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Bonnie G. Waring
Utah State University

Daniel Pérez-Aviles
University of Minnesota

Jessica G. Murray
Utah State University

Jennifer S. Powers
University of Minnesota

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Plant community responses to stand-level nutrient fertilization in a secondary tropical dry forest

BONNIE G. WARING,^{1,4,5} DANIEL PÉREZ-AVILES,¹ JESSICA G. MURRAY,² AND JENNIFER S. POWERS^{1,3}

¹Departments of Ecology, Evolution, and Behavior and Plant and Microbial Biology, University of Minnesota, Saint Paul, Minnesota 55108 USA

²Department of Biology and Ecology Center, Utah State University, Logan, Utah 84321 USA

³Smithsonian Tropical Research Institute, Panamá, República de Panamá

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Abstract. The size of the terrestrial carbon (C) sink is mediated by the availability of nutrients that limit plant growth. However, nutrient controls on primary productivity are poorly understood in the geographically extensive yet understudied tropical dry forest biome. To examine how nutrients influence above- and belowground biomass production in a secondary, seasonally dry tropical forest, we conducted a replicated, fully factorial nitrogen (N) and phosphorus (P) fertilization experiment at the stand scale in Guanacaste, Costa Rica. The production of leaves, wood, and fine roots was monitored through time; root colonization by mycorrhizal fungi and the abundance of N-fixing root nodules were also quantified. In this seasonal forest, interannual variation in rainfall had the largest influence on stand-level productivity, with lower biomass growth under drought. By contrast, aboveground productivity was generally not increased by nutrient addition, although fertilization enhanced growth of individual tree stems in a wet year. However, root growth increased markedly and consistently under P addition, significantly altering patterns of stand-level biomass allocation to above- vs. belowground compartments. Although nutrients did not stimulate total biomass production at the community scale, N-fixing legumes exhibited a twofold increase in woody growth in response to added P, accompanied by a dramatic increase in the abundance of root nodules. These data suggest that the relationship between nutrient availability and primary production in tropical dry forest is contingent on both water availability and plant functional diversity.

Key words: carbon; fertilization experiment; nitrogen; nutrient limitation; phosphorus; primary productivity; tropical dry forest.

INTRODUCTION

Soil nutrient availability regulates the exchange of carbon (C) between terrestrial ecosystems and the atmosphere (Fernández-Martínez et al. 2014). In earth system models, representing limitation of plant growth by nitrogen (N) and phosphorus (P) can alter the sign and magnitude of the land sink response to rising atmospheric CO₂ (Wieder et al. 2015). This suggests that accurate predictions of carbon cycle–climate interactions hinge on our understanding of plant nutrient limitation. Surprisingly, however, we do not know the identity of the element(s) that constrain net primary production (NPP) in many widespread terrestrial biomes; tropical forests in particular represent a major knowledge gap. This is especially concerning given that tropical

ecosystems are undergoing rapid transitions in land use, nutrient deposition, and climate (Bonan 2008, Hietz et al. 2011), dominate CO₂ exchange between the land sink and atmosphere (Cleveland et al. 2011) and are expected to drive terrestrial ecosystem feedbacks to rising atmospheric CO₂ (Bonan and Levis 2010).

A common biogeochemical paradigm (Walker and Syers 1976) holds that N should regulate plant growth in ecosystems on geologically “young” soils, whereas plant communities on older substrates should be limited by rock-derived nutrients such as P. This conceptual model led to the prediction that tropical forest growth is largely P limited, given that most such forests grow on highly weathered soils (Crews et al. 1995). Just a handful of tropical fertilization experiments have been conducted to test the P limitation hypothesis directly; of these, a minority have examined both above- and belowground responses (Wright et al. 2018). Unfortunately, the results of these experiments have not been straightforward. In the longest-running tropical fertilization experiment, conducted in a Panamanian moist forest, production of leaf litter, wood, and roots responded individually

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⁴ Present address: Department of Biology and Ecology Center, Utah State University, Logan, Utah 84321 USA.

⁵ E-mail: bonnie.waring@gmail.com

to different nutrients after 11 yr (Wright et al. 2011). A similar experiment in a Costa Rican wet forest found no stand-level responses to N or P, although smaller stems exhibited faster wood growth with P addition (Alvarez-Clare et al. 2013). A long-term fertilization experiment in a tropical montane forest found no net effect of nutrients on aboveground productivity, reflecting both positive and negative growth responses of individual species (Baez and Homeier 2017). Finally, two recent meta-analyses have failed to detect significant responses of tropical tree growth to added nutrients (Schulte-Uebbing and de Vries 2017, Wright et al. 2018). Although growth responses to both nutrients tend to be positive, there is no evidence that the response to P is stronger than the response to N. These muted and complex responses to nutrient addition suggest one of the three potential explanations: (1) NPP in tropical forests is limited by a nonmacronutrient resource (e.g., micronutrients, water, or light); (2) strong signals of nutrient limitation only emerge at timescales greater than those used in fertilization experiments to date; or (3) physiological or ecological mechanisms adjust to maintain colimitation by all major plant resources. Each of these mechanisms has distinct implications for the way nutrient limitation of NPP should be measured in situ and represented in predictive models.

Weak stand-level responses to N and/or P fertilization may indicate that these macronutrients are not the primary limiting resource in tropical forests (Jordan and Herrera 1981). There is some evidence that micronutrients can indirectly impact productivity in tropical forests; for example, molybdenum regulates free-living N fixation and therefore macronutrient inputs in some tropical forests (Reed et al. 2013), and sodium may affect decomposer activity and thereby the recycling of macronutrients to plants (Kaspari et al. 2009). There is also evidence that the micronutrient boron may directly structure the composition of tropical tree communities (Steidinger 2015), which could in turn affect community-level productivity. Moreover, light rather than nutrients is likely to constrain the growth of many tropical trees, especially in older forests (Graham et al. 2003). This may explain why responses to nutrients are more pronounced in secondary forests and in smaller (younger) stems, which commonly occupy canopy gaps (Wright et al. 2018). Water availability may also shape forest responses to nutrient addition. In central Panama, the distribution of many tree species is sensitive to dry-season intensity (Condit et al. 2013), suggesting some degree of water limitation even in the relatively moist forests examined. However, despite the fact that over 40% of tropical forests are highly seasonal with pronounced dry seasons (Murphy and Lugo 1986), no large-scale, stand-level fertilization experiments have examined nutrient effects on both above- and belowground productivity in tropical dry forest (TDF). This precludes our ability to examine how water and nutrient availability jointly shape patterns of plant productivity

across the wide spectrum of seasonality exhibited across tropical forests (Powers et al. 2015).

Even if macronutrients such as N and P do ultimately constrain productivity in tropical forests, detecting stand-level responses to fertilization in ecosystems dominated by long-lived trees may require long-term studies (Sullivan et al. 2014). The absence of nutrient response in tropical fertilization studies could be an artifact of insufficient experimental duration (Wright et al. 2018). However, given the relatively long time frame of the tropical forest fertilization studies described above, it is unlikely that the weak responses of NPP to nutrients can be ascribed entirely to experimental timing. Although of course a decade-long experiment is too short to identify shifts in long-lived tree community composition, physiological responses (growth, biomass allocation, nutrient uptake, etc.) can be observed at annual or even monthly timescales (Santiago 2015). Therefore, although increases in stand-level productivity may take decades to manifest (especially in older stands, where growth is slower and nutrient demand lower), shifts in biomass allocation or plant–microbe interactions that presage changes in NPP should be observed much more rapidly. This hypothesis is difficult to evaluate, however, given that many tropical fertilization experiments have only quantified aboveground responses to nutrients.

Finally, studies that seek to identify single-factor nutrient limitation by adding N, P, or other nutrients individually may provide an incomplete picture of carbon–nutrient interactions in tropical forests. It is increasingly recognized that plant physiology and growth are regulated by multiple resources simultaneously, at the level of the individual (Reich 2014) and the community (Danger et al. 2008). Species may experience limitation by different nutrients, even in an identical resource environment, due to variation in their tissue stoichiometry, nutrient use efficiency, or nutrient uptake strategies (Townsend et al. 2007, Townsend and Asner 2013). For example, many plants in the family Leguminosae associate with N-fixing bacteria and are therefore expected to escape N limitation (Houlton et al. 2008, Tiruvaimozhi et al. 2018), and trees that associate with N-mining ectomycorrhizal fungi are also thought to have a competitive advantage in N-poor environments (Phillips et al. 2013). By contrast, because arbuscular mycorrhizal fungi (AMF) are thought to promote P uptake, increased investment in AMF may represent a viable plant strategy to cope with P limitation (Johnson 2010). Nutrient limitation may also vary temporally (Farrion et al. 2013), as plant communities are continually re-optimizing allocation strategies to maintain maximum growth rates (Bloom et al. 1985).

In summary, most plant communities display complex responses to nutrient addition, and these responses are likely mediated by the availability of other resources (such as water and light), as well as the taxonomic identity and functional traits of species present. To examine how nutrients, climatic conditions, plant functional

diversity, and their interactions affect productivity in drier tropical forests, we conducted a fully factorial N and P addition experiment in a regenerating TDF in northwest Costa Rica. Our study represents the first large-scale, stand-level fertilization experiment in the TDF biome. Understanding carbon–nutrient interactions in TDF is important because of the size of the biome and because these ecosystems capture tremendous plant functional diversity. Tree species in TDF encompass a broad spectrum of leaf habits, from highly deciduous to evergreen, and exhibit a variety of microbial symbioses: legumes, arbuscular mycorrhizal, and ectomycorrhizal tree species are all common (Eamus 1999, Waring et al. 2016a). This functional variation makes TDF ecosystems excellent natural laboratories in which to examine plasticity in plant nutrient acquisition strategies.

Over a 3-yr period, we examined temporal dynamics in the production of leaves, wood, and fine roots, along with changes in root nodulation and colonization by mycorrhizal fungi. These data allowed us to examine any nutrient-induced changes in total NPP, as well as shifts in C allocation between above- and belowground biomass compartments, against the backdrop of large interannual variation in rainfall. Finally, we examined woody-growth responses as a function of plant functional types as classified by leaf habit (evergreen vs. [semi]-deciduous) and symbiont association (N-fixing legumes, ectomycorrhizal trees, and arbuscular mycorrhizal trees).

METHODS

Study site

Our experiment was conducted at Estación Experimental Forestal Horizontes, in a ~30-yr regenerating tropical dry forest in Guanacaste, Costa Rica. Mean annual temperature at the site is approximately 25°C, and mean annual precipitation is 1,800 mm, nearly all of which falls between May and November. Interannual variability in total rainfall is high, as precipitation is highly sensitive to the El Niño Southern Oscillation. Soils at the site are Andic and Typic Haplustepts (Alfaro et al. 2001), with a high clay content ($38 \pm 1\%$) and a total N:P of 8.3 ± 0.4 , which is slightly lower than the global mean (Cleveland and Liptzin 2007).

The forest at Horizontes is approximately 30 yr old and has regenerated naturally following cessation of several decades of rice, cotton, and sorghum production as well as cattle grazing (Werden et al. 2018). This secondary forest is quite biodiverse (Appendix S1: Table S1); across the 1-ha area contained within the experimental plots (described below), we encountered 60 tree species representing 23 families. However, 32% of species belonged to the Leguminosae, and legumes represent an average of $17 \pm 4\%$ of total basal area across our study plots (range: 1–53%). The distribution of

species and plant functional groups at Horizontes is similar to that observed across nearby regenerating forests in northwestern Costa Rica (Powers and Tiffin 2010). The majority of trees are deciduous and arbuscular mycorrhizal, although eight species are evergreen and one of these is known to associate with ectomycorrhizal fungi (*Pisonia aculeata*, Hayward and Horton 2014).

Experimental design

The experiment consists of 16 plots, each measuring 25×25 m. Because of the small size of most stems in this forest (Appendix S1: Fig. S1), each plot contained approximately 70 stems ≥ 5 cm diameter at breast height (DBH). Plots were randomly assigned to one of four treatments: control, nitrogen addition ($150 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), phosphorus addition ($45 \text{ kg P}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$), and addition of N and P together at the aforementioned rates. Nutrients were broadcast over the entire 625-m^2 plot area, and all plots were separated by a buffer zone of at least 50 m on each side. Nutrient addition rates were similar to those used in two other large-scale tropical forest fertilization experiments (Wright et al. 2011, Alvarez-Clare et al. 2013). N was supplied as urea, and P as phosphoric acid, the only form of P-only fertilizer available in the region of Costa Rica where we worked. Our data show that neither N nor P treatments had significantly reduced soil pH over the experimental period ($P = 0.83$). Plots were fertilized with back-mounted sprayers three times per year, in early, middle, and late wet seasons. Nutrient additions began in June 2015, immediately after the first productivity measurements were recorded. At the start of the experiment, there were no significant differences among experimental plots in soil texture, pH, or concentrations of organic C, N, P, Ca, K, or Mg (all P values >0.05). Similarly, there was no significant pre-existing variation in plant community structure among treatments.

Productivity measurements

This paper reports stand-level productivity data collected from June 2015 through March 2018 (i.e., three consecutive wet seasons). For all stems greater than 5 cm (DBH), we identified the individual to species and measured diameter increments at 6-mo intervals (June and November of a given year). For stems <10 cm DBH, diameter was measured at a marked point 1.5 m above the ground (trees in this forest do not have buttresses). For stems >10 cm DBH, we tracked growth using band dendrometers. We used the allometric equations presented in Chave et al. (2014) to convert stem-diameter increments to woody biomass.

Leaf production was measured using litterfall traps. We deployed three 0.25-m^2 traps in a transect running through the center of each plot. Litter was collected from each trap monthly, dried to constant weight, and sorted to separate leaves, small branches, flowers, fruits,

and frass. Each of these components was weighed separately.

Fine root productivity was determined using the root ingrowth core method (Waring et al. 2016b). We deployed seven ingrowth cores in each plot: four located 2 m from each plot corner, and three in a transect running along the plot center. Cores were constructed of 2 mm flexible mesh fabric and had a diameter of 8 cm. Upon deployment, each core was filled with sieved, root-free soil collected on site, and installed to a depth of 15 cm. Root ingrowth cores were harvested in June, August, and November of each year, capturing fine root production over the entire wet season. We did not measure root growth during the dry season, because these clay-rich soils harden so completely during the dry season that sieving soils and installing new cores would be impossible. However, our measurements capture the bulk of root production, which is highly biased toward the wet season (J. S. Powers, *unpublished data*). After collection, soils were carefully removed from each core and washed over a 2-mm sieve to isolate clean roots. We examined all roots collected in this way to identify and count rhizobial nodules and ectomycorrhizal hyphal mantles. Subsequently, root samples were dried, weighed, and archived for quantification of arbuscular mycorrhizal colonization via staining and microscopy (Koske and Gemma 1989, McGonigle et al. 1990).

To determine total net primary productivity, we summed total leaf, wood, and root production in each plot for each year. In this highly seasonal forest, new leaves are produced in April and May and shed between January and March; therefore, “annual” leaf production was calculated as the sum of litterfall between April and March of the following year. Note that for 2016 and 2017, wood productivity data used in these calculations represent the biomass increment in June through November of a given year (“wet season growth”), because stems did not grow (or even shrank) during the dry season. To verify that our biomass increment data captured true stem growth (rather than shrinking/swelling of wood associated with plant water status), we also calculated and analyzed net stem growth over the entire 3-yr study interval, and at annual intervals (using data from June censuses only). These results were entirely consistent with analyses performed on more temporally resolved biomass increment data, confirming that the patterns we observed reflect true wood growth and not dimensional swelling. Finally, aboveground:belowground biomass productivity ratios, or AGB:BGB, were calculated as total leaf and wood production divided by root production in each plot for each year.

Soil biogeochemistry

To ensure that fertilization treatments were in fact altering nutrient availability, we measured NH_4 , NO_3 , and PO_4 in each plot ($N = 5$ samples per plot) during the wet and dry season of 2016. We also quantified

microbial biomass C, N, and P pools with the fumigation and direct extraction method (Vance et al. 1987). Inorganic N was extracted from soils with 2 mol/L KCl, and phosphate was extracted with NaCO_3 . Nutrient concentrations in soil extracts were determined colorimetrically following standard methods (Doane and Horwath 2003, Sims et al. 2003, Jeannotte et al. 2004). Additionally, in 2018, we measured soil pH in water annually in each plot using a 1:2.5 soil to solution ratio to verify that fertilizers did not acidify the soil.

Statistical analysis

We used repeated-measures nested analyses of variance (ANOVAs) to analyze variation in soil chemistry, aboveground productivity (leaves, flowers, and fruits), belowground productivity (fine roots), and mycorrhizal colonization among treatments. For all these analyses, plot identity was nested within treatment. For wood productivity analyses, we standardized incremental growth of each individual stem to initial stem biomass to control for autocorrelation in biomass increment and tree size: larger stems will add more total biomass each year than smaller stems, regardless of treatment or environmental conditions (see Appendix S1: Fig. S1 for the distribution of stem size classes). Henceforth, we will refer to this standardized growth metric as “relative wood growth” (i.e., relative wood growth of 0.10 indicates that a given stem increased its woody biomass by 10% of initial biomass in a given year). This metric allows us to explore how nutrients stimulate growth of individual stems independently of their size class. Relative wood growth was analyzed with a mixed-effects model that included interactions between the fixed effects of treatment and leaf habit (deciduous, semideciduous, and evergreen, sensu Powers and Tiffin 2010) and between treatment and N-fixer status. “N fixers” were defined as legume species with the potential to form N-fixing symbioses, vs. non-legumes and legumes that do not form nodules (Gei et al. 2018). Individual tree identity was included in this model as a random effect. There was high plant diversity at the site, so we had limited statistical power to test nutrient effects on the growth of individual species. However, we calculated mean overall growth rates in each nutrient treatment for the four species that were most widely distributed across all experimental plots: *Cupania guatemalensis*, *Enterolobium cyclocarpum*, *Guzmania ulmifolia*, and *Pisonia aculeata*.

Because total productivity and biomass allocation (aboveground:belowground biomass productivity ratios) were measured at the plot scale, these response variables were analyzed with two-way ANOVAs with nutrient treatment and year as fixed factors. The same analyses were also conducted for leaf, wood, and root production, summed at the plot level within each year. Root nodule counts and stem mortality events were analyzed with Poisson regression (a generalized linear model used for count data) with the same predictors (fertilization

treatment and year). Mortality rates reflect the death of separate stems, not necessarily entire trees, as a high proportion of the individuals in each plot were multi-stemmed. Note that nodulation and mycorrhizal colonization were effectively measured at the stand scale, because we examined all root-ingrowth cores for the presence of nodules rather than targeting the rhizosphere of individual trees. For all parametric analyses, data were log or square-root transformed to meet assumptions of normality. All statistical analyses were conducted in R Version 3.3.2.

RESULTS

Climate and soil conditions

Our site experienced dramatic variation in rainfall over the study interval. In 2015, Costa Rica endured one of the most severe El Niño events on record, with only 628 mm of rain falling at nearby Sector Santa Rosa of Área Conservación Guanacaste during that calendar year. Precipitation patterns returned to normal in 2016 (1,754 mm of rain) and above normal in 2017 (2,050 mm; M. M. Chavarría, *personal communication*).

The fertilization treatments impacted pools of plant-available nutrients. By the second year of treatment, all measured soil phosphorus pools (including microbial biomass P, PO₄, and Bray P) increased three- to sixfold in the +P and +NP treatments. In contrast, pools of microbial biomass C and N, NH₄, and NO₃ did not change in response to fertilization. This may indicate that some portion of the added N was lost to denitrification and/or rapid plant immobilization. All measured soil nutrient pools varied significantly between wet and dry seasons (Appendix S1: Table S2a, & Table S1a&b).

Aboveground responses

Production of leaves, flowers, and fruit varied at monthly timescales, reflecting seasonal patterns of leaf senescence and plant reproduction (Appendix S1: Table S3; Fig. S2). Total annual leaf production in each plot was not affected by treatments and did not vary among years (Table 1; Fig. 1A). Total plot-scale wood production varied from year to year and increased nearly fivefold in 2016 vs. 2015, the drought year (Table 1; Fig. 1B). Fertilization had no effect on overall plot-scale wood production. However, a more nuanced treatment response is apparent when examining patterns of relative wood growth for each stem (i.e., annual wood production divided by initial stem biomass; Appendix S1: Table S4). Interannual variation in relative stem growth was similar to that observed for total wood production, averaging 0.050 ± 0.004 in the drought year of 2015, and increased up to threefold in wetter years (0.135 ± 0.009 and 0.085 ± 0.006 in 2016 and 2017, respectively). These patterns of relative wood growth from year to year were affected by stem size. Following

the cessation of drought in 2016, the greatest relative growth increase was observed in the 10–20-cm size class (Appendix S1: Table S5). The effects of nutrients on relative growth of individual stems were detectable in 2016 only, when the +N and +NP treatments significantly stimulated relative growth (0.172 ± 0.023) in comparison to treatments where no N was added (0.101 ± 0.011 ; Appendix S1: Table S4). Relative growth responses to nutrients did not vary by stem-size class (Appendix S1: Table S5).

Finally, stem mortality was greater in 2015 (when 10.6% of stems died) vs. 2016 and 2017 (when 6.0 and 4.6% of stems died, respectively; $P < 0.001$). Mortality events (i.e., stem deaths) were 1.3 to 1.8 times more frequent in the +NP treatment vs. the others ($P = 0.047$).

Belowground responses

Plot-level root production varied idiosyncratically across the nine sampling time points (Appendix S1: Table S3; Fig. S3). Annual root production varied by up to 80% among years (Table 2; Fig. 1C) and peaked in 2016, the year following drought. When added alone or in combination with N, P increased root production by an average of 40%. By contrast, root colonization by mycorrhizal fungi did not vary among nutrient treatments (Table 2; Fig. 2B; Appendix S1: Table S3). However, the abundance of root nodules increased nearly threefold in the +P treatment relative to control ($P < 0.001$), and decreased approximately 40% when N was added alone ($P = 0.006$) or in combination with P ($P = 0.005$; Table 2; Fig. 2A). Both mycorrhizal root colonization and root nodulation were greatest in 2016, when both wood and root productivity were also highest.

Total productivity and biomass allocation

There was no overall effect of nutrient addition on total annual productivity (the sum of leaf, stem, and wood production in each plot). However, total productivity was nearly twofold greater in 2016 vs. 2015, when a major drought occurred (Fig. 3A; Appendix S1: Table S6). By contrast, the ratio of aboveground:belowground productivity (AGB:BGB) in each year was strongly affected by nutrient addition. Because adding P increased root productivity while leaf and wood production were unchanged, AGB:BGB decreased twofold in the +P treatment and was 25% lower in the +NP treatment vs. the control treatment (Fig. 3B; Appendix S1: Table S6). The AGB:BGB ratio also increased continuously among years, and increased nearly threefold in 2017 vs. 2015 (Fig. 3B).

Functional group and species responses

When we examined stem-growth responses by plant functional type, we found that the +P treatment

TABLE 1. Mean (\pm standard error) aboveground biomass produced annually in each of the four nutrient fertilization treatments in 2015–2017.

	Leaves			Flowers		
	2015	2016	2017	2015	2016	2017
Control	0.59 \pm 0.04	0.62 \pm 0.04	0.65 \pm 0.06	7.18 \pm 2.52	39.60 \pm 13.19	45.17 \pm 24.56
+N	0.60 \pm 0.07	0.68 \pm 0.05	0.61 \pm 0.04	21.11 \pm 11.02	37.29 \pm 27.16	16.01 \pm 6.77
+P	0.48 \pm 0.06	0.57 \pm 0.03	0.58 \pm 0.08	4.79 \pm 2.71	26.69 \pm 14.63	19.08 \pm 9.43
+NP	0.59 \pm 0.06	0.63 \pm 0.09	0.73 \pm 0.07	19.10 \pm 15.42	34.36 \pm 19.02	5.67 \pm 3.36

Notes: All data are reported as kg (biomass)/m², except flower and fruit production, which are reported in g/m². Capital letters indicate significant differences in annual productivity among years.

increased relative growth of N-fixing legumes by over twofold vs. the control treatment (Table 3; Fig. 4; Appendix S1: Table S4). This effect was independent of time; thus, P fertilization enhanced the growth of N-fixing trees from year to year and over the entire 3-yr study interval ($P = 0.008$). Non-N-fixing stems responded to the interactive effects of nutrient fertilization and year; as these individuals made up the majority of basal area, their relative growth patterns were very similar to those observed at the entire stand scale (Table 3). There was no indication that trees with different leafing phenologies responded differentially to fertilization (Appendix S1: Table S4). However, among the four most common tree species at our site, we observed growth trends that indicate very different responses to fertilization (Appendix S1: Fig. S4). These ranged from a twofold increase in the relative wood growth of *G. ulmifolia* in the +N treatment ($P = 0.060$), to a tendency toward growth inhibition by nutrients in an ectomycorrhizal evergreen species (*P. aculeata*). There was high variance in growth rates among individuals, so treatment effects on stem growth within each species were not significant.

DISCUSSION

The handful of tropical forest fertilization experiments performed to date have demonstrated subtle or insignificant effects of nutrient addition on stand-level productivity. These muted responses may indicate that another resource (e.g., light or water) exerts the dominant control on plant growth in mature tropical forests, at least at the annual to decadal timescales typical of such experiments. By contrast, in this secondary tropical dry forest, we observed remarkably strong belowground responses to nutrients after just 3 yr of fertilization. We also found that nutrient addition enhanced the growth of many individual stems when trees were recovering from drought stress. However, echoing patterns observed in other tropical forests, these patterns of stand-level growth dynamics were shaped by diverse responses of individual plant species or functional groups. Below, we further explore how interactions among nutrient availability, rainfall, and plant functional diversity mediate productivity and ecosystem-scale biogeochemical cycles.

Changes in above and belowground productivity in response to fertilization

Unlike most previous fertilization experiments in tropical forests, which have been conducted in mature forests, this study was performed in a young secondary forest, where nutrient capital was relatively recently lost to deforestation (Powers and Marín-Spiotta 2017). As such, we expected relatively pronounced aboveground responses to nutrient addition. Yet at the stand scale, aboveground productivity (i.e., production of leaves, flowers, fruits, and wood) was not strongly influenced by nutrients overall, and much of the intra-annual variation in productivity was observed among plots (Appendix S1: Fig. S5). However, an extreme drought in the first year of the study may have suppressed nutrient responses, and the +N and +NP treatments did stimulate relative wood growth (although not overall wood biomass production) in the year immediately following the drought. Overall, these patterns suggest that water and nutrient availability may exert interactive effects on aboveground biomass production in this tropical dry forest.

Our results highlight a discrepancy between patterns in total wood production vs. relative wood growth by individual stems. The total amount of new wood biomass produced each year varied over time, but was unresponsive to nutrient addition (Table 1). Meanwhile, when we examined biomass increment of individual stems, we found that N-fixing legumes responded positively to P addition, whereas the addition of N (alone or in combination) enhanced relative wood growth of many nonfixing stems in 2016 alone (Appendix S1: Table S4). This discrepancy may occur because the growth responses of a few very large individuals dominate the signal in total annual wood production in each treatment, obscuring the responses of smaller, more numerous stems. Although we did not find evidence for an interaction between stem-size class and fertilization treatment (Appendix S1: Table S5), this finding may well reflect low statistical power, as a small minority of stems were >30 cm. It is possible that some of the largest trees that dominated the total wood productivity signal were especially unresponsive to fertilization, as has been observed in other tropical

Fruits			Wood		
2015	2016	2017	2015 ^A	2016 ^B	2017 ^B
6.12 ± 2.18	46.12 ± 39.06	9.11 ± 1.57	0.32 ± 0.05	1.26 ± 0.35	0.98 ± 0.33
9.26 ± 1.98	7.32 ± 3.88	9.08 ± 2.85	0.24 ± 0.10	1.28 ± 0.42	0.82 ± 0.11
4.12 ± 2.15	14.16 ± 4.30	14.06 ± 3.45	0.22 ± 0.09	0.87 ± 0.33	0.49 ± 0.11
12.58 ± 6.36	17.18 ± 9.33	14.62 ± 5.11	0.29 ± 0.06	1.69 ± 0.49	0.76 ± 0.24

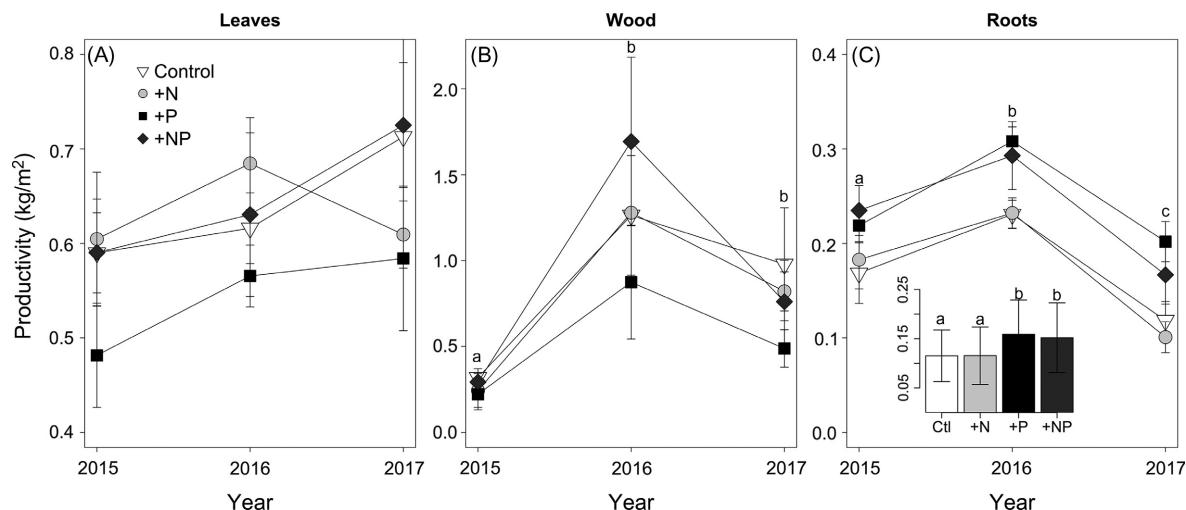


FIG. 1. Mean annual biomass production (in kg/m²) of (A) leaves, (B) wood, and (C) roots in each of the four fertilization treatments. Data represent means across the four plots in each treatment; error bars indicate ±1 standard error. The inset panel shows data averaged over the entire study interval (2015–2017). Letters in main panels indicate significant productivity differences among years (determined via Tukey’s honestly significant difference post hoc tests); letters in the inset panel indicate significant variation among treatments.

TABLE 2. Mean (±1 standard error) fine root biomass, root mycorrhizal colonization, and root nodulation observed annually in each of the four nutrient fertilization treatments in 2015–2017.

	Roots kg/m ²			Mycorrhizal colonization % root length			Root nodules N observed per root core		
	2015 ^A	2016 ^B	2017 ^C	2015	2016	2017	2015 ^A	2016 ^B	2017 ^C
Control	0.17 ^a ± 0.03	0.23 ^a ± 0.02	0.12 ^a ± 0.02	28.5 ^a ± 9.7	35.3 ^a ± 7.5	27.4 ^{ab} ± 9.9	0.40 ^a ± 0.70	0.67 ^a ± 1.62	0
+N	0.18 ^a ± 0.03	0.23 ^a ± 0.02	0.10 ^a ± 0.02	28.7 ^a ± 9.0	29.9 ^a ± 10.4	19.8 ^{ab} ± 9.4	0.16 ^b ± 0.48	0.44 ^b ± 1.24	0
+P	0.22 ^b ± 0.02	0.31 ^b ± 0.02	0.20 ^b ± 0.02	27.8 ^{ab} ± 10.6	32.3 ^a ± 9.9	26.0 ^{ab} ± 8.7	0.94 ^c ± 1.76	1.67 ^c ± 3.19	0.29 ± 1.29
+NP	0.23 ^b ± 0.03	0.29 ^b ± 0.04	0.17 ^b ± 0.03	12.3 ^b ± 6.2	33.7 ^a ± 8.2	25.2 ^{ab} ± 10.1	0.09 ^b ± 0.22	0.45 ^b ± 0.73	0

Note: Capital letters indicate significant differences among years, and lowercase letters indicate significant differences among nutrient fertilization treatments.

forest fertilization studies (Alvarez-Clare et al. 2013). On the other hand, the strong positive responses of legumes to added P may not have manifested at the stand scale, as these trees occupied, on average, just one-fifth of total stand basal area. In summary, although we did not detect nutrient-induced changes

in total wood biomass over the 3-yr study interval, there is strong evidence that many individual trees responded to fertilization. Whether such responses will ultimately affect stand-level wood production will depend on demographic and ecological dynamics, which may play out over longer timescales.

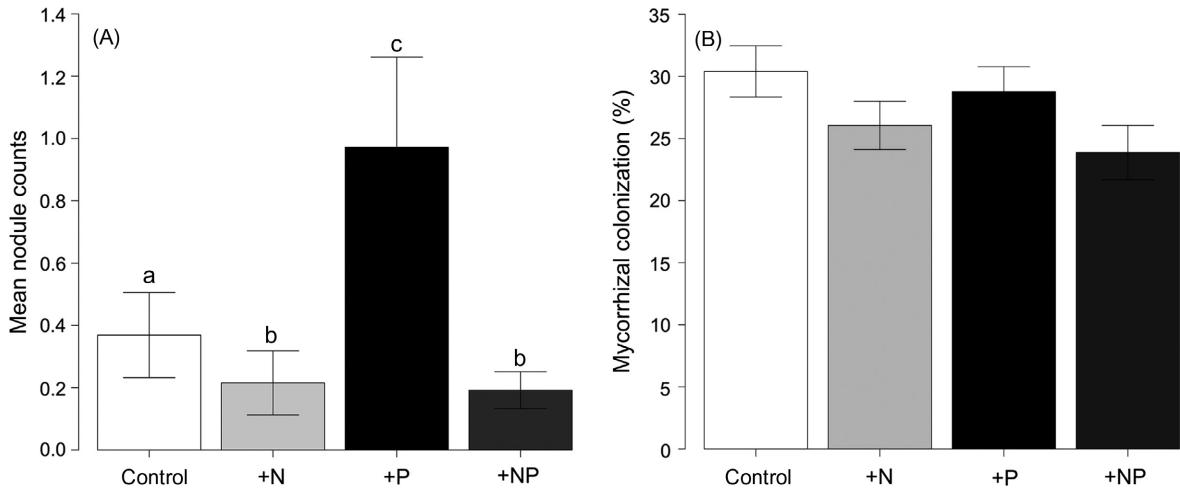


FIG. 2. (A) Mean root nodule counts (number of nodules observed in each root-ingrowth core) and (B) percent root colonization by arbuscular mycorrhizal fungi in each of the four treatment groups. Data are averaged over the entire study interval (2015–2017). Letters indicate significant differences among treatments.

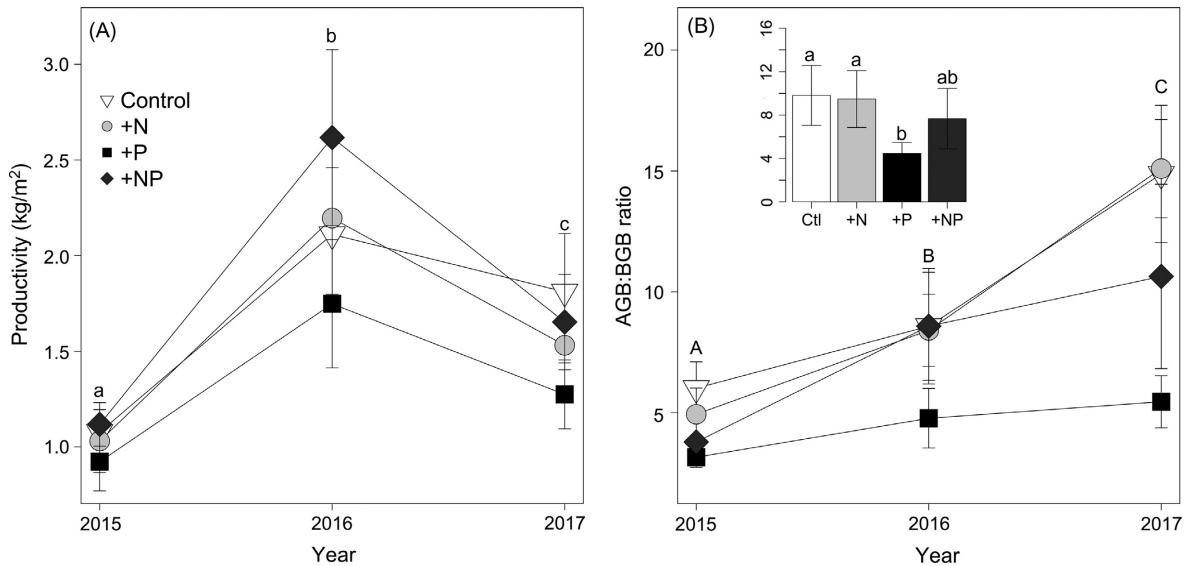


FIG. 3. (A) Total annual biomass production (in kg/m²) and (B) aboveground:belowground productivity ratios in each of the four fertilization treatments. Data represent means across the four plots in each treatment; error bars in all figures indicate ±1 standard error. The inset panel shows data averaged over the entire study interval (2015–2017). Letters in main panels indicate significant productivity differences among years, and letters in the inset panel indicate significant variation among treatments.

Belowground responses to fertilization also suggest that water and nutrients jointly shape patterns of plant growth in this highly seasonal ecosystem. In contrast to the weak aboveground responses to nutrients, belowground productivity strongly increased under P fertilization. Enhanced root production following nutrient addition seems paradoxical: when belowground resource limitation is relieved, plants should invest more in the acquisition of aboveground resources (i.e., light; Poorter et al. 2012). Indeed, in fertilization experiments in a

tropical moist forest, root production declined when nutrient limitation was alleviated (Wurzburger and Wright 2015), and stand-level fine root biomass decreases along soil fertility gradients in Neotropical rain forests (Powers et al. 2005). However, plants use roots for both nutrient and water acquisition. In this seasonally dry forest, it is possible that fertilized plants could invest their nutrient capital in fine root production in order to promote water uptake. Water availability is known to regulate the production and turnover of fine

TABLE 3. Mean (± 1 standard error) relative wood growth in each of the four nutrient treatments in 2015–2017.

	N-fixing legumes			Nonfixers		
	2015 ^A	2016 ^B	2017 ^B	2015	2016	2017
Control	0.042 ^a \pm 0.016	0.111 ^a \pm 0.032	0.065 ^a \pm 0.025	0.053 ^a \pm 0.006	0.112 ^{bc} \pm 0.014	0.103 ^{bcc} \pm 0.013
+N	0.057 ^a \pm 0.024	0.134 ^a \pm 0.038	0.104 ^a \pm 0.055	0.046 ^a \pm 0.010	0.175 ^{bd} \pm 0.032	0.057 ^{ac} \pm 0.008
+P	0.110 ^b \pm 0.027	0.190 ^b \pm 0.049	0.292 ^b \pm 0.221	0.039 ^a \pm 0.006	0.082 ^{abcc} \pm 0.012	0.066 ^{acc} \pm 0.009
+NP	0.049 ^{ab} \pm 0.024	0.112 ^{ab} \pm 0.023	0.127 ^{ab} \pm 0.030	0.057 ^a \pm 0.012	0.185 ^d \pm 0.025	0.081 ^{acc} \pm 0.013

Notes: Relative wood growth is expressed as a proportion: annual wood biomass increment (kg) divided stem biomass at the start of that year (kg). Data are presented separately for N-fixing legumes vs. nonfixers, as these groups responded differently to nutrient treatments. Capital letters indicate significant differences among years, and lowercase letters indicate significant differences among nutrient fertilization treatments. There were 25, 28, 18, and 39 N-fixing stems in the control, +N, +P, and +NP treatments, respectively. The corresponding sample sizes for nonfixing stems are 304, 228, 240, and 254 stems, respectively.

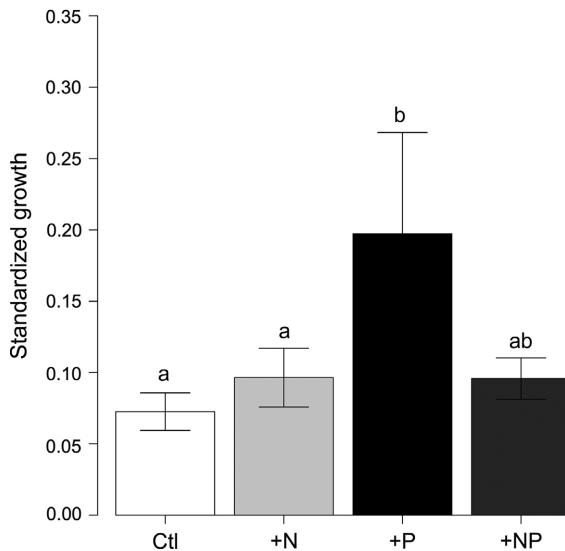


FIG. 4. Relative wood growth (i.e., growth standardized to initial stem biomass) in each of the four treatment groups, for N-fixing legumes only. Data are averaged across stems in each treatment group over the entire study interval (2015–2017). Letters indicate significant differences among treatments determined with Tukey's honestly significant difference post hoc tests.

roots in wet and seasonal tropical forests (Espeleta and Clark 2007). Increased belowground allocation to facilitate water acquisition may also explain observed patterns of root colonization by arbuscular mycorrhizae. In our study, root colonization did not decline in response to nutrient fertilization, as has been repeatedly observed elsewhere (Treseder 2004, Johnson 2010). However, arbuscular mycorrhizae can enhance plant water status (Delavaux et al. 2017); therefore, it is possible that trees maintained investment in their fungal symbionts to promote water rather than nutrient uptake. If our results can be generalized to other tropical dry forests (which we admit is speculative), this would imply a fundamental difference between how wet forests vs. seasonally dry, water-limited forests respond to nutrient addition.

The ratio of above- vs. belowground productivity was also jointly controlled by water and nutrient availability. Because P addition increased root biomass, but had no effect on wood or leaf production, AGB:BGB was significantly lower in the +P and +NP treatments. The strong effect of P addition on stand-level biomass was superimposed over a steady increase in AGB:BGB through time. This increase in allocation to aboveground productivity may reflect ongoing forest recovery from the severe drought in 2015, when trees presumably directed more resources to acquisition of water belowground. These patterns echo those observed at the pan-tropical scale: across broad climatic gradients, AGB:BGB ratios of individual trees are positively correlated with precipitation (Waring and Powers 2017).

Functional group and species responses

Our data provide clear evidence that plant functional traits mediate their responses to nutrient fertilization. Even though we found no overall response of aboveground productivity to fertilization, woody growth of N-fixing legumes was strongly enhanced by P addition. This response can be explained from a stoichiometric perspective (e.g., Batterman et al. 2013), as observed increases in stand-scale nodulation under P addition suggest that N-fixing trees leverage added P to enhance N fixation and growth. We also found preliminary evidence for species-specific responses to nutrients. Although fertilization did not significantly affect woody growth within any single taxon, there are trends towards divergent responses among the four most common species in our plots. Highly species-specific responses to nutrients have been observed across many tropical fertilization experiments (e.g., Chou et al. 2018). For example, in a wet tropical forest, P addition doubled growth rates of a common palm, but had no effect on wood production of the dominant tree species, *Pentaclethra macroloba* (Alvarez-Clare et al. 2013). Even subtropical tree species within the same genus (*Eucalyptus*) exhibited highly divergent responses to N and P addition in a shadehouse experiment (Wooliver et al. 2017). These

data are consistent with an emerging picture of nutrient limitation in tropical forests, where weak responses to nutrient availability at the stand or community scale mask heterogeneous and contrasting responses of individual species within communities (Chou et al. 2018, Turner et al. 2018). When plant species exhibit opposing growth responses to nutrient availability, high species turnover can effectively buffer variation in NPP along steep gradients of soil fertility (Turner et al. 2018). Presumably, these contrasting species-specific growth responses could also occur within a single site, precluding a stand-level biomass increase following fertilization. Ultimately, because plant species or functional groups may have different stoichiometric requirements, the concept of a single “limiting nutrient” may not be meaningful for such a diverse plant community.

The role of nutrients in mediating ecosystem carbon cycling in tropical dry forest

The responses of this seasonally dry forest to fertilization have implications for our understanding of coupled biogeochemical cycles across the tropical forest biome. First, even over this relatively short study interval, it is obvious that NPP is mediated by precipitation as well as nutrients. Water limitation of plant growth is widespread across tropical forests, even in wet forests where there are no pronounced dry seasons (Clark et al. 2010, Vasconcelos et al. 2012, Condit et al. 2013, Fisher et al. 2018). The duration of this study was not sufficient to tease apart the effects of dry season length, dry season intensity, and total rainfall on plant nutrient uptake and growth. However, it is clear that forest responses to nutrients must be interpreted in the context of interannual variation in rainfall: nutrients do not appear to boost overall productivity when water is also limiting.

Next, our data suggest that the response of the plant C sink to nutrients is highly dependent on plant community composition. Our data clearly show that the growth of N-fixing trees is stimulated by P addition; therefore, the extent to which phosphorus enhances stand-level productivity is dependent on the relative abundance of legumes. Meanwhile, growth of the most common species at our site (*G. ulmifolia*) was most sensitive to N, a response which may have underpinned enhanced relative woody growth in the +N and +NP treatments in the year following the extreme drought. Identifying the plant traits that mediate variation in responses to nutrients is a critical next step toward predicting ecosystem-scale productivity along gradients of soil fertility or in response to nutrient inputs.

Finally, our study revealed that nutrient fertilization may shift plant biomass allocation, even in the absence of overall increases in productivity, with the potential for additional direct or indirect effects on other ecosystem processes. For example, increased root allocation under P fertilization may have longer-term implications for ecosystem carbon balance. On one hand, increases in

root exudation can prime the decomposition of stable soil C (Dijkstra and Cheng 2007, Pausch and Kuzakov 2017); on the other, it is increasingly recognized that soil organic matter itself is predominantly derived from roots (Rasse et al. 2005, Jackson et al. 2017). Although the net effects of increased root production on the terrestrial C sink are unclear, it is likely that changes in plant biomass allocation will have longer-term impacts on ecosystem biogeochemical cycles.

CONCLUSIONS

In this highly seasonal tropical dry forest, P addition strongly increased fine root growth, possibly as a mechanism to enhance plant water uptake, whereas N had subtle effects on patterns of aboveground productivity. The asymmetry in the strength of above- vs. belowground responses led to a shift in stand-level plant biomass allocation, which may have longer-term impacts on biogeochemical cycles and the strength of the forest C sink. Although in general plant growth appeared to be more sensitive to drought stress than nutrient availability, there is evidence that specific plant species and functional groups—notably N-fixing legumes—respond more strongly to P fertilization. Therefore, our results highlight that the relationship between the plant C sink and nutrient availability will depend on the identity and relative abundance of the tree species present, as well as climatic factors. For diverse tropical forests, identifying the functional traits that dictate species’ responses to nutrients is critical for forecasting ecosystem responses to altered belowground resource availability.

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LITERATURE CITED

- Alfaro, E. A., A. Alvarado, and A. Chaverri. 2001. Cambios edaficos asociados a tres etapas sucesionales de bosque tropical seco en Guanacaste, Costa Rica. *Agronomía Costarricense* 25:7–20.
- Alvarez-Clare, S., M. Mack, and M. Brooks. 2013. A direct test of nitrogen and phosphorus limitation to net primary productivity in a lowland tropical wet forest. *Ecology* 94:1540–1551.
- Baez, S., and J. Homeier. 2017. Functional traits determine tree growth and ecosystem productivity of a tropical montane forest: Insights from a long-term nutrient manipulation experiment. *Global Change Biology* 24:399–409.
- Batterman, S. A., N. Wurzburger, and L. O. Hedin. 2013. Nitrogen and phosphorus interact to control tropical symbiotic N₂ fixation: a test in *Inga punctata*. *Journal of Ecology* 101:1400–1408.

- Bloom, A., F. S. Chapin III, and H. A. Mooney. 1985. Resource limitation in plants: an economic analogy. *Annual Review of Ecology and Systematics* 16:363–392.
- Bonan, G. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320:1444.
- Bonan, G. B., and S. Levis. 2010. Quantifying carbon–nitrogen feedbacks in the community land model (CLM4). *Geophysical Research Letters* 37:L07401.
- Chave, J. et al. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* 20:3177–3190.
- Chou, C. B., L. O. Hedin, and S. W. Pacala. 2018. Functional groups, species, and light interact with nutrient limitation during tropical rainforest sapling bottleneck. *Journal of Ecology* 106:157–167.
- Clark, D., D. Clark, and S. Oberbauer. 2010. Annual wood production in a tropical rain forest in NE Costa Rica linked to climatic variation but not to increasing CO₂. *Global Change Biology* 16:747–759.
- Cleveland, C., and D. Liptzin. 2007. C:N:P stoichiometry in soil: is there a ‘Redfield ratio’ for the microbial biomass? *Biogeochemistry* 85:235–252.
- Cleveland, C. et al. 2011. Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. *Ecology Letters* 14:939–947.
- Condit, R., B. Engelbrecht, D. Pino, R. Pérez, and B. 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* 110:5064–5068.
- Crews, T. et al. 1995. Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* 76:1407–1424.
- Danger, M., T. Daufresne, F. Lucas, S. Pissard, and G. Lacroix. 2008. Does Liebig’s law of the minimum scale up from species to communities? *Oikos* 117:1741–1751.
- Delavaux, C. S., L. M. Smith-Ramesh, and S. E. Kuebbing. 2017. Beyond nutrients: a meta-analysis of the diverse effects of arbuscular mycorrhizal fungi on plants and soils. *Ecology* 98:2111–2119.
- Dijkstra, F. A., and W. Cheng. 2007. Interactions between soil and tree roots accelerate long-term soil carbon decomposition. *Ecology Letters* 10:1046–1053.
- Doane, T., and W. Horváth. 2003. Spectrophotometric determination of nitrate with a single reagent. *Analytical Letters* 36:2713–2722.
- Eamus, D. 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology and Evolution* 14:11–16.
- Espeleta, J. F., and D. A. Clark. 2007. Multi-scale variation in fine-root biomass in a tropical rain forest: a seven-year study. *Ecological Monographs* 77:377–404.
- Farrior, C., et al. 2013. Resource limitation in a competitive context determines complex plant responses to experimental resource additions. *Ecology* 94:2505–2517.
- Fernández-Martínez, M. et al. 2014. Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change* 4:471–476.
- Fisher, R. A. et al. 2018. Vegetation demographics in earth system models: A review of progress and priorities. *Global Change Biology* 24:35–54.
- Gei, M. G. et al. 2018. Legume abundance along successional and rainfall gradients in Neotropical forests. *Nature Ecology and Evolution* 2:1104–1111.
- Graham, E. A., S. S. Mulkey, K. Kitajima, N. G. Phillips, and S. J. Wright. 2003. Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences* 100:572–576.
- Hayward, J., and T. R. Horton. 2014. Phylogenetic trait conservation in the partner choice of a group of ectomycorrhizal trees. *Molecular Ecology* 23:4886–4898.
- Hietz, P. et al. 2011. Long-term change in the nitrogen cycle of tropical forests. *Science* 334:664–666.
- Houlton, B., Y.-P. Wang, P. Vitousek, and C. Field. 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature* 454:327–330.
- Jackson, R. B. et al. 2017. The ecology of soil carbon: Pools, vulnerabilities, and biotic and abiotic controls. *Annual Review of Ecology Evolution and Systematics* 48:419–445.
- Jeannotte, R., D. W. Sommerville, C. Hamel, and J. K. Whalen. 2004. A microplate assay to measure soil microbial biomass phosphorus. *Biology and Fertility of Soils* 40:201–205.
- Johnson, N. 2010. Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. *New Phytologist* 185:631–647.
- Jordan, C. F., and R. Herrera. 1981. Tropical rain forests: Are nutrients really critical? *American Naturalist* 117:167–180.
- Kaspari, M., S. P. Yanoviak, R. Dudley, M. Yuan, and N. A. Clay. 2009. Sodium shortage as a constraint on the carbon cycle in an inland tropical rainforest. *Proceedings of the National Academy of Sciences* 106:19405–19409.
- Koske, R., and J. Gemma. 1989. A modified procedure for staining roots to detect VA mycorrhizas. *Mycological Research* 92:486–488.
- McGonigle, T., M. Miller, D. Evans, G. Fairchild, and J. Swan. 1990. A new method which gives an objective measure of colonization of roots by vesicular–arbuscular mycorrhizal fungi. *New Phytologist* 115:495–501.
- Murphy, P. G., and A. E. Lugo. 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17:67–88.
- Pausch, J., and Y. Kuzyakov. 2017. Carbon input by roots into the soil: Quantification of rhizodeposition from root to ecosystem scale. *Global Change Biology* 24:1–12.
- Phillips, R., E. Brzostek, and M. Midgley. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytologist* 199:41–51.
- Poorter, H. et al. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* 193:30–50.
- Powers, J. S., and E. Marín-Spiotta. 2017. Ecosystem processes and biogeochemical cycles in secondary tropical forest succession. *Annual Review of Ecology Evolution and Systematics* 48:497–519.
- Powers, J., and P. Tiffin. 2010. Plant functional type classifications in tropical dry forests in Costa Rica: leaf habit versus taxonomic approaches. *Functional Ecology* 24:927–936.
- Powers, J., K. Treseder, and M. Lerdau. 2005. Fine roots, arbuscular mycorrhizal hyphae and soil nutrients in four neotropical rain forests: patterns across large geographic distances. *New Phytologist* 165:913–921.
- Powers, J. S. et al. 2015. Nutrient addition effects on tropical dry forests: a mini-review from microbial to ecosystem scales. *Frontiers in Earth Science* 3:1–8.
- Rasse, D., C. Rumpel, and M.-F. Dignac. 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant and Soil* 269:341–356.
- Reed, S. C., C. C. Cleveland, and A. R. Townsend. 2013. Relationships among phosphorus, molybdenum and free-living nitrogen fixation in tropical rain forests: results from observational and experimental analyses. *Biogeochemistry* 114:135–147.

- Reich, P. B. 2014. The worldwide fast-slow plant economics spectrum: a traits manifesto. *Journal of Ecology* 102:275–301.
- Santiago, L. S. 2015. Nutrient limitation of eco-physiological processes in tropical trees. *Trees* 29:1291–1300.
- Schulte-Uebbing, L., and W. de Vries. 2017. Global-scale impacts of nitrogen deposition on tree carbon sequestration in tropical, temperate, and boreal forests: A meta-analysis. *Global Change Biology* 24:e416–e431.
- Sims, G. K., T. R. Ellsworth, and R. L. Mulvaney. 2003. Micro-scale determination of inorganic nitrogen in water and soil extracts. *Communications in Soil Science and Plant Analysis* 26:303–313.
- Steidinger, B. 2015. Qualitative differences in tree species distributions along soil chemical gradients give clues to the mechanisms of specialization: why boron may be the most important soil nutrient at Barro Colorado Island. *New Phytologist* 206:895–899.
- Sullivan, B. W., S. Alvarez-Clare, S. C. Castle, S. Porder, S. C. Reed, L. Schreeg, A. R. Townsend, and C. C. Cleveland. 2014. Assessing nutrient limitation in complex forested ecosystems: alternatives to large-scale fertilization experiments. *Ecology* 95:668–681.
- Tiruvaimozhi, Y. V., V. Varma, and M. Sankaran. 2018. Nitrogen fixation ability explains leaf chemistry and arbuscular mycorrhizal responses to fertilization. *Plant Ecology* 219:391–401.
- Townsend, A. R., and G. P. Asner. 2013. Multiple dimensions of resource limitation in tropical forests. *Proceedings of the National Academy of Sciences* 110:4864–4865.
- Townsend, A. R., C. C. Cleveland, G. P. Asner, and M. M. C. Bustamante. 2007. Controls over foliar N:P ratios in tropical rain forests. *Ecology* 88:107–118.
- Treseder, K. 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO₂ in field studies. *New Phytologist* 164:347–355.
- 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.
- Vance, E., P. Brookes, and D. Jenkinson. 1987. An extraction method for measuring soil microbial biomass C. *Soil Biology and Biochemistry* 19:703–707.
- Vasconcelos, S. S., D. J. Zarin, M. M. Araujo, and I. D. Miranda. 2012. Aboveground net primary productivity in tropical forest regrowth increases following wetter dry-seasons. *Forest Ecology and Management* 276:82–87.
- Walker, T., and J. Syers. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15:1–19.
- Waring, B. G., and J. S. Powers. 2017. Overlooking what is underground: Root:shoot ratios and coarse root allometric equations for tropical forests. *Forest Ecology and Management* 385:10–15.
- Waring, B. G., R. Adams, S. Branco, and J. S. Powers. 2016a. Scale-dependent variation in nitrogen cycling and soil fungal communities along gradients of forest composition and age in regenerating tropical dry forests. *New Phytologist* 209:845–854.
- Waring, B. G., M. G. Gei, L. Rosenthal, and J. S. Powers. 2016b. Plant–microbe interactions along a gradient of soil fertility in tropical dry forest. *Journal of Tropical Ecology* 32:314–323.
- Werden, L. K., J. P. Alvarado, S. Zarges, M. E. Calderón, E. M. Schilling, L. M. Gutiérrez, and J. S. Powers. 2018. Using soil amendments and plant functional traits to select native tropical dry forest species for the restoration of degraded Vertisols. *Journal of Applied Ecology* 55:1019–1028.
- Wieder, W., C. Cleveland, and W. Smith. 2015. Future productivity and carbon storage limited by terrestrial nutrient availability. *Nature Geoscience* 8:441–444.
- Wooliver, R. C. et al. 2017. Phylogeny is a powerful tool for predicting plant biomass responses to nitrogen enrichment. *Ecology* 98:2120–2132.
- 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.
- Wurzburger, N., and S. J. Wright. 2015. Fine-root responses to fertilization reveal multiple nutrient limitation in a lowland tropical forest. *Ecology* 96:2132–2146.

SUPPORTING INFORMATION

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DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mq62g78>.