutrient and the strength of species-specific reproductive responses to addition of that nutrient could identify a developing shift in species composition and a possible ultimate limiting nutrient.

We have maintained a factorial N–P–potassium (K) addition experiment for 21 yr in a mature lowland tropical forest growing on a nutrient poor Oxisol in central Panama. Each added nutrient increased plant tissue concentrations of that nutrient; K addition decreased fine root biomass and increased fine root turnover and seedling growth rates; P addition increased fine litter production, photosynthesis, and stomatal conductance; and combined N and P addition increased seedling 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). These responses demonstrate proximate limitation of different plant functions by N, P, and K.

This study evaluates reproductive responses. We examine levels of reproduction realized by individual trees of 38 species during the 21st year of nutrient addition and the reproductive component of fine litter production over the first 20 yr. An increase in reproductive activity in response to P addition provides evidence of proximate limitation by P. We also evaluate the interaction between species-specific reproductive responses to P addition and the P effect size from Condit et al. (2013). A significant positive interaction would be consistent with a developing shift in species composition and could provide the first stand-level experimental evidence consistent with ultimate nutrient limitation of species composition in a tropical forest.

METHODS

Study site

The study site is on the Gigante Peninsula within the Barro Colorado Nature Monument in central Panama (9°06′31″ N, 79°50′37″ W). Temperature averages 26°C, and annual precipitation averages 2,600 mm. Tree species and structural composition are characteristic of seasonal, old-growth forest, with canopy heights up to 43 m. The youngest soil charcoal ^{14}C dates indicate the most recent fire occurred 650 YBP (Crystal H. McMichael, *unpublished data*). The soils are Oxisols (Typic Hapludox in Soil Taxonomy; Soil Survey Staff 1999) over most of the 38.4-ha experimental plot and transition to Inceptisols (Aeric Epiaquepts) in the poorly drained, low-lying, southwest corner (Benjamin L. Turner, *unpublished data*).

Experimental design

We replicated the eight treatments of a 2 × 2 × 2 factorial NPK experiment four times, with replicates placed along a 36-m topographic gradient. Soil properties (Yavitt et al. 2009) and tree distributions (S. Joseph Wright, *unpublished data*) parallel the topographic gradient. Within each replicate, we blocked the N, P, K, and NPK treatments vs. the NP, NK, PK, and control treatments (see Appendix S1: Fig. S1). 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). For this reason, we do not evaluate the three-way interaction. The 32 experimental plots are each 40 × 40 m and are separated by a minimum distance of 40 m, except two plots separated by 20 m and a 2 m deep streambed.

Nutrient treatments

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). We added N as coated urea ($(NH_2)_2CO$), P as triple superphosphate ($Ca(H_2PO_4)_2 \cdot H_2O$), and K as potassium chloride (KCl). Annual doses were 125 kg $N \cdot ha^{-1} \cdot yr^{-1}$, 50 kg $P \cdot ha^{-1} \cdot yr^{-1}$, and 50 kg $K \cdot ha^{-1} \cdot yr^{-1}$, 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 doses of P are standard practice in tropical nutrient addition experiments (see Data S1 in Wright 2019) because many tropical soils, including the soils at our site, sequester large amounts of added P in forms believed to be inaccessible to plants (Mirabello et al. 2013).

Reproductive measurements

We identified, mapped, and measured diameter at breast height (DBH) for trees with DBH ≥ 10 cm throughout each plot and trees with DBH ≥ 1 cm for a central 20 × 30 m subset of each plot in 2018 using the methods of Condit (1998). We assessed the reproductive status of mapped trees during 13 censuses at approximately 3-week intervals between January and September 2019. Most plant species reproduce between December and August in central Panama (Croat 1978, Zimmerman et al. 2007), so our censuses covered flowering and/or fruiting in most species. During each census, we focused on species known to reproduce at that time of year from our own observations and published records (Croat 1978, Zimmerman et al. 2007). Reproductive scores were zero for sterile trees and 1, 2, 3, or 4 for trees with 1–25%, 26–50%, 51–75%, or 76–100% of the canopy bearing flowers or fruit, respectively (follows Wright et al. 2005*a*).

Tree condition

We sought to explain as much of the background variation in reproductive scores as possible to evaluate nutrient addition effects better. Tree size (quantified by DBH), liana infestation, sun exposure, and crown damage are known to explain variation in levels of reproduction (Graham et al. 2003, Wright et al. 2005*a*, León et al. 2018) and are covariates in our analyses. We scored every tree for liana infestation, sun exposure, and canopy damage. Liana scores were 0 for trees without lianas and 1, 2, 3, or 4 for trees with 1–25%, 26–50%, 51–75%, or 76–100% of their canopy covered by lianas, respectively (follows Clark and Clark [1990]). Sun exposure scores were integers from 1 to 5, with 1 for understory plants lacking direct sunlight except during sun flecks and 5 for canopy emergents (follows Dawkins and Field [1978]). Crown damage scores were 0 for intact crowns and 1 or 2 for damaged crowns retaining more or less than 50% of their major limbs, respectively. We dichotomized liana, sun exposure, and crown damage scores for analyses. The dichotomized scores were 0 for liana scores ≤1, sun exposure scores ≤3, and crown damage scores ≤1 and 1 otherwise (follows Wright et al. [2005*a*]).

Reproductive litter production

We quantified fine litter production with litter traps censused on the final Thursday of each month from July 1998 through October 2018. Each trap had a surface area of 0.57 m^2 and consisted of a 1-mm mesh bag suspended 80 cm above the ground on a PVC frame. We placed traps randomly but with 10-m minimum spacing in the inner 30 by 30 m of each plot. There were three traps per plot from June 1998 through January 2007 and five traps per plot thereafter. We oven dried trap contents to constant mass at 60°C. We separated leaves, reproductive material, branches (<2 cm diameter) and "dust" starting in November 1998. Thus, annual production was for years beginning on the final Thursday in October. This choice captures interannual variation because reproductive litter production is minimal in late October/early November (Wright et al. 1999). We stopped in October 2018 because a windstorm on 23 August 2018 damaged many trees causing large among-plot variation later in 2018 and in 2019.

Data analysis—Focal trees

We analyzed reproductive scores with mixed effects ordinal logistic regressions and cumulative link functions. The response variable was the ordinal reproductive score (R). We first identified and retained covariates (DBH and indices for CROWN damage, SUN exposure and LIANA infestation) with significant effects on R. We then added the fixed nutrient addition treatments and their two-way interactions as well as random effects.

We evaluated species-specific responses to nutrient addition for seven species that averaged five or more individuals per plot (160 total individuals). To account for spatial variation, a random effect nested plot within block and replicate. The model equation including all covariates follows:

$$\begin{aligned} \mathrm{R} = {} & \mathrm{DBH} + \mathrm{CROWN} + \mathrm{SUN} + \mathrm{LIANA} + \mathrm{N{*}P} + \mathrm{N{*}K} \\ & + \mathrm{P{*}K} + (1|\mathrm{REP/BLOCK/PLOT}). \end{aligned}$$

We then evaluated community-wide responses for the 38 species with five or more sterile and five or more reproductive trees (following sample size recommendations of Bolker et al. [2009]). The model equation was as above but with a second random intercept to account for interspecific variation. We calculated odds ratios for each nutrient treatment and their two-way interactions.

We performed a second community-wide analysis to evaluate the relationship between species-specific responses to P addition and species-specific associations with soil P availability (P_{affinity}). We used P effect sizes from Condit et al. (2013) to quantify P_{affinity} (see Introduction for further explanation). This analysis retained random effects and significant covariates and nutrient treatments from the first community-wide analysis and added the covariate P_{affinity}, the interaction between P_{affinity} and the main effect of P addition, and a random slope for species. The P * P_{affinity} interaction addresses the prediction that reproductive responses to P addition change with species-specific P requirements. The random slope for species estimates species-specific responses to P addition. The model equation follows:

$$R = \mathrm{DBH} + \mathrm{CROWN} + \mathrm{SUN} + \mathrm{LIANA} + P_{\mathrm{affinity}} + P + P^{*}P_{\mathrm{affinity}} + (1 + P|\mathrm{SP}) + (1|\mathrm{REP/BLOCK/PLOT}).$$

We calculated species-specific odds ratios to visualize the relationship between P_{affinity} and reproductive responses to P addition.

Data analysis—Reproductive litter production

We evaluated community-level reproductive litter production ($\mathrm{Mg \cdot ha^{-1} \cdot yr^{-1}}$), using repeated-measures ANOVA. Allocation to reproduction expressed as a proportion of total fine litter production increases with soil fertility in natural tropical forests (Chave et al. 2010). To evaluate the possibility that nutrient addition shifts allocation towards reproduction, we repeated the repeated-measures ANOVA with reproductive litter production expressed as a proportion of total fine litter production. Repeated measures were on year, with 20 levels. Fixed effects included the N, P, and K treatments and their two-way interactions. We used the Greenhouse–Geisser epsilon to adjust *P* values of within-subjects effects for violations of the sphericity assumption. We performed analyses in R using the aov, glm, and clmm functions (R Development Core Team 2018).

RESULTS

We scored reproduction for 3,603 individuals representing 38 species (Appendix S1: Table S1). The 1,830 sterile trees accounted for slightly more than half of the assessed trees. The 1,773 fertile trees received scores of 1 ($n = 632$), 2 (342), 3 (399), or 4 (400).

Single-species responses

The main effect of P addition was positive for six of the seven abundant species with five or more individuals per plot, significantly positive for *Sorocea affinis*, and marginally significantly positive for *Heisteria concinna* (Appendix S2: Table S1, Figs. S1, S2). In contrast, the main effects of N and K addition were each positive for four species and negative for three species (Appendix S2: Table S1). The only significant responses involving N and K addition were reduced reproduction with N addition for *Mabea occidentalis* (Appendix S2: Fig. S3) and reduced reproduction with combined N and K addition for *Talisia nervosa* (Appendix S2: Fig. S4). Neither response is consistent with N or K limitation, and their significance may reflect chance, the large number of tests performed, and Type 1 statistical error (Appendix S2: Table S1). The remaining nutrient interactions were all insignificant (Appendix S2: Table S1). The single species analyses suggest a consistent positive response to P addition.

Community wide responses

The main effect of P addition was significantly positive in the community-wide analysis that included 38 species with five or more sterile and five or more reproductive individuals ($P = 0.024$, Appendix S1: Table S2). None of the remaining nutrient treatments were significant (Appendix S1: Table S2). The odds ratio of 1.43 for the main effect of P addition indicates that plants with added P were 1.43 times more likely to receive a higher reproductive score than plants without added P (Fig. 1).

We removed insignificant nutrient treatments from the previous model and added a covariate that quantifies species-specific associations with soil P availability (P_{affinity}; see Methods: Data analysis—Focal trees) and its interaction with the main effect of P addition ($P * P_{\mathrm{affinity}}$). The main effect of P addition remained significant ($P = 0.042$), whereas P_{affinity} and $P * P_{\mathrm{affinity}}$ were insignificant (Appendix S1: Table S3). Species-specific reproductive responses to P addition and regional associations with P-rich soils were unrelated (Fig. 2).

Reproductive litter production

Reproductive litter production varied widely among years (Fig. 3; $P < 0.001$, Appendix S1: Table S4). Between-plot effects, which evaluate whether nutrient treatments had consistent effects across years, were all

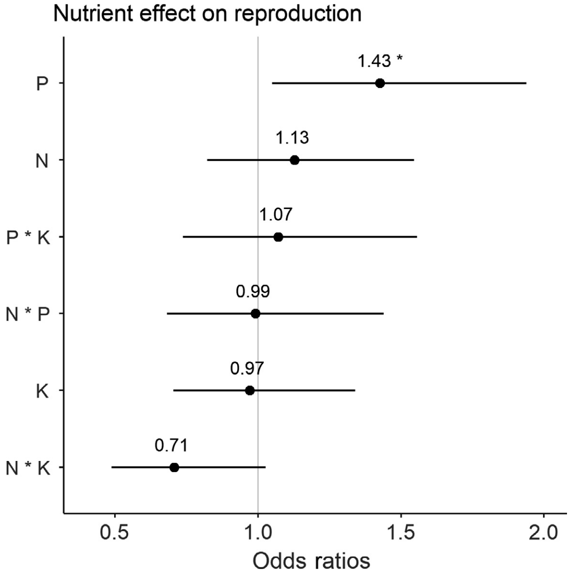

FIG. 1. Forest plot of odds ratios (95% confidence interval [CI]) for each nutrient treatment for the community-wide ordinal logistic regression. An odds ratio of 1 indicates no change in the probability of a plant being scored in a higher reproductive category. Odds ratios larger than 1 indicate the added nutrient increased reproductive scores. Phosphorus (P) was the only nutrient that significantly affected reproductive scores (P value = 0.024). Plants exposed to added P were 1.43 times more likely to receive a higher score than plants not exposed to added P.

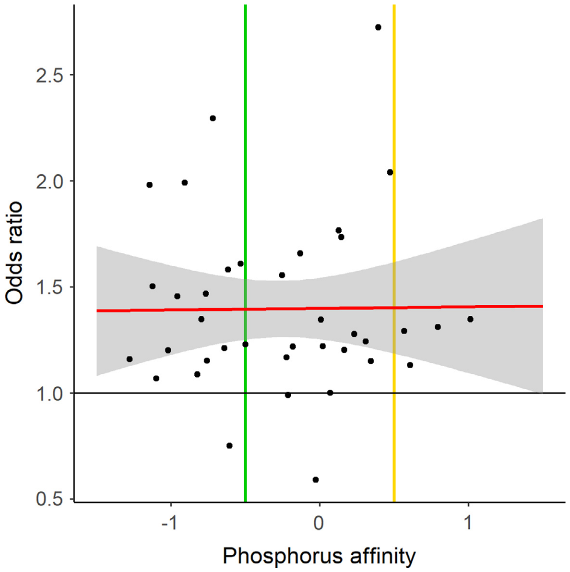

FIG. 2. Scatterplot showing the relationship between species-specific phosphorus affinity ($P_{affinity}$) and reproductive responses to phosphorus (P) addition. Reproductive responses are represented by odds ratios calculated from species-specific coefficients for the main effect of P addition. The $P_{affinity}$ scores are effect sizes relating regional distributions to soil P availability from Condit et al. (2013). $P_{affinity}$ values ≤ -0.5 (green vertical line) and ≥ 0.5 (yellow vertical line) indicate species strongly associated with P-poor and P-rich soils, respectively. The red line represents the linear relationship between phosphorus affinity and odds ratios, with gray shading representing the 95% confidence interval (P value = 0.95). The black horizontal line represents an odds ratio of 1, which corresponds to identical reproductive scores with and without added P.

insignificant (Appendix S1: Table S4) even though reproductive litter production was greater with N addition in every year (Fig. 3B, $P = 0.16$ for the main effect of N addition). Between-plot effects were also insignificant for reproductive litter production expressed as a proportion of total fine litter production (Appendix S1: Table S5, Fig. S2). Within-plot effects of nutrient treatments, which evaluate interactions between treatments and year, were also all insignificant when the Greenhouse–Geisser correction was implemented (Appendix S1: Tables S4, S5).

DISCUSSION

We explored plant reproductive responses to a 21-yr, factorial nitrogen–phosphorus–potassium (NPK) addition experiment conducted in an old-growth lowland tropical forest growing on a nutrient-poor Oxisol. None of the nutrient treatments significantly affected community-wide reproductive litter production over the first 20 yr of the experiment (Fig. 3; Appendix S1: Table S4). A significant increase in reproductive litter production with N addition, reported for the first 5 yr of the experiment (Kaspari et al. 2008), is no longer significant, even though N addition was associated with enhanced reproductive litter production in all 20 yr (Fig. 3B). Tremendous interspecific, spatial, and temporal variation characterizes plant reproduction in central Panama (Wright et al. 1999, 2005*b*), and it is perhaps unsurprising that this variation overwhelms treatment effects in community-wide analyses. Focal tree responses provided a very different outcome. Reproductive responses to P addition were consistently positive and significant across 38 focal species (Figs. 1, 2; Appendix S2). In contrast, reproductive responses to N and K addition were weak, inconsistent, and insignificant (Fig. 1; Appendix S2). After 21 yr of nutrient addition, our experiment provides evidence that P limits tree reproduction, whereas N and K do not.

Four previous experiments evaluated plant reproductive responses to nutrient addition in tropical forests with similar results for community-wide vs. species-specific analyses. Community-wide reproductive litter production was unaffected by N addition in an N-limited montane forest (Adamek et al. 2009) or by P addition in a P-limited lowland forest (Alvarez-Clare et al. 2013). In contrast, an epiphytic bromeliad in Puerto Rico increased reproduction after fertilization (Lasso and Ackerman 2013) and the dominant tree species in a Hawaiian forest increased inflorescence production after N and P addition (DiManno and Ostertag 2016). Significant reproductive responses to nutrient addition have been detected in analyses that control interspecific variation (Lasso and Ackerman 2013, DiManno and Ostertag 2016, Fig. 1 in this study) but not in community-wide analyses that pool species (Adamek et al. 2009, Alvarez-Clare et al. 2013, Fig. 3 in this study). Future attempts to evaluate nutrient limitation of reproduction in diverse tropical forests should control interspecific variation.

We have experimentally demonstrated proximate limitation of reproduction by P in a species-rich tropical forest for the first time. Interspecific variation in the degree to which P limits reproduction will influence species composition. Interspecific variation in the strength of reproductive responses to P addition could provide experimental evidence consistent with ultimate control of species composition by P. Specifically, stronger responses to P addition among species associated with P-rich soils could presage a shift in species composition towards the species composition characteristic of P-rich soils. We found no evidence for this effect for reproduction (Fig. 2) nor for tree growth rates (Wright et al. 2018). An important caveat is that species associated with P-poor soils dominate our study site (Wright et al. 2018). For example, 17 and just 4 of our focal tree species are strongly associated with P-poor and P-rich soils, respectively (Fig. 2; Appendix S1: Table S1). Our experiment provides limited information about the responses of species associated with P-rich soils. To overcome limitations imposed by local species composition, Zalamea et al. (2016) took central Panama tree species associated with a wide range of soil P availability into a growing

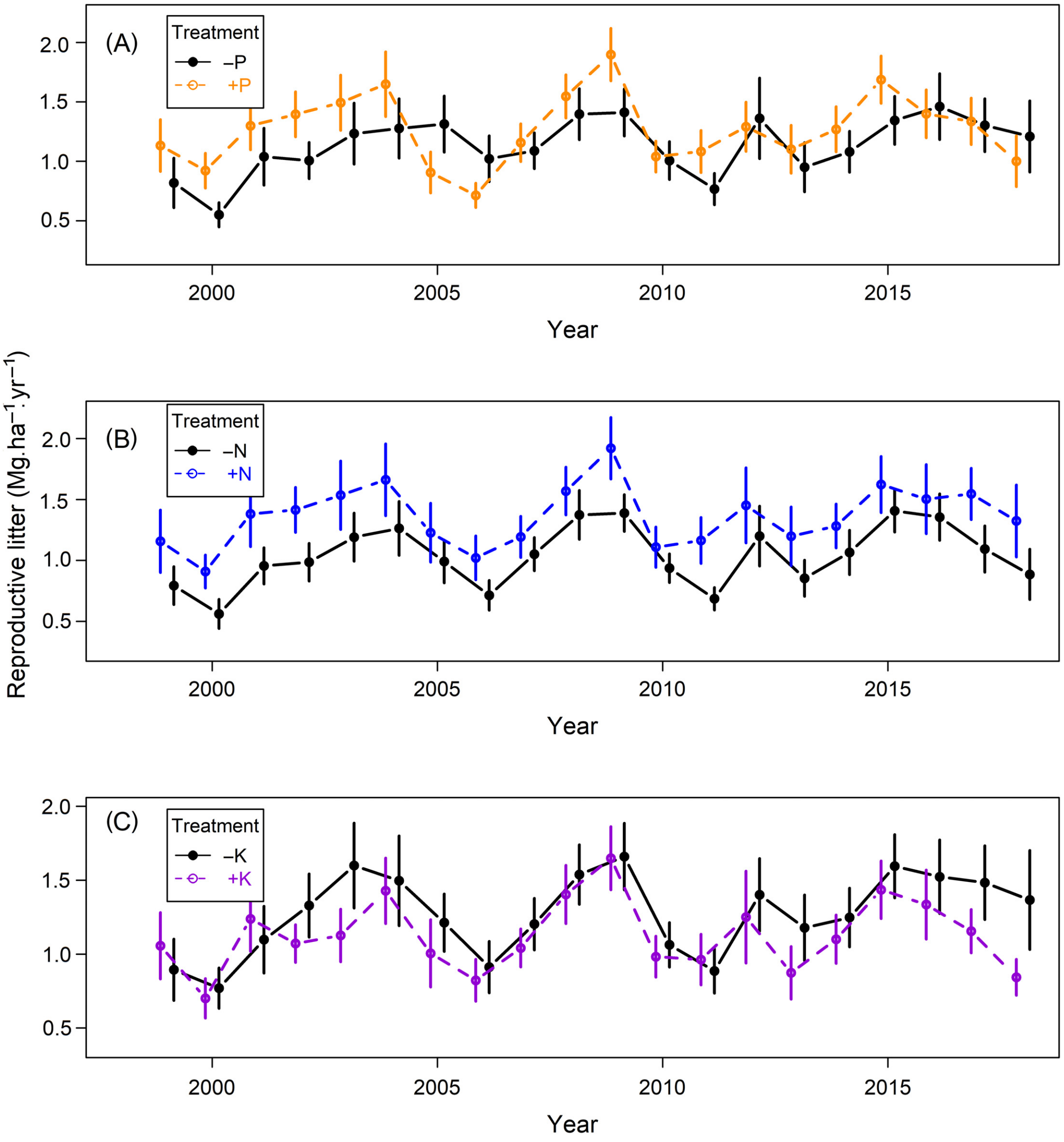

FIG. 3. Annual reproductive litter production contrasting (A) −P and +P treatments, (B) −N and +N treatments, and (C) −K and +K treatments (C). In each panel, the colorful dashed and solid black lines represent the addition and control treatments, respectively. Values are means (±1 SE) for 16 plots.

house, where seedling growth responses to P addition are stronger for species associated with P-rich soils. We could overcome limitations imposed by local species composition by planting species associated with a wide range of soil P availability into common gardens within our stand-level experimental plots. This new experiment could provide the first experimental evidence consistent with ultimate limitation of species composition by P under forest conditions.

Proximate limitation of plant processes by N and P is well documented for tropical forests. In recent meta-analyses of nutrient addition experiments conducted in tropical forests, foliar N and P concentrations increase significantly after N and P addition, respectively (Ostertag and DiManno 2016); productivity increases significantly after N addition (LeBauer and Treseder 2008); and tissue nutrient concentrations, fine litter production, and plant growth rates increase significantly after N and P addition (Wright 2019). Our experiment also manipulates K availability and provides evidence that K, N, and P limit different functions at a single site (Kaspari et al. 2008, Wright et al. 2011, Yavitt et al. 2011, Pasquini and Santiago 2012, Santiago et al. 2012, Mayor et al. 2014, Schreeg et al. 2014, Pasquini et al. 2015, Wurzburger and Wright 2015, this study). Nitrogen addition increases tissue N concentrations and, when added together with P, seedling growth rates. Potassium addition decreases fine root biomass and increases tissue K concentrations, seedling growth rates, and fine root turnover rates. Phosphorus addition increases tissue P concentrations, photosynthesis, stomatal conductance, fine litter production, and reproduction by focal trees. Experiments demonstrate proximate limitation of a wide range of plant functions by N, P, and K in tropical forests. Possible proximate limitation by other nutrients remains unexplored, and experiments cannot yet demonstrate ultimate limitation of species composition and ecosystem structure by any nutrient for any tropical forest.

Acknowledgments

We thank Edwin Perez and Rodolfo Perez for assistance in the field and Milton Garcia, Omar Hernandez, and Sebastian Bernal for maintaining the treatments for 21 yr. An internship from the Smithsonian Tropical Research Institute funded RF. A grant from the Scholarly Studies Program of the Smithsonian Institution funded the 2018 tree census and determinations of crown condition, light exposure, and liana infestation indices.

Literature Cited

Adamek, M., M. D. Corre, and D. Hölscher. 2009. Early effect of elevated nitrogen input on above-ground net primary production of a lower montane rain forest, Panama. Journal of Tropical Ecology 25:637–647.

Alvarez-Clare, S., M. Mack, and M. Brooks. 2013. A direct test of nitrogen and phosphorus limitation to net primary production in a lowland tropical wet forest. Ecology 94:1540–1551.

Bloom, A. J., F. Chapin, and H. A. Mooney. 1985. Resource limitation in plants—an economic analogy. Annual Review of Ecology and Systematics 16:363–392.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.

Chapin, F., P. Vitousek, and K. Cleve. 1986. The nature of nutrient limitation in plant communities. American Naturalist 127:48–58.

Chave, J., et al. 2010. Regional and seasonal patterns of litterfall in tropical South America. Biogeosciences 7:43–55.

Clark, D. B., and D. A. Clark. 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. Journal of Tropical Ecology 6:321–331.

Condit, R. 1998. Tropical forest census plots. Springer-Verlag and RG Landes Company, Berlin, Germany.

Condit, R., B. M. J. Engelbrecht, D. Pino, R. Perez, and B. L. Turner. 2013. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. Proceedings of the National Academy of Sciences of the United States of America 110:5064–5068.

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, California, USA.

Dawkins, H. C., and D. R. B. Field. 1978. A long-term surveillance system for British woodland vegetation. Department of Forestry, Oxford University, Oxford, England, UK.

DiManno, N., and R. Ostertag. 2016. Reproductive response to nitrogen and phosphorus fertilization along the Hawaiian archipelago's natural soil fertility gradient. Oecologia 180:245–255.

Farrior, C. E., D. Tilman, R. Dybzinski, P. B. Reich, S. A. Levin, and S. W. Pacala. 2013. Resource limitation in a competitive context determines complex plant responses to experimental resource additions. Ecology 94:2505–2517.

Field, C. B., F. S. Chapin, P. A. Matson, and H. A. Mooney. 1992. Responses of terrestrial ecosystems to the changing atmosphere—a resource-based approach. Annual Review of Ecology and Systematics 23:201–235.

Graham, E. A., S. S. Mulkey, K. Kitajima, N. G. Phillips, and S. J. Wright. 2003. Cloud cover limits net CO_2 uptake and growth of a rainforest tree during tropical rainy seasons. Proceedings of the National Academy of Sciences of the United States of America 100:572–576.

Kaspari, M., S. J. Wright, J. B. Yavitt, K. E. Harms, M. Garcia, and M. Santana. 2008. Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecology Letters 11: 35–43.

Lasso, E., and J. Ackerman. 2013. Nutrient limitation restricts growth and reproductive output in a tropical montane cloud forest bromeliad: Findings from a long-term forest fertilization experiment. Oecologia 171:165–174.

LeBauer, D. S., and K. K. Treseder. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89:371–379.

León, M. M. G., L. I. Martínez, F. N. A. Mello, J. S. Powers, and S. A. Schnitzer. 2018. Lianas reduce community-level canopy tree reproduction in a Panamanian forest. Journal of Ecology 106:737–745.

Mayor, J. R., S. J. Wright, and B. L. Turner. 2014. Species-specific responses of foliar nutrients to long-term nitrogen and phosphorus additions in a lowland tropical forest. Journal of Ecology 102:36–44.

Mirabello, M. J., J. B. Yavitt, M. Garcia, K. E. Harms, B. L. Turner, and S. J. Wright. 2013. Soil phosphorus responses to chronic nutrient fertilisation and seasonal drought in a humid lowland forest, Panama. Soil Research 51:215–221.

Muller-Landau, H. C., K. C. Cushman, E. E. Arroyo, I. M. Cano, K. J. Anderson-Teixeira, and B. Backiel. 2020. Patterns and mechanisms of spatial variation in tropical forest productivity, woody residence time, and biomass. New Phytologist 229:3065–3087.

Ostertag, R., and N. M. DiManno. 2016. Detecting terrestrial nutrient limitation: a global meta-analysis of foliar nutrient concentrations after fertilization. Frontiers in Earth Science 4:1–14.

Pasquini, S. C., and L. S. Santiago. 2012. Nutrients limit photosynthesis in seedlings of a lowland tropical forest tree species. Oecologia 168:311–319.

Pasquini, S. C., S. J. Wright, and L. S. Santiago. 2015. Lianas always outperform tree seedlings regardless of soil nutrients: results from a long-term fertilization experiment. Ecology 96:1866–1876.

R Development Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Sanchez, P. A. 1976. Properties and management of soils in the tropics. Wiley, New York, New York, USA.

Santiago, L. S., S. J. Wright, K. E. Harms, J. B. Yavitt, C. Korine, M. N. Garcia, and B. L. Turner. 2012. Tropical tree seedling growth responses to nitrogen, phosphorus and potassium addition. Journal of Ecology 100:309–316.

Schreeg, L. A., L. S. Santiago, S. J. Wright, and B. L. Turner. 2014. Stem, root, and older leaf N:P ratios are more responsive indicators of soil nutrient availability than new foliage. Ecology 95:2062–2068.

Soil Survey Staff. 1999. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. United States Department of Agriculture, Natural Resources Conservation Service, Washington, DC, USA.

Tully, K. L., T. E. Wood, A. M. Schwantes, and D. Lawrence. 2013. Soil nutrient availability and reproductive effort drive patterns in nutrient resorption in *Pentaclethra macroloba*. Ecology 94:930–940.

Turner, B. L., T. Brenes-Arguedas, and R. Condit. 2018. Pervasive phosphorus limitation of tree species but not communities in tropical forests. Nature 555:367–370.

Vitousek, P. M., S. Porder, B. Z. Houlton, and O. A. Chadwick. 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. Ecological Applications 20:5–15.

Vitousek, P. M., and R. L. Sanford. 1986. Nutrient cycling in moist tropical forest. Annual Review of Ecology and Systematics 17:137–167.

Winer, B. J. 1971. Statistical principles in experimental design. McGraw-Hill Book Company, New York, New York, USA.

Wright, S. J. 2019. Plant responses to nutrient addition experiments conducted in tropical forests. Ecological Monographs 89:1–18.

Wright, S. J., et al. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92:1616–1625.

Wright, S. J., et al. 2018. Plant responses to fertilization experiments in lowland, species-rich, tropical forests. Ecology 99:1129–1138.

Wright, S. J., C. Carrasco, O. Calderón, and S. Paton. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. Ecology 80:1632–1647.

Wright, S. J., M. A. Jaramillo, J. Pavon, R. Condit, S. P. Hubbell, and R. B. Foster. 2005*a*. Reproductive size thresholds in tropical trees: Variation among individuals, species and forests. Journal of Tropical Ecology 21:307–315.

Wright, S. J., H. C. Muller-Landau, O. Calderón, and A. Hernandéz. 2005*b*. Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. Ecology 86:848–860.

Wurzburger, N., and S. J. Wright. 2015. Fine-root responses to fertilization reveal multiple nutrient limitation in a lowland tropical forest. Ecology 96:2137–2146.

Yavitt, J. B., K. E. Harms, M. N. Garcia, M. J. Mirabello, and S. J. Wright. 2011. Soil fertility and fine root dynamics in response to 4 years of nutrient (N, P, K) fertilization in a lowland tropical moist forest, Panama. Austral Ecology 36:433–445.

Yavitt, J. B., K. E. Harms, M. N. Garcia, S. J. Wright, F. He, and M. J. Mirabello. 2009. Spatial heterogeneity of soil chemical properties in a lowland tropical moist forest, Panama. Australian Journal of Soil Research 47:674–687.

Yavitt, J. B., S. J. Wright, and R. K. Wieder. 2004. Seasonal drought and dry-season irrigation influence leaf-litter nutrients and soil enzymes in a moist, lowland forest in Panama. Austral Ecology 29:177–188.

Zalamea, P. C., B. L. Turner, K. Winter, F. A. Jones, C. Sarmiento, and J. W. Dalling. 2016. Seedling growth responses to phosphorus reflect adult distribution patterns of tropical trees. New Phytologist 212:400–408.

Zimmerman, J. K., S. J. Wright, O. Calderón, M. A. Pagan, and S. Paton. 2007. Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: The role of annual changes in irradiance. Journal of Tropical Ecology 23:231–251.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3469/suppinfo