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Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest

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Abstract. We maintained a factorial nitrogen (N), phosphorus (P), and potassium (K) addition experiment for 11 years in a humid lowland forest growing on a relatively fertile soil in Panama to evaluate potential nutrient limitation of tree growth rates, fine-litter production, and fine-root biomass. We replicated the eight factorial treatments four times using 32 plots of 40 × 40 m each. The addition of K was associated with significant decreases in stand-level fine-root biomass and, in a companion study of seedlings, decreases in allocation to roots and increases in height growth rates. The addition of K and N together was associated with significant increases in growth rates of saplings and poles (1–10 cm in diameter at breast height) and a further marginally significant decrease in stand-level fine-root biomass. The addition of P was associated with a marginally significant ($P = 0.058$) increase in fine-litter production that was consistent across all litter fractions. Our experiment provides evidence that N, P, and K all limit forest plants growing on a relatively fertile soil in the lowland tropics, with the strongest evidence for limitation by K among seedlings, saplings, and poles.

Key words: Barro Colorado Nature Monument, Panama; fertilization; fine litter; fine roots; nitrogen; nutrient limitation; phosphorus; potassium; tree growth; tropics.

INTRODUCTION

Fertilizers that combine nitrogen (N), phosphorus (P), and potassium (K) are routinely required to maintain agricultural productivity. The role of nutrient limitation is less certain in natural ecosystems for at least two reasons. First, nutrients are recycled through decomposition rather than being removed in harvests. Second, most wild plants tolerate lower nutrient supplies than do most agricultural species. In natural ecosystems, nutrients are supplied by weathering rock, atmospheric deposition, and, in the case of N, biological fixation. All ecosystems lose nutrients through gaseous emission, leaching to groundwater, and overland export to streams and rivers. The potential for nutrient limitation in wild plants reflects the ability of plants to adjust to the local balance of nutrient supply and loss.

The balance of nutrient supply and loss changes as soils age and, in the case of N, with latitude (Walker and

Syers 1976, Vitousek 1984, Vitousek and Sanford 1986, Hedin et al. 2009, Vitousek et al. 2010). Weathering bedrock is the primary source of P and K, and their availability tends to decline as soils age (Walker and Syers 1976, Hedin et al. 2003). In regions of active geological uplift, ongoing erosion continues to supply rock-derived nutrients (Porder et al. 2007). Elsewhere as soils age, long-distance transport in dust and precipitation becomes the principal source of rock-derived nutrients. In contrast, N is largely absent from igneous and metamorphic rock, its primary sources are biological fixation and atmospheric deposition, and its supply initially increases in young soils, reaches maximum levels in moderately weathered soils, and declines in some highly weathered soils as other nutrients come to limit biological N fixation (Vitousek 2004, Lambers et al. 2008, Barron et al. 2009). Some lowland tropical forests sustain levels of N cycling, N losses, N:P ratios in leaves and fine litter, and C:P ratios in fine litter that far exceed levels observed in temperate and boreal forests (Vitousek 1984, McGroddy et al. 2004). A latitudinal gradient in soil age contributes to this trend, with lower N and greater P availability on younger soils initiated by repeated glacial cycles and the widespread deposition of

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glacial dust at higher latitudes (Vitousek and Sanford 1986). In addition, N fixation by heterotrophic bacteria and epiphytes that are decoupled from soil N supplies and up-regulation of biological N fixation by abundant legumes should disturbance reduce N availability are hypothesized to sustain high N losses from N-rich tropical forests (Hedin et al. 2009). For these reasons, supplies of N, P, and K are all likely to be relatively high in N-rich, lowland tropical forests growing in regions of active geological uplift.

Plants adjust to local nutrient availability through changes in species composition, phenotypic plasticity, and adaptation. As an example of changes in species composition, tree species characterized by dense wood and low foliar nutrient concentrations dominate forests on nutrient-poor soils in the geologically stable eastern and central Amazon and tend to be replaced by tree species characterized by lighter wood and larger foliar nutrient concentrations on richer soils influenced by the rapidly eroding Andes in the western Amazon (Fyllas et al. 2009, Patiño et al. 2009). As an example of a likely mix of phenotypic plasticity and local adaptation, widespread Amazonian species tend to have denser wood and lower foliar nutrient concentrations when growing on poorer soils (Fyllas et al. 2009, Patiño et al. 2009). Collectively, these adjustments mediate the potential limitation of primary production by nutrients and are likely to lead to simultaneous limitation by multiple nutrients. Simultaneous limitation can arise through physiological responses that maintain homeostasis at the level of individual plants, limitation of different species by different nutrients at the level of plant communities, and positive feedbacks among nutrient supply rates at the level of ecosystems (Vitousek et al. 2010).

Recent meta-analyses of fertilization experiments are broadly consistent with the hypothesis that multiple nutrients limit plant growth in natural communities. A meta-analysis of 38 potassium fertilization experiments involving 26 forest tree species demonstrates that K addition tends to increase growth rates (69% of studies) and tissue K concentrations (76%; Tripler et al. 2006). A meta-analysis of 126 terrestrial N fertilization experiments demonstrates that N is equally likely to limit aboveground net primary production at all latitudes (LeBauer and Treseder 2008). Finally, a meta-analysis of 173 terrestrial studies that included independent manipulations of N and P or factorial manipulation of N and P demonstrates that N and P tend to co-limit plant biomass or plant productivity (Elser et al. 2007).

Unfortunately, lowland tropical forests are underrepresented in these meta-analyses. There has not been a single K fertilization experiment in a tropical forest. Just five P fertilization experiments and four N fertilization experiments have evaluated community-level responses in lowland tropical forests. Most of these experiments took place in young secondary forests, where reduced organic matter pools limit nutrient availability and rapid

increases in plant biomass sustain high nutrient demand (Campo and Vazquez-Yanes 2004, Davidson et al. 2004). The only fertilization experiments conducted in old-growth, lowland tropical forests are a four-year factorial manipulation of N and P on a relatively infertile soil in Borneo (Mirmanto et al. 1999) and a two-year manipulation of P on a relatively infertile soil in Cameroon (Newbery et al. 2002). We lack a single fertilization experiment that has lasted more than four years in a lowland tropical forest.

For these reasons, we initiated a chronic NPK factorial fertilization experiment in an old-growth tropical forest in the lowlands of Panama in 1998. Here, we report the first 10 to 11 years of responses for fine-root biomass, fine-litter production, and tree growth rates. We evaluate radial growth responses of saplings, poles, and larger trees separately because they experience contrasting light levels, and light availability is likely to limit potential responses to fertilization in shaded plants. We expected the strongest responses for P and K addition in this N-rich forest and for progressively larger trees that experience progressively higher light levels.

METHODS

Study site

The 38.4-ha study site (9°06'31" N, 79°50'37" W) is located on the mainland in the Barro Colorado Nature Monument in the Republic of Panama (Appendix A: Fig. A1). Tree species composition and stature (canopy heights up to 40 m) are characteristic of very old (>200 yr), secondary forest. Aerial photographs confirm the presence of tall forest at the site in 1927 (S. J. Wright, *personal observation*).

Table 1 summarizes concentrations of N, P, and K in bedrock and fine litter and in plant available forms in surface soils (0–10 cm depth) in our control plots. The bedrock is an 85-m thick Miocene basalt (Stewart et al. 1980) and is relatively rich in P (Table 1). Elevation grades from 25 m in the southwest to 61 m in the northeast corner of the study site (Appendix A: Fig. A1). In the FAO classification, the soils are Endogleyic Cambisols and Acric Nitisols in the lower and upper parts of the landscape, respectively (Koehler et al. 2009, who accidentally reverse the position of the soil types). These soil types are widespread in Mesoamerica (IUSS Working Group WRB 2006). Plant available soil nutrient concentrations are representative of forest soils in central Panama (B. L. Turner, *unpublished data*), and soil K concentrations are representative of Mesoamerica (Barthold et al. 2008). Total P and total reserve base concentrations are 600 mg/kg and 97 mmol_c/kg, respectively, for the upper 30 cm of soil (J. B. Yavitt, *unpublished data*). Total P and reserve base concentrations are smaller for >92% and 60% of 63 Amazonian sites (Fyllas et al. 2009), respectively. Soils at the study site are relatively fertile for the lowland tropics.

TABLE 1. Nutrient status in bedrock, fine litter, and surface soils of the study site in the Barro Colorado Nature Monument, Panama.

Element	Bedrock (ppm) [†]	Input in litter (kg·ha ⁻¹ ·yr ⁻¹) [‡]	Concentration in control soils (mg element/kg dry soil) [§]
K	3410	57	84–131
N		180	5.3–5.6 nitrate; 6.2–15.5 ammonium
P	1600	11	1.4–2.2

[†] Mean value for Miocene basalts in the Panama Canal area (C. Jaramillo, *unpublished data*).

[‡] Measured for forest 3 km from our site on Barro Colorado Island (Yavitt et al. 2004).

[§] For samples stored at 2–4°C for 24–48 h and extracted in 2 mol/L KCl for ammonium and nitrate, Mehlich III for the smaller K and P values, Bray 1 for the larger P value, and 1 mol/L NH₄Cl for the larger K value (Yavitt et al. 2009, Sayer and Tanner 2010).

Experimental design

We replicated the eight treatments of a 2 × 2 × 2 factorial NPK experiment four times. We placed the four replicates perpendicular to the 36-m topographic gradient because soil properties (Yavitt et al. 2009) and tree distributions (S. J. Wright, *unpublished data*) parallel the gradient. Within each replicate, we blocked the N, P, K, and NPK treatments vs. the NP, NK, PK, and control treatments (Appendix A: Fig. A1). This balanced, incomplete-block design minimizes uncontrolled error associated with spatial variation, enables evaluation of main effects and two-way interactions, but limits power to evaluate the three-way interaction (Winer 1971). The 32 experimental plots each measured 40 × 40 m. The minimum distance between plots was 40 m, excepting two plots separated by 20 m and a 3 m deep streambed (Appendix A: Fig. A1).

Beginning in 1998, we added fertilizer by hand in four equal doses each wet season with 6–8 weeks between applications (15–30 May, 1–15 July, 1–15 September, and 15–30 October). Nitrogen was added as coated urea ((NH₂)₂CO), P as triple superphosphate (Ca(H₂PO₄)₂·H₂O), and K as potassium chloride (KCl). Annual doses were 125 kg N·ha⁻¹·yr⁻¹, 50 kg P·ha⁻¹·yr⁻¹, and 50 kg K·ha⁻¹·yr⁻¹, which equals 69%, 470%, and 88% of annual inputs from fine litter at a nearby site (3 km), respectively (Table 1). Similar large additions of P relative to annual litter inputs are standard practice in forestry and in previous tropical nutrient addition experiments (Tanner et al. 1992, Mirmanto et al. 1999, Fisher and Binkley 2000) because many soils, including soils at our site, sequester large amounts of added P in forms that are inaccessible to plants (Yavitt et al. 2010). After nine years, N addition had reduced soil pH and base saturation and increased nitrate leaching, N-oxide emissions, and aluminum saturation (Corre et al. 2010).

Tree growth

We measured diameter at breast height (dbh) or just above buttresses for all free-standing woody plants with dbh > 10 cm in the central 30 × 30 m and with dbh ≥ 1 cm in the central 20 × 30 m of each 40 × 40 m plot in 1997, 2000, and 2008 (see Plate 1). All measured trees were > 5 m from the nearest plot boundary. For

analyses of relative growth rates (RGR), we excluded trees with multiple stems, broken stems, and buttresses or other deformities whose growth prevented measurements at the same height in consecutive censuses. The 9551 trees that remained included those that first recruited to the 1-cm dbh minimum size threshold and those that died between 2000 and 2008. We calculated RGR for 1997–2000 and 2000–2008 as $RGR_{i-f} = \log(\text{dbh}_f/\text{dbh}_i)/((\text{DC}_f - \text{DC}_i)/365)$, where DC represents day of century and the subscripts *i* and *f* represent initial and final values, respectively. We performed separate analyses for four tree size classes (1.0 cm ≤ dbh ≤ 2.4 cm, 2.5 cm ≤ dbh ≤ 4.9 cm, 5.0 cm ≤ dbh ≤ 9.9 cm, and dbh ≥ 10 cm) to isolate trees with contrasting levels of shading and to control size-related variation in RGR. Response variables were mean RGR for each plot, census interval, and size class. The median (minimum) number of trees used to calculate RGR for each plot and census interval was 75 (36), 47 (19), 23 (10), and 19 (7) for the smallest to largest size classes, respectively.

Fine-root biomass

We collected soil to 10 cm depth from four (six in 2009) random locations in the central 20 × 20 m of each plot with a 5 cm diameter split-sleeve core in April 2000, November 2008, and April 2009. We washed soils through a 0.5-mm sieve leaving roots and coarse sand. We oven-dried fine (<2 mm diameter) and coarse (2–5 mm) roots to constant mass at 60°C. We performed separate analyses for 0–5 and 5–10 cm depths and for fine roots only because many cores lacked coarse roots. Response variables were mean dry mass for each plot, year, and depth.

Fine-litter production

We randomly located three litter traps in the central 30 × 30 m of each plot on 1 July 1998. The minimum distance between traps was 10 m. Each trap had an effective surface area of 0.58 m² composed of an open bag of 1-mm mesh window screen raised 80 cm above the ground on a PVC frame. We collected litter once each month following the methods of Proctor (1983), oven-dried litter to constant mass at 60°C, and, beginning in November 1998, weighed leaves, wood, reproductive material, and other fine litter or “dust”

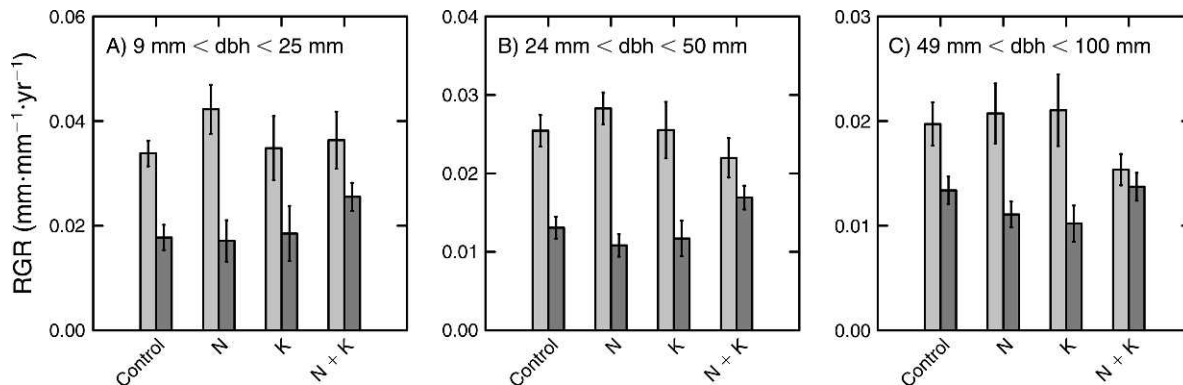


FIG. 1. Tree growth responses to nitrogen (N) and potassium (K) addition for three subcanopy size classes. Each panel illustrates a significant $N \times K \times$ census interaction ($F_{1,18} = 5.45, 8.34,$ and 6.82 ; $P = 0.031, 0.010,$ and 0.018 in panels (A), (B), and (C), respectively). Relative growth rates (RGR) declined significantly from 1997–2000 (light bars) to 2000–2008 (dark bars) for each size class. N plus K addition ameliorated the decline for all three size classes. The full experiment included eight factorial N, K, and phosphorus (P) treatments. P addition had no significant effects on RGR, and the four P addition treatments (P, N + P, K + P, and N + K + P) are pooled with the appropriate treatment without P (control, N, K, and N + K, respectively). Thus, bars represent RGR (mean \pm SE) for eight plots. Above each panel are the diameter at breast height (dbh) limits for the tree size class.

separately. The response variable was mean dry mass production ($\text{Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) for each plot and year. Years extended from 1 November to 31 October.

Aboveground net primary production (ANPP)

We summed fine-litter and wood production to estimate ANPP. To estimate wood production, we estimated the aboveground biomass (AGB) of each tree at each census (1997, 2000, and 2008) using its dbh, wood density ($\text{g dry mass}/\text{cm}^3$ fresh volume) determined for each species (Wright et al. 2010), and the “best predictive equation” for tropical moist forest from Chave et al. (2005). Mean wood density was substituted for six rare species that lacked a wood density measurement. Stand-level wood production equaled the sum of $\text{AGB}_f - \text{AGB}_i$ for trees that survived from census i to census f and the AGB of trees that recruited during the census interval. The response variable was dry mass production of wood plus fine litter ($\text{Mg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) for each plot and year.

Analyses

We performed repeated-measures analyses of variance (ANOVA) for each response variable to control spatial variation among plots and to evaluate temporal variation. Between-subject (henceforth, between-plot) effects evaluate responses over the entire experiment. Within-subject (henceforth, within-plot) effects evaluate variation among years and interactions among treatments and year. A nutrient response that lagged behind the initial addition of nutrients might be insignificant over the entire experiment but lead to a significant treatment \times year interaction. Such lags characterize tree responses to fertilization (Tanner et al. 1992). Repeated-measures ANOVA assumes compound symmetry of the variance-covariance matrix if there are more than two repeated measures. We therefore used the conservative

Greenhouse-Geisser correction for violations of the compound symmetry assumption to evaluate the significance of all within-plot effects for fine-root biomass and fine-litter production, which had three and 11 repeated measures, respectively. All analyses were performed with SYSTAT 11.0 (Richmond, California, USA).

RESULTS

Tree growth

Tree growth rates decreased through time (Figs. 1 and 2). $\text{RGR}_{2000-2008}$ was significantly smaller than $\text{RGR}_{1997-2000}$ for all four tree size classes ($F_{1,18} > 15.0$, $P < 0.001$; Appendix B: Tables B1–B4).

A single consistent response to nutrient addition characterized the three smaller size classes (Fig. 1). The $N \times K \times$ year interaction was significant for each of these size classes ($F_{1,18} = 6.82, 8.34,$ and 5.45 ; $P = 0.018, 0.010,$ and 0.031 ; Appendix B: Tables B2, B3, and B4, respectively). The combined N + K treatment ameliorated the temporal decline in RGR. The pattern of similar growth rates for control, N, K, and combined N + K treatments in the first interval and larger growth rates for the combined N + K treatment in the second interval indicates a positive lagged response to the combined N + K treatment (Fig. 1).

The response of large trees (dbh > 10 cm) to nutrient addition was more complicated (Fig. 2; Appendix B: Table B1). The between-plot, $N \times K$ interaction was marginally significant (Appendix B: Table B1; $F_{1,18} = 4.41$, $P = 0.050$) because RGR was similar for the control and combined N + K treatments but larger for the N and K treatments (Fig. 2B).

The $P \times$ year interaction was also significant for large trees (Fig. 2C; $F_{1,18} = 7.95$, $P = 0.011$; Appendix B: Table B1); however, the pattern of growth rates underlying this interaction is inconsistent with a positive response to P addition. Added P appears to have depressed

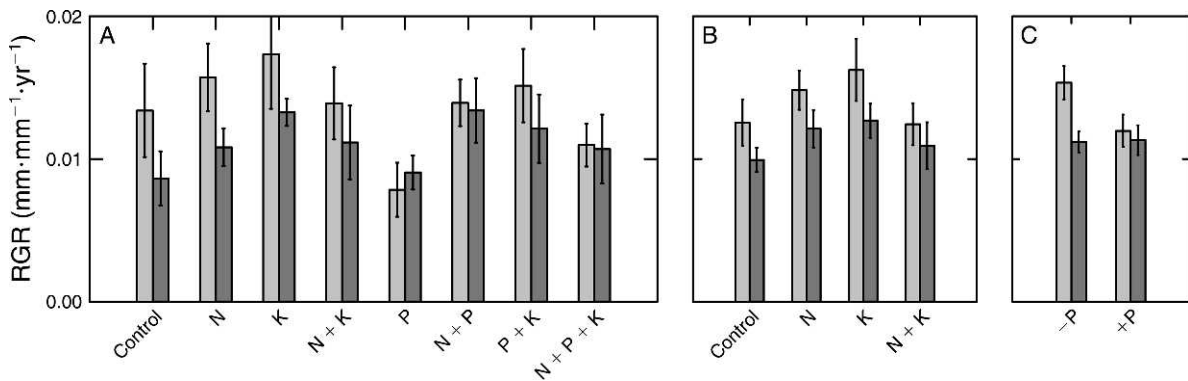


FIG. 2. Growth responses of large trees (>10 cm dbh) to phosphorus (P), nitrogen (N), and potassium (K) addition. Relative growth rates (RGR) declined significantly from 1997–2000 (light bars) to 2000–2008 (dark bars). Panel (A) presents the eight treatments in the full factorial NPK design, and bars represent RGR (mean \pm SE) for four plots. Panel (B) presents the marginally significant $N \times K$ interaction ($F_{1,18} = 4.41$, $P = 0.050$). The P addition treatments (P, N + P, K + P, and N + K + P) are pooled with the appropriate treatment without P (control, N, K, and N + K, respectively), and bars represent RGR (mean \pm SE) for eight plots. Panel (C) presents the significant $P \times$ census interaction ($F_{1,18} = 7.95$, $P = 0.011$). The four P addition treatments (P, N + P, K + P, and N + K + P) are pooled, the four treatments without P (control, N, K, and N + K) are pooled, and bars represent RGR (mean \pm SE) for 16 plots.

RGR_{1997–2000} and to have had no effect on RGR_{2000–2008} (Fig. 2C). The arrangement of treatments in Fig. 2A also illustrates the effect of added P. The control, N, K, and combined N + K treatments are arranged from left to right first without and then with added P (Fig. 2A). Added P did not increase tree growth rates.

Fine-root biomass

Fine-root biomass in surface soils (0–5 cm depth) varied significantly with K addition. The addition of K was associated with a significant reduction in fine-root biomass (Fig. 3A; $F_{1,18} = 9.69$, $P = 0.006$; Appendix B: Table B5). The $N \times K \times$ year interaction was also marginally significant ($F_{2,36} = 3.22$, $P = 0.064$; Appendix B: Table B5), with fine-root biomass in surface soils reduced in one year with N addition alone, in two years with K addition alone, and in all three years with combined NK addition (Fig. 3B). Fine-root biomass in subsurface soils (5–10 cm depth) was unaffected by nutrient additions (Appendix B: Table B6).

Fine-root biomass also varied significantly among years. Fine-root biomass was approximately twice as large in April 2000 as in November 2008 and April 2009 (Fig. 3B; Appendix B: Tables B5 and B6). Similar large temporal variation in fine-root biomass has been observed previously in a nearby forest (Cavelier et al. 1999).

Fine-litter production

There was a marginally significant increase in fine-litter production with P addition (Fig. 4A; $F_{10,180} = 4.10$, $P = 0.058$; Appendix B: Table B7). We also examined the four fractions that comprise fine-litter production separately (Fig. 4B–E). The mean level of production was larger where P was added and smaller where P was not added for 39 of the 44 combinations of year and

litter fraction (Fig. 4B–E). Two of the five exceptions were for the first year of the experiment (Fig. 4D–E). The three remaining exceptions were for reproductive structures (Fig. 4C). Reproductive output varies widely in space and time in central Panama (Wright et al. 2005). As an example, the coefficient of variation (SD/mean) of annual production (averaged over the 32 experimental plots) was 250% to 500% greater for reproductive structures (0.203) than for total fine litter (0.040), leaf litter (0.055), or small branches (0.080). It is not surprising that the spatial and temporal variation in reproductive output sometimes overwhelmed the effect of added P. The consistent increase in the three remaining fractions of fine-litter production after the first year of P addition (30 out of 30; Fig. 4B, D, and E) suggests that the marginally significant effect of P addition on total fine-litter production is real.

Aboveground net primary production (ANPP)

ANPP averaged 14.7 ± 4.0 Mg·ha⁻¹·yr⁻¹ (mean \pm SD). This included 11.4 ± 3.2 and 4.2 ± 2.7 Mg·ha⁻¹·yr⁻¹ of fine-litter and wood production, respectively. There were no significant effects of nutrient treatments for ANPP (Appendix B: Table B8); however, we have little confidence in our plot-level estimates of wood production and hence ANPP. Our plot-level estimates of wood production were highly variable. As an example, the overall coefficient of variation (SD/mean) for plots was 0.64 and 0.28 for wood and fine-litter production, respectively. We believe our plots are too small to estimate wood production accurately because just 3% of the trees larger than 10 cm dbh account for 50% of the aboveground biomass (Muller-Landau et al. 2006) and a similar percentage of wood production in mature forests in central Panama. Our effective plot size was just 0.09 ha because trees were not

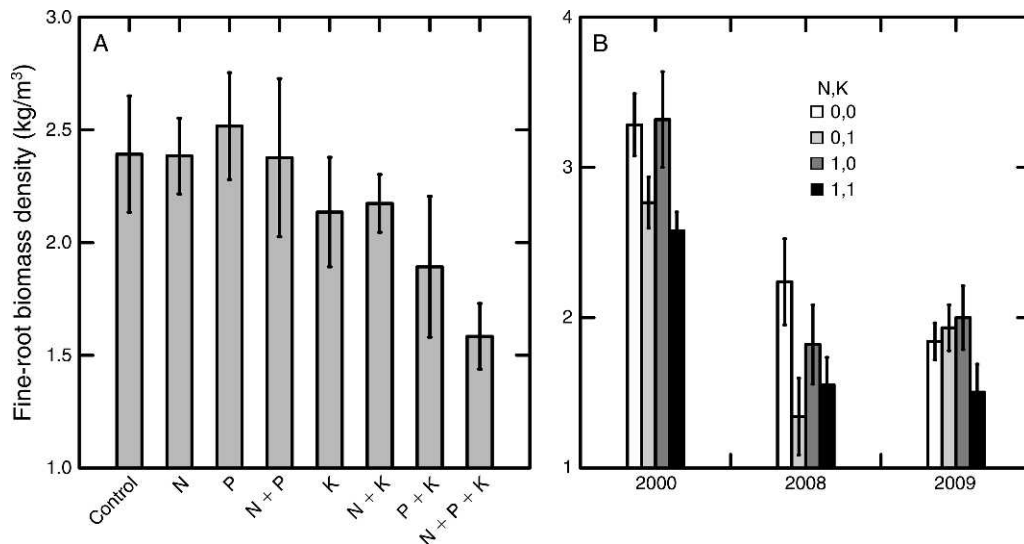


FIG. 3. Fine-root biomass responses to nutrient addition for surface soils (0–5 cm depth). Panel (A) presents the eight treatments in the factorial NPK design. The four treatments with K addition are to the right to illustrate the significant effect of K addition ($F_{1,18} = 9.69$, $P = 0.006$). Bars represent values (mean \pm SE) for four plots and three years. Panel (B) isolates the marginally significant $N \times K \times \text{year}$ interaction ($F_{2,36} = 3.22$, $P = 0.064$). The inset key matches the shading of the bars with the four factorial combinations of N and K, where 1's and 0's represent plots where N or K were added or not added, respectively. P addition had no significant effects on fine-root biomass, and the four P addition treatments (P, N + P, K + P, and N + K + P) are pooled with the appropriate treatment without P (control, N, K, and N + K, respectively). Bars represent values (mean \pm SE) for eight plots in panel (B).

measured in a 5-m fertilized buffer. A plot of 0.09 ha might or might not contain a large tree, and this ensured highly variable plot-level estimates of wood production. We do not mention ANPP again.

DISCUSSION

The addition of N, P, and K increased concentrations of the same nutrient in soils, leaves, and fine litter in an old-growth, lowland tropical forest growing on a relatively fertile soil in Panama (Table 2). Experimental increases in tissue concentrations might represent luxury consumption or might enable additional plant responses if nutrients limit plant function. We evaluated community-level responses to nutrient addition including fine-root biomass, fine-litter production, and tree growth rates.

Relative growth rates (RGR) declined significantly during the 11-year study (Figs. 1 and 2; Appendix B: Tables B1–B4). This is the fourth tropical forest for which a decadal trend toward slower tree growth rates has been observed (Feeley et al. 2007, Clark et al. 2010). Possible mechanisms include rising temperatures and temperature-dependent respiration rates and/or temperature-dependent photosynthetic rates, increasing abundance of competing woody vines, increasing competition among trees in the final stages of secondary succession, natural decadal climate variation, and cumulative effects of trampling (Wright 2010). Regardless of its cause, slowing tree growth rates affect the interpretation of responses to nutrient addition. A positive response to nutrient addition that lags behind the initial application

of nutrients might be expressed as a relatively small decline in RGR and not as an increase in RGR. We performed repeated-measures analyses with repeated measures on census intervals to evaluate temporal variation in each response variable and possible lagged responses to nutrient addition.

Responses to phosphorus addition

It is widely hypothesized that P limits primary production on highly weathered tropical soils (see *Introduction*; Vitousek 1984, Lambers et al. 2008, Hedin et al. 2009). Six P fertilization experiments have now been conducted in lowland tropical forests. Three of the six took place in young secondary forests (Campo and Vazquez-Yanes 2004, Davidson et al. 2004), where relatively small organic matter pools limit nutrient availability, rapid biomass accumulation provides a strong nutrient sink, and nutrient limitation is to be expected regardless of soil weathering status. Not surprisingly, tree growth rates and/or fine-litter production increased after 3–4 years of P addition in these 4-, 12-, and 60-year-old secondary forests (Campo and Vazquez-Yanes 2004, Davidson et al. 2004).

The three remaining P addition experiments took place in old-growth forests and provide an opportunity to evaluate the hypothesis that P limits tree growth and fine-litter production in mature lowland, tropical forests. The three experiments took place on soils with total P concentrations of 80 mg P/kg (upper 10 cm; Mirmanto et al. 1999), 277 mg P/kg (average of upper 5 cm and 15–20 cm; Newbery et al. 2002), and 484 mg P/kg (upper 15

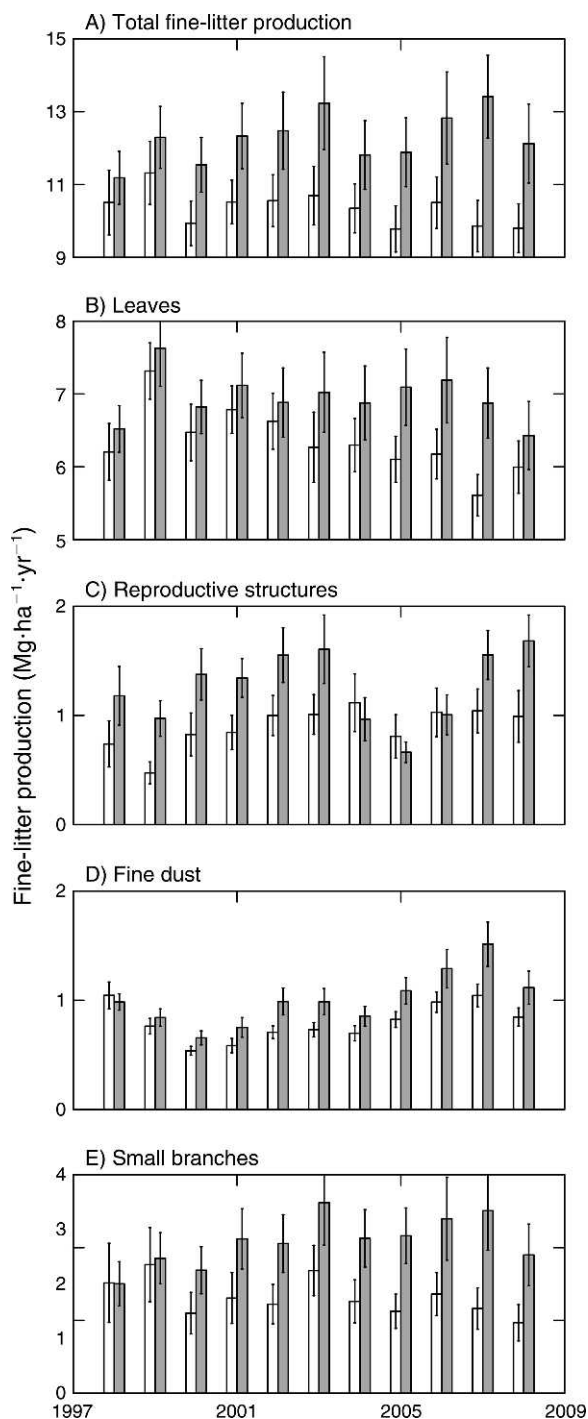


FIG. 4. Responses to phosphorus (P) addition for total fine-litter production (panel A, $F_{1,18} = 4.10$, $P = 0.058$) and its four fractions (panels B–E) over 11 years. Solid and open bars represent pooled treatments with and without added P, respectively. The four litter fractions are (B) leaves, (C) reproductive structures, (D) fine material or dust, and (E) twigs and small branches. The addition of N and K had no significant effects. Therefore, the four P addition treatments (P, N + P, K + P, and N + K + P) are pooled, the four treatments without P (control, N, K, and N + K) are pooled, and each bar represents production (mean \pm SE) for 16 plots.

cm, see *Results*; Yavitt et al. 2010). P addition had no significant effect on tree growth at any of these sites. At the low-P site, fine-litter production averaged 25% greater with P addition than in controls just 8–20 months after the first P application (Mirmanto et al. 1999). At the intermediate-P site, there was no significant effect on fine-litter production; however, fine litter was measured for just one month \sim 2.5 years after the initial P application and 0.5 years after the final P application (Newbery et al. 2002). Finally at our high-P site, fine-litter production averaged 25% greater with P addition than in controls for years eight through 11 after the first P application (Fig. 4A). The obvious conclusion is that more and longer P fertilization experiments will be required before generalization is possible. In the meantime, the evidence that P limits fine-litter production at a P-poor site in Borneo and a relatively P-rich site in Panama suggests that P is likely to limit plant production in many tropical forests.

Responses to nitrogen addition

It is widely hypothesized that N is available in excess of plant demand in lowland tropical forest soils (see *Introduction*; Vitousek 1984, Hedin et al. 2009). LeBauer and Treseder (2008) rejected this hypothesis and concluded that N limitation was equally strong for temperate and tropical forests. Their conclusion is based on a meta-analysis of N addition experiments that included 15 tropical forest experiments; however, just four of these 15 experiments took place in the lowlands. The remaining 11 experiments took place in montane forests. The N cycles and C:N ratios of fine litter in montane tropical forests are similar to those in temperate forests (Vitousek 1984, Tanner et al. 1998, Hedin et al. 2009). Montane forests should therefore be excluded to evaluate the hypothesis that N is available in excess of plant demand in lowland tropical forests. In addition, three of the four lowland experiments evaluated by LeBauer and Treseder (2008) were conducted in

TABLE 2. Increases (%) with nutrient addition in concentrations of the added nutrient for soils, fine litter, and sun-exposed canopy leaves.

Element	Increase with addition of same nutrient (%)		
	Soil [†]	Fine litter [‡]	Canopy leaves [§]
K	24	16	18
N	47	7	5
P	34	27	38

[†] For samples stored at 2–4°C for 24–48 h and extracted in 2 mol/L KCl for ammonium and nitrate, Bray's P1 solution for P, and 1 mol/L NH₄Cl for K. The value for N refers to nitrate; ammonium was unaffected (Koehler et al. 2009, Yavitt et al. 2010).

[‡] Kaspari et al. (2008).

[§] Mean value for one individual of each of three species for each 40 \times 40 m plot. The increase for N is only marginally significant ($P = 0.087$).

young secondary forests, where nutrient limitation is expected as previously discussed (see *Discussion: Responses to phosphorus addition*).

Just two N fertilization experiments have evaluated community-level responses in old-growth, lowland tropical forests (Mirmanto et al. 1999; see *Results*). Fine-litter production increased significantly with N addition just 8–20 months after the first N application in Borneo (Mirmanto et al. 1999). In contrast in our experiment, N alone had no significant effects on fine-root biomass, fine-litter production, and tree growth rates; however, the combined addition of N and K was associated with a significant increase in the growth rates of the three smaller size classes of trees (Fig. 1) and a marginally significant reduction in fine-root biomass (Fig. 3B).

Co-limitation by N and K is indicated, especially for sapling and pole-sized trees. Thus, the two experiments conducted in mature, lowland tropical forests suggest limitation by N (Mirmanto et al. 1999) or co-limitation by N and K (see *Results*). The hypothesis that N is available in excess of plant demand in mature lowland tropical forests is not supported.

Responses to potassium addition

In contrast to N and P, the possibility that K might limit tropical forest plants has been entirely overlooked and there are no prior K addition experiments from lowland tropical forests to compare with our results (Tripler et al. 2006). This is surprising because K, like P, is derived from rock and monovalent K^+ ions are particularly prone to leaching losses in the humid tropics (Veldkamp et al. 1990, Hedin et al. 2003). In our experiment, K addition decreased fine-root biomass (Fig. 3A), increased fine-root turnover (Yavitt et al. 2010), decreased seedling allocation to roots, increased seedling height growth rates (L. Santiago, *unpublished data*), and when combined with N addition increased growth rates of smaller trees (Fig. 1). Limitation by K is clearly indicated. The possibility that K might limit plants in tropical forests deserves greater attention.

The mechanism linking K addition to root dynamics is unclear. In the laboratory, K-deficient plants are unable to increase allocation to root growth because K^+ is required to load sucrose into the phloem, and K deficiency impedes sucrose export from leaves to support increased allocation to roots (Hermans et al. 2006). Nonetheless, the addition of K was associated with strong and consistent changes in root dynamics in our experiment. These included significant decreases in seedling allocation to roots (L. Santiago, *unpublished data*) and in stand-level fine-root biomass detected with both root cores and minirhizotrons (Fig. 3A; Yavitt et al. 2010). Allocation shifted away from roots with K addition. The discrepancy with laboratory experiments (Hermans et al. 2006) suggests unknown links between root allocation and K availability.



PLATE 1. Most mature tropical forests include a small number of very large trees. These largest trees make disproportionate contributions to stand-level wood production, and their rarity introduces large variation in wood production among our experimental plots. Three technicians are required to measure the diameter of the largest trees above buttresses and other deformities of the lower trunk. The photograph shows a canopy emergent *Cavanillesia platanifolia* (Bonpl.) Kunth being measured above the swollen lower trunk characteristic of many species in the family Bombacaceae. Photo credit: Marcos Guerra, STRI.

CONCLUSIONS

After 11 years of chronic nutrient addition, our experiment provides evidence for co-limitation of plants growing on a relatively fertile lowland tropical forest soil by N, P, and K. The addition of K reduced fine-root biomass at the community level, reduced allocation to roots in seedlings, and increased seedling height growth rates. The simultaneous addition of K plus N increased growth rates of small saplings and pole-sized trees. And, the addition of P increased fine-litter production, which is dominated by large trees and lianas. Thus, there is also a suggestion that different nutrients limit different forest strata and/or plants of different sizes.

Clearly many more fertilization experiments must be conducted in mature, lowland tropical forests before the hypothesis that P limits primary production while N is available in excess of plant demand on moderately to

highly weathered tropical soils can be fully evaluated (Vitousek 1984, Vitousek and Sanford 1986, Hedin et al. 2009). In the meantime, the three fertilization experiments that evaluated community-level responses in mature, lowland tropical forests (Mirmanto et al. 1999, Newbery et al. 2002; see *Results*) suggest that N ($N = 2$ out of two experiments), P ($N = 2$ out of three experiments), and a second rock-derived nutrient, K ($N = 1$; see *Results*) limit plant growth and/or fine-litter production. These results and long-standing observations that nutrients other than N, P, and K influence plant function and plant distributions in lowland tropical forests (e.g., Baillie et al. 1987, Cuevas and Medina 1988) suggest that the full range of nutrients that might limit plants in lowland tropical forests should now be considered.

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APPENDIX A

Maps showing the location of the study site, its topography, and locations of each experimental plot (*Ecological Archives* E092-136-A1).

APPENDIX B

ANOVA tables for the factorial, incomplete block design for the eight response variables analyzed in this article (*Ecological Archives* E092-136-A2).

SUPPLEMENT

All data sets analyzed in this article (*Ecological Archives* E092-136-S1).