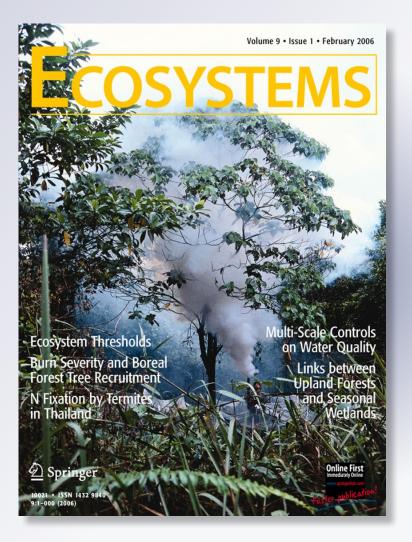# *Variable Responses of Lowland Tropical Forest Nutrient Status to Fertilization and Litter Manipulation*

Emma J. Sayer, S. Joseph Wright, Edmund V. J. Tanner, Joseph B. Yavitt, Kyle E. Harms, Jennifer S. Powers, Michael Kaspari, Milton N. Garcia, et al.

Volume 9 • Issue 1 • February 2006

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Variable Responses of Lowland Tropical Forest Nutrient Status to Fertilization and Litter Manipulation

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ABSTRACT

Predicting future impacts of anthropogenic change on tropical forests requires a clear understanding of nutrient constraints on productivity. We compared experimental fertilization and litter manipulation treatments in an old-growth lowland tropical forest to distinguish between the effects of inorganic nutrient amendments and changes in nutrient cycling via litterfall. We measured the changes in soil and litter nutrient pools, litterfall, and fine root biomass in plots fertilized with nitrogen (N), phosphorus (P), or potassium (K), and in litter addition and litter removal treatments during 7 years. Soil inorganic N and litter N increased in double-litter plots but not in N-fertilized plots. Conversely, litter P and soil pools of P and K increased in fertilized plots but not in the double-litter plots. Soil and litter pools of N and K decreased in the no-litter plots.

Changes in litterfall with added nutrients or litter were only marginally significant, but fine root biomass decreased with both the litter and the K addition. Differences between the two experiments are mostly attributable to the coupled cycling of carbon and nutrients in litter. Increased nutrient inputs in litter may improve plant uptake of some nutrients compared to fertilization with similar amounts. The litter layer also appears to play a key role in nutrient retention. We discuss our findings in the context of possible impacts of anthropogenic change on tropical forests.

Key words: nutrient limitation; Panama; litter addition; litter removal; nitrogen; phosphorus; potassium; litterfall; soil nutrients; fine root biomass.

INTRODUCTION

Tropical forest growth currently represents the largest terrestrial sink for anthropogenic CO_2 emissions but forest productivity under rising atmospheric CO_2 may eventually become constrained by nutrient availability (Oren and others 2001; Beedlow and others 2004). Enhanced forest

growth not only alters forests' nutrient demands but also alters nutrient cycles through greater inputs of organic matter and indirect effects on microbial processes and soil chemistry (Sayer 2006). At the same time, human activities are rapidly increasing the atmospheric nutrient deposition across the globe (Galloway and others 2004; Phoenix and others 2006). Recent research has shown that anthropogenic nitrogen (N) deposition in particular is increasing dramatically in tropical regions (Galloway and others 2004; Hietz and others 2011) and phosphorus (P) deposition may already play an important role as a source of P in tropical regions (Okin and others 2004). It has been proposed that atmospheric nutrient deposition may, to some extent, alleviate nutritional constraints on increased growth under elevated CO_2 (Beedlow and others 2004). However, large inputs of specific nutrients (such as reactive N) can change the stoichiometric ratios of nutrients in plant matter, which causes nutrient imbalances in plants (Vitousek and others 1997), alters decomposition processes (Güsewell 2004), and can result in deficiencies of other elements (Loladze 2002).

Despite the importance of tropical forests in global biogeochemical cycles, there remain major knowledge gaps in our understanding of tropical forest nutrient cycling. This confounds attempts to predict the effects of anthropogenic change on tropical forest nutrient cycling and carbon sequestration. The maintenance of productive forests with large biomass on seemingly infertile soils is one such conundrum. This apparent paradox can be attributed in part to the major difficulties in assessing nutrient availability to plants. For example, lowland tropical forests are thought to have a large pool of soil N owing to N accumulation from biological fixation and atmospheric deposition during the course of soil development (Robertson and Vitousek 1981). In contrast, P is mainly derived from the weathering of parent material during the initial stages of soil development, and the size of the available soil P pool decreases over time due to erosion, leaching (Walker and Syers 1976), sorption to secondary soil minerals, and incorporation into organic compounds (for example, Turner and Engelbrecht 2011). Consequently, lowland tropical forests on old, highly weathered soils are generally thought to be rich in N but poor in plant-available P and possibly other rock-derived nutrients (Vitousek 1984; Vitousek and Sanford 1986; Townsend and others 2007; Vitousek and others 2010). However, recent research has shown that N cycling in lowland tropical forests can be relatively conservative, despite large soil pools of inorganic N (Koehler and

others 2009) and that N limitation remains an important control on tropical forest productivity (LeBauer and Treseder 2008; Wright and others 2011). Conversely, other studies have shown relatively high returns of P in litterfall despite low concentrations of extractable P in the soil (Kaspari and others 2008; Sayer and Tanner 2010), indicating that the size of the measurable or extractable soil nutrient pool does not necessarily reflect nutrient availability to plants. Further, plant adaptation strategies to nutrient limitation, including increased nutrient uptake and use efficiency can lead to higher productivity than expected on nutrient poor soils (Paoli and others 2005).

The great heterogeneity of tropical forests further complicates efforts to make meaningful generalizations because they grow on a very broad range of different soils (Townsend and others 2008) and because not all species need be limited by the same nutrient (Grubb 1989). In addition, multiple resource limitation is common (Bloom and others 1985; Field and others 1992; Wright and others 2011), and the alleviation of limitation by one nutrient will likely immediately lead to limitation by another (Davidson and Howarth 2007; Vitousek and others 2010).

Fertilizer experiments have greatly advanced our understanding of tropical forest mineral nutrition because they make it possible to directly measure the response of nutrient pools to changes in nutrient inputs. These responses can then be used to draw conclusions about the availability of nutrients to plants. Fertilizer experiments have also proven invaluable in identifying process-limiting nutrients, whereby additions of a given nutrient cause an increase in the rate of a biological process (Vitousek and others 2010)—usually measured as increased growth, biomass (Elser and others 2007; LeBauer and Treseder 2008), or decomposition rates (Ostertag and Hobbie 1999; Hobbie and Vitousek 2000). Single nutrients and combinations of nutrients can be added in a highly controlled manner and treatment responses are often easily interpreted.

One of the drawbacks of fertilizer studies is that the application of one or two specific inorganic nutrients (often in large quantities) alters nutrient ratios in the soil and litter. This can have wide-reaching consequences for the interpretation of changes in nutrient cycles because of the crucial role of the stoichiometric nutrient requirements of microbes controlling the dynamics of elements during decomposition processes (Manzoni and others 2010). However, such effects as these may

also be a common consequence of atmospheric nutrient deposition (Güsewell 2004). Furthermore, both the fertilization and the atmospheric nutrient deposition can substantially alter the timing of nutrient pulses, which is a critical mechanism for maintaining productivity in many tropical forests (Lodge and others 1994). Thus, experimental fertilization treatments can also be applied in natural ecosystems to elucidate the effects of atmospheric nutrient deposition on tropical forest nutrient cycling (for example, Hall and Matson 2003; Wullaert and others 2010).

Recently, a different experimental approach has been adopted in tropical forests, which involves removing or adding litterfall (for example, Sayer and others 2006a, b; Vasconcelos and others 2008; Wood and others 2009; Sayer and Tanner 2010). These experiments are useful for determining the importance of litterfall in forest nutrient cycling (Sayer 2006; Sayer and Tanner 2010). In the first instance, litter can be regarded as a natural, complete fertilizer that provides all the elements plants need for growth and the slow release of nutrients from decomposing litter plays a role in the retention of nutrients that are otherwise quickly leached from the system (Qualls and others 1991; Tobón and others 2004). Moreover, litter addition treatments also introduce large amounts of carbon to the system. This not only provides an energy source for the soil microbial populations controlling nutrient immobilization and mineralization but can also alter soil chemical and physical properties (Sayer 2006). Indeed, increased litter inputs, for example as a response to CO_2 fertilization, may be more likely to alter ecosystem nutrient cycling than changes in litter quality (Liu and others 2009), which has been shown to have little effect on decomposition under elevated CO_2 (Norby and others 2001). In contrast, litter removal treatments provide a way to reduce the recycling of nutrients from plants to the soil and measure to what extent soil nutrient pools can compensate and support plant nutrient requirements for growth.

Litter manipulation experiments differ greatly from fertilization studies in that they cannot identify limiting nutrients, and they impose additional variation because of the high spatial and temporal heterogeneity of litter quantity and quality. Furthermore, the forest floor fulfills many other functions besides being a source of nutrients (Sayer 2006), which often makes treatment responses difficult to interpret. Litter removal presents an additional challenge as the loss of organic matter deprives microbial decomposers of energy in addition to nutrients.

Given the differences in nutrient augmentation by fertilization versus litter addition treatments, we are in a unique position to compare and contrast complementary fertilization and litter manipulation experiments in a lowland tropical forest in Panama because our experiments were set up side by side at the same study site and the sampling dates and methodology have been largely coordinated. An estimate of the annual nutrient return by litter at the study site (Sayer and Tanner 2010) shows that experimentally doubling the annual litterfall supplies approximately the same amount of N and potassium (K) to the plots as the fertilizer treatments (143 vs. 125 kg N ha^{-1} y^{-1} and 39 vs. 50 kg K ha^{-1} y^{-1} for the double-litter and fertilizer treatments, respectively) and around 12% of the P added in the fertilization experiment (5.8 kg ha^{-1} y^{-1} vs. 50 kg ha^{-1} y^{-1}).

Here, we evaluate the differences between the effects of inorganic nutrient inputs and the increased inputs of nutrients cycled in organic matter to suggest possible pathways by which anthropogenic change could affect tropical forest nutrient cycles. First, we considered the level of extractable soil nutrients in response to nutrient augmentation. We hypothesized that for process-limiting nutrients at our study site (P and K) we would see a relatively rapid increase in pool size, whereas for those nutrients thought to be readily available (N, calcium, and magnesium) the response time would be longer than the time-frame of the study. The effects of fertilization and litter manipulation on N and K pools should be similar, as the two experiments added similar amounts of these nutrients. Correspondingly, we expected a greater response of P pools to fertilization with P.

We then evaluated the concentration of nutrients returned through litterfall, which can, to some extent, reflect the availability of nutrients in the soil (Vitousek and Sanford 1986; Aerts and Chapin 2000). We hypothesized that if the extractable pool size of a given nutrient were related to its availability to plants, we would expect changes in the soil nutrient pool to be reflected in the nutrient concentrations of the litter.

Net primary productivity is notoriously difficult to measure in tropical forests (Clark and others 2001); we therefore considered litterfall as a measure of productivity and also assessed fine root biomass, as fine roots are the primary plant part responsible for nutrient uptake. Plants can maintain a small fine root biomass when nutrients are plentiful, whereas they tend to allocate a larger proportion of resources to fine root biomass when nutrients are scarce (Bloom and others 1985).

Hence, we hypothesized that an increase in the availability of limiting soil nutrients would reduce fine root biomass while increasing aboveground productivity (litterfall).

MATERIALS AND METHODS

Study Site

The study site is located on the Gigante Peninsula (9°06′ N, 79°54′ W) in the Barro Colorado Nature Monument (BCNM) in Panama. The species composition and stature of the forest are characteristic of mature seasonally evergreen lowland tropical forest (Wright and others 2011). The soils are classed as Endogleyic Cambisols to Acric Nitrisols (FAO classification; Koehler and others 2009), with moderate to low concentrations of extractable inorganic nitrogen, phosphorus, and potassium (Sayer and Tanner 2010; Yavitt and others 2011). Nearby Barro Colorado Island (c. 5 km from the study site) has a mean annual rainfall of 2600 mm with a strong dry season from January to April and a mean temperature of 26°C (Leigh 1999). Between 1996 and 1997, a 38.4-ha area (480 m × 800 m) of forest was mapped and all trees with a diameter at breast height (DBH) greater than 20 cm were tagged, identified, and measured for DBH. Within this site the fertilization and litter manipulation experiments were initiated in 1998 and 2003, respectively.

Gigante Fertilization Project (GFP)

The GFP consists of a factorial NPK fertilization with an additional micronutrient treatment. Each of the 36 plots measures 40 m × 40 m and nine fertilizer treatments (N, P, K, NP, NK, PK, NPK, micronutrients, and control) were each applied to four replicate plots beginning in June 1998. The micronutrient treatment will not be addressed here. Fertilizers are applied by hand four times a year during the wet season. The experimental design and fertilizers used are described in detail in Kaspari and others (2008) and Wright and others (2011).

Gigante Litter Manipulation Project (GLMP)

The GLMP consists of 15 plots, each measuring 45 m × 45 m. Starting in January 2003, the litter in five plots was raked up once a month (no-litter plots) and immediately added to five plots (double-litter plots), and five plots were left undisturbed as controls. The experimental design is described in detail in Sayer and Tanner (2010).

Comparisons Between the Experiments

As the experiments were initiated in different years, we compared treatment responses after a common number of years since the start of treatments. We compared fine and small root biomass after about 20 months of treatments; soil organic carbon, total nitrogen, and microbial biomass after 6 years; litter nutrient concentrations after 3 and 5 years; soil nutrients after 3 and 7 years; and litter production annually over 7 years of treatments. Some of these data have been previously reported in different forms (Sayer and others 2006a, 2007; Kaspari and others 2008; Sinsabaugh and others 2008; Sayer and Tanner 2010; Wright and others 2011; Yavitt and others 2011; Online Appendix Tables 1–4).

Nutrients in Soil and Litter

We compared N, P, K, calcium (Ca), magnesium (Mg), and zinc (Zn) in the soil after 3 and 7 years of treatments (Online Appendix Table 1). All the soil samples were collected during the late rainy season at 0–10-cm depth and at least 10 m from the nearest edge of a treatment plot. Four to nine individual samples were combined to make one composite sample per plot as described below.

After 3 years of treatments, four soil samples were taken in each GFP plot and eight in each GLMP plot. For all plots, nitrate and ammonium were extracted from fresh soil in a 2 M KCl solution within 48 h of collection and soil pH was measured on a 1:3 soil solution in distilled water. In the GFP plots, extractable P was determined by Bray's P-1 test and cation concentrations were determined by NH_4Cl extraction from dried (45°C) soil. In the GLMP plots, extractable P and cations were determined by Mehlich III extraction. Problems with contamination with ammonium-N obliged us to discard the 3-year results for ammonium-N and total inorganic N (N_{inorg}) in the GLMP plots.

After 7 years of treatments, nine soil samples were collected from each GFP and GLMP plot. Fresh-soil extracts for mineral nutrients were prepared within 24 h of collection and soil pH was measured on a 1:3 fresh soil solution in distilled water. Nitrate-N and ammonium-N were extracted from fresh soil in a 2 M KCl solution and determined by automated colorimetry; soil P and cations were determined by Mehlich III extraction and analyzed by ICP-OES.

We also compared total organic carbon (TOC), total nitrogen (N_{TOT}), and microbial biomass C and N at 0–10-cm depth in the soil after 6 years of treatments (Online Appendix Table 2). In the GFP

plots, four soil samples were collected in each plot during the rainy season in August 2004. In the GLMP plots, eight samples were collected in April 2008. Samples were pooled to give one composite sample per plot and extractions for analysis were performed within 2 days of sampling. Microbial biomass was estimated via the fumigation extraction technique using identical protocols to those reported in Sayer and others (2007). TOC and N_{TOT} were extracted in 0.5 M K_2SO_4 solution and measured simultaneously on a TOC VCPH/CPN Analyzer (Schimadzu, Kyoto, Japan; Online Appendix Table 2).

Nutrient concentrations in mixed forest litter collected from litter traps (see below) were compared after 3 and 5 years of treatments (Online Appendix Table 3). For the GFP plots, litter samples collected in September and October were pooled to make one sample per plot and year. For the GLMP plots, litter samples collected in September were pooled by plot and year. All the samples were finely ground for nutrient analysis. Phosphorus and cations were determined by ICP after acid digestion and total nitrogen was determined by complete combustion gas chromatography (Kaspari and others 2008; Sayer and Tanner 2010).

Fine Root Biomass and Litterfall

We compared fine root biomass (<2-mm diameter) after 19–22 months of treatments (Online Appendix Table 2) by taking 5-cm diameter intact soil cores at 0–10-cm depth. All the sampling sites were located randomly in the inner 20 m × 20 m and 30 m × 30 m of the GFP and GLMP plots, respectively. In the GFP plots, four soil cores were taken per plot in April 2000 (22 months after the start of treatments); in the GLMP plots, ten cores were taken in each plot in June and July 2004 (19 months after the start of treatments). Each soil core was cut into two equal segments, giving nominal sampling depths of 0–5 cm and 5–10 cm. Live roots were separated from the soil as described by Sayer and others (2006a) and dried to constant weight at 60°C.

We compared litterfall annually over 7 years of treatments. Small litterfall (sensu Proctor 1983) was collected in all GFP and GLMP plots on the last Thursdays and Fridays of every month; litter traps measured 0.76 m × 0.76 m and were mounted approximately 0.7 m above the soil surface. Three and ten litter traps were located randomly in the inner 30 m × 30 m of each GFP and GLMP plot, respectively. Woody debris with a diameter greater than 20 mm was discarded during collection; the

remaining small litter was oven-dried at 60°C and weighed (Sayer and Tanner 2010; Wright and others 2011). We divided total annual small litterfall into dry season and rainy season litterfall to differentiate between changes in leaf turnover during the rainy season and leaf shedding due to phenological cues or water stress during the dry season (Sayer and Tanner 2010). Dry season litterfall was defined as small litterfall from January to April for each year, whereas rainy season litterfall was defined as small litterfall from May to December for each year (Online Appendix Table 4).

Data Analysis

To facilitate the comparison of treatment effects and effect size between experiments, log response ratios were calculated for N addition, P addition, K addition, litter addition, and litter removal treatments. Log response ratios represent the proportional response to experimental treatments: $RR_X = \ln(R_X/R_C)$, where R_X is the measured value of the response variable in the experimental treatment and R_C is its value in the untreated control (Elser and others 2007). An RR_X of zero represents ''no treatment response'', values greater than zero represent positive responses, and values less than zero represent negative responses (Harpole and others 2011). Absolute values of measured variables are given in Online Appendix Tables 1–4.

Data with repeated measures (soil nutrients, pH, litter nutrients, litterfall) were analyzed using mixed effects models (lme command in R, Pinheiro and Bates 2000) with treatment and time as fixed effects and plot as the random effect. Data with only one time point (fine root biomass, microbial biomass, TOC, and N_{TOT}) were analyzed by one-way analysis of variance (lm command in R). Interactions between fertilizer treatments (N + P, N + K, and P + K) were evaluated in preliminary models; none of the interactions was significant when compared to the main treatment effect and interactions were therefore excluded from further analysis. Main treatment effects were assessed by comparing null models to full models (with treatment as a factor/fixed effect) using likelihood ratio tests and were considered only if including treatment significantly improved the model. Significance levels and t values for individual treatments were derived from the full models. All analyses were performed in R 2.13.2 (R Development Core Team 2010).

As we evaluated differences between experiments using only those time points at which the variables were directly comparable, the significance levels of effects for individual treatments differ
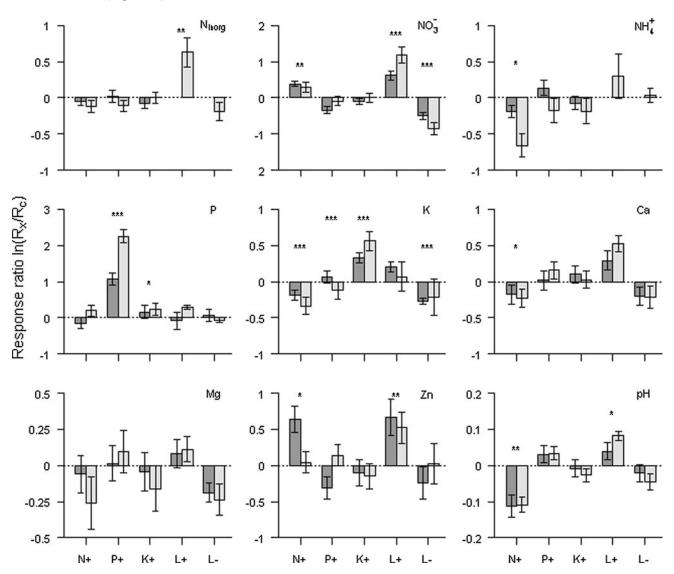
from previously published results from the two experiments (see Sayer and others 2006a, 2007; Kaspari and others 2008; Corre and others 2010; Sayer and Tanner 2010; Wright and others 2011; Yavitt and others 2011).

RESULTS

Soil Nutrients and pH

Litter manipulation treatments had a greater effect on inorganic N concentrations in the soil, whereas fertilization had a greater effect on soil P and K concentrations (Figure 1).

Total inorganic N (N_{inorg}) was unchanged by fertilization but ammonium-N in the soil decreased in the plots with added N ($t = -2.04$, $P = 0.047$), whereas nitrate-N increased ($t = 3.14$, $P = 0.003$). In contrast, the concentration of N_{inorg} doubled in the double-litter plots ($t = 3.39$, $P = 0.001$) and nitrate-N was threefold higher after 7 years of litter addition ($t = 5.36$, $P < 0.001$). Nitrate-N had also decreased in the no-litter plots ($t = -3.53$, $P < 0.001$) whereas ammonium-N was not significantly affected by litter manipulation.

Extractable soil P increased tenfold in the plots with added P ($t = 7.63$, $P < 0.001$) and there was a

Figure 1. Changes in soil nutrient concentrations in response to fertilization and litter manipulation experiments in old-growth lowland tropical forest, Panama, Central America, expressed as log response ratios relative to controls; *N+* = nitrogen fertilization; *P+* = phosphorus fertilization; *K+* = potassium fertilization; *L+* = litter addition; *L−* = litter removal; *dark gray bars* show effects after 3 years of treatments and *light gray bars* show effects after 7 years of treatments; values shown are means ± standard errors for *n* = 16 (fertilizer treatments) and *n* = 5 (litter manipulation treatments); significance levels for individual treatments are given as ***P < 0.001, **P < 0.01, *P < 0.05.
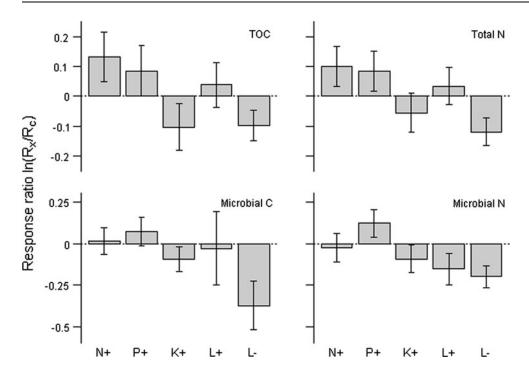
Figure 2. Changes in TOC, N_{TOT}, microbial biomass C, and microbial biomass N in the mineral soil in response to 6 years of fertilization and litter manipulation treatments in old-growth lowland tropical forest in Panama, Central America, expressed as log response ratios relative to controls (see Figure 1 for a description of symbols and abbreviations).

small but significant increase in soil P in the plots with added K ($t = 2.01$, $P = 0.049$). The concentration of K in the soil doubled in the plots with added K ($t = 4.12$, $P < 0.001$) and decreased in the plots with added N ($t = -5.50$, $P < 0.001$). Soil K was slightly higher in the plots with added P and the no-litter plots after 3 years of treatments, but had decreased significantly after 7 years of treatments ($t = -3.66$, $P < 0.001$ and $t = -3.70$, $P < 0.001$, respectively). There was no effect of litter addition on soil P or soil K concentrations. The Ca and Mg concentrations in the soil were not affected by any treatment, whereas Zn increased in the plots with added N and in the double-litter plots ($t = 2.56$, $P = 0.013$ and $t = 2.72$, $P = 0.009$, respectively; Figure 1).

Soil pH (0–10-cm depth) decreased by half a unit (from 5.4 to 4.9) in the plots with added N ($t = -3.3$, $P = 0.002$) and soil pH was higher (5.8) in the double-litter plots ($t = 2.19$, $P = 0.033$; Figure 1). Total organic C, total N, and microbial biomass C and N in the mineral soil were not affected by any treatment (Figure 2).

Litter Nutrients

Litter N concentrations were not affected by fertilization with N but increased in the plots with added K ($t = 2.07$, $P = 0.043$). There was a trend towards higher litter N concentrations in the double-litter plots and a significant decrease in the no-litter plots ($t = 1.86$, $P = 0.069$ and $t = -2.21$, $P = 0.031$,

respectively). Litter P concentrations were higher in the plots with added P ($t = 3.70$, $P < 0.001$; Figure 3) but there were no significant effects of any other treatment. Litter K concentrations were not significantly affected by K fertilization but there was a strong trend towards lower litter K in the plots with added P ($t = -1.99$, $P = 0.052$) and a significant decrease in the no-litter plots after 7 years of litter removal ($t = -2.15$, $P = 0.036$). The concentration of Ca in litter decreased in the plots with added N ($t = -2.08$, $P = 0.042$) but there were no effects of any treatment on the concentration of Mg or Zn in litter (Figure 3).

Fine Roots and Litterfall

Fine roots in the surface soil (0–5 cm) responded rapidly to fertilization with K and to the litter addition treatment (Sayer and others 2006a; Yavitt and others 2011). After less than 2 years of treatments, fine root biomass at 0–5-cm depth was significantly lower in the plots with added K and in the double-litter plots ($t = -2.54$, $P = 0.014$ and $t = -2.49$, $P = 0.016$; Figure 4).

Annual litterfall and dry season litterfall were not affected by any treatment but rainy season litterfall was higher in the plots with added N or P ($t = 2.2$, $P = 0.032$ and $t = 2.46$, $P = 0.017$) and there was a marginally significant increase in rainy season litterfall in the double-litter plots ($t = 1.74$, $P = 0.087$; Figure 5).
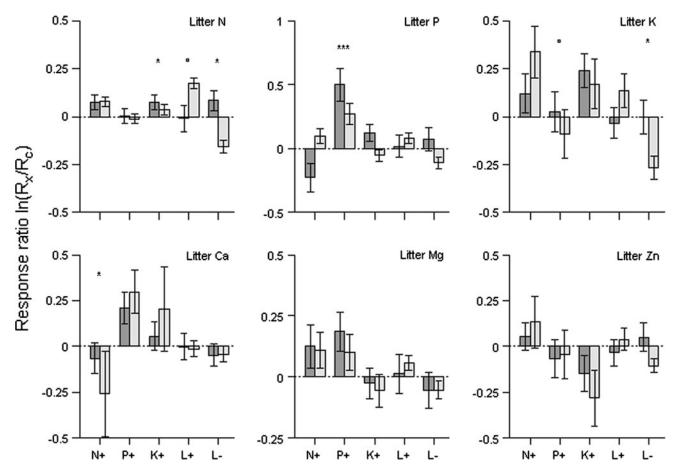
Figure 3. Changes in litter nutrient concentrations in response to fertilization and litter manipulation treatments in old-growth lowland tropical forest in Panama, Central America, expressed as log response ratios relative to controls; *dark gray bars* show effects after 3 years of treatments and *light gray bars* show effects after 5 years of treatments; marginally significant effects ($P < 0.1$) are denoted by °; see Figure 1 for a description of other symbols and abbreviations.

DISCUSSION

The amounts of nutrients and litter added in this study are much greater than the projected inputs by atmospheric deposition or increased growth in response to elevated CO_2 levels. Nevertheless, litter inputs can increase dramatically after extreme weather events such as hurricanes or drought (Lodge and others 1994) and a recent research has shown that changes in litter chemistry in the N-fertilization treatments are very similar to the effects of chronic low-level N deposition in the region since the 1960s (Hietz and others 2011). We observed several unexpected differences between the two experiments, most notably the contrasting effects of fertilization and litter addition treatments on N and K pools. We propose that these differences can be largely explained by the addition of extra carbon in the double-litter plots. The additional organic carbon affects not only the cycling of the added nutrients by providing energy to

decomposers (Fontaine and others 2004) but also through changes in soil chemical and physical properties (Sayer 2006). Although substantial changes in soil respiration rates indicate that litter addition and removal treatments have affected carbon dynamics in the litter manipulation plots (Sayer and others 2007, 2011), it is important to note that neither TOC nor microbial biomass in the mineral soil (0–10 cm) changed significantly in the experimental treatments (Figure 2).

Changes in Nutrient Pools

Nitrogen

We hypothesized that we would see little change in soil extractable N pools following nutrient augmentation. Although this largely held true for the N-fertilized plots, we observed a substantial increase in extractable inorganic N in the soil in the double-litter plots. This is surprising because both
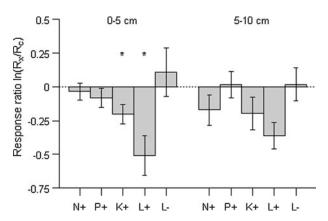
Figure 4. Changes in fine root biomass at 0–5-cm and 5–10-cm depth in response to 19–22 months of fertilization and litter manipulation treatments in old-growth lowland tropical forest in Panama, Central America, expressed as log response ratios relative to controls (see Figure 1 for a description of symbols and abbreviations).

the treatments added roughly the same amount of N.

In the N-fertilized plots, the decrease in ammonium-N can be attributed to reduced immobilization of ammonium and increased gross nitrification rates under chronic N-fertilization (Corre and others 2010). Nitrate leaching also increased in the plots with added N (Corre and others 2010),

resulting in a relatively small effect of N-fertilization on the soil nitrate-N pool (Figure 1). In the double-litter plots, the higher concentrations of nitrate-N could reflect increased nitrification rates without the corresponding losses because the slow release of inorganic N during litter decomposition reduces nitrate leaching (Qualls and others 1991; Chang and others 2007). Although nitrification is generally thought to be an autotrophic process, heterotrophic nitrification is common in acid soils and may even be the dominant pathway for the production of nitrate-N in mature forest soil (Pedersen and others 1999). It is conceivable that litter addition increased heterotrophic nitrification in the forest floor because heterotrophic nitrification is stimulated by the presence of organic C (Focht and Verstraete 1977; Adams 1986) and uses organic N compounds as a substrate instead of ammonium (Schimel and others 1984; Pedersen and others 1999). Thus, high rates of mineralization and nitrification in the forest floor would continuously replenish the soil nitrate-N pool with minimal losses through leaching; this possibility merits further attention in future. Litter N concentrations were shown to increase in the plots with added N in previous comparisons of the fertilized plots (Kaspari and others 2008; Corre and others 2010). Here we show that the increase in litter N concentrations
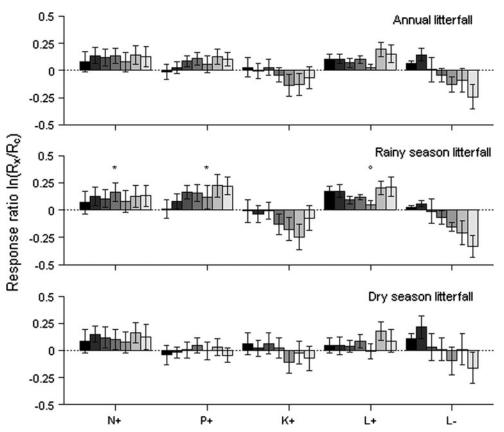

Figure 5. Changes in total annual fine litterfall, rainy season litterfall, and dry season litterfall during 7 years of fertilization and litter manipulation treatments in old-growth lowland tropical forest in Panama, Central America, expressed as log response ratios relative to controls. *Different shades* of *gray* denote individual years from 1999 to 2005 for the fertilizer treatments and from 2003 to 2009 for the litter manipulation treatments (see Figures 1 and 3 for a description of symbols and abbreviations).

was greater in the double-litter plots (Figure 3), indicating greater long-term availability of N to plants in the litter addition treatment.

The litter removal treatment resulted in lower concentrations of nitrate-N but not ammonium-N in the soil. As N in forest ecosystems is mainly cycled in organic form through litterfall (Attiwill and Adams 1993), the available soil N pool in the no-litter plots is gradually being depleted by plant uptake and leaching. Decreased nitrification rates and greater immobilization of ammonium-N represent mechanisms to conserve inorganic N as the system becomes N-limited. Thus, it appears that on the one hand, chronic additions of inorganic N result in the forest N cycle becoming progressively "leaky" with major losses of N from the system (Koehler and others 2009; Corre and others 2010). On the other hand, the natural forest N cycle is relatively conservative and the retention and availability of N is largely dependent on the cycling of N in organic matter, to the extent that the withdrawal of N from the system by litter removal rapidly induces N-conserving mechanisms.

Phosphorus

Phosphorus is often considered the main growth-limiting element in lowland tropical forests (Vitousek 1984; Townsend and others 2011), especially because a large proportion of inorganic P in tropical soils is usually bound in forms of low biological availability (Sanchez 1976; Vitousek and Sanford 1986). Nutrient limitation can sometimes be inferred from the size of soil and litter nutrient pools (Vitousek and Sanford 1986; Aerts and Chapin 2000) but in our study forest the concentrations of extractable phosphate in the topsoil are low (≤ 2 mg kg^{-1}; Sayer and Tanner 2010) whereas the amounts of P being returned by litterfall (c. 5–6 kg ha^{-1} y^{-1}, Kaspari and others 2008; Sayer and Tanner 2010) are more characteristic of moderately fertile soils (Vitousek and Sanford 1986). This strongly suggests that the size of the extractable soil P pool does not accurately reflect P availability to plants.

Fertilization with P caused a rapid and substantial increase in soil P with a corresponding increase in litter P concentrations (Figures 1, 3). The large additions of P in the fertilized plots were deemed necessary to saturate soil colloids (Ingestad 1974; Ostertag 2010) and to overcome the high phosphate sorption in the soils at our study site (L. Schreeg, unpublished data). Even so, the high concentration of extractable P in the soil of the P-fertilized plots demonstrates that much of the

added P was not taken up by plants and Yavitt and others (2011) showed that approximately 81% of the added P remained in the soil after 7 years of fertilization. Consequently, although the amounts of P added as fertilizer in our study are not representative of atmospheric P deposition, much smaller inputs of P may indeed have a positive effect on P availability in tropical forests in the future (Okin and others 2004).

The litter addition treatment provided only about 12% of the P added as fertilizer, but the increase in litterfall in the double-litter plots required an additional uptake of approximately 1.2 kg P ha^{-1} y^{-1}, which is very similar to the additional 1.4 kg P ha^{-1} y^{-1} returned in litter in the plots with added P. This implies that a greater proportion of the P from the litter was available for plant uptake. Most of the demand for P in natural forests can be met by rapid cycling of P in organic matter (Attiwill and Adams 1993; Turner and Engelbrecht 2011) and fine roots growing into the organic horizons acquire P directly from decomposing litter as it is mineralized (Herrera and others 1978; Stark and Jordan 1978; Tobón and others 2004), bypassing the mineral soil (Witkamp 1971). The increase in P uptake despite the lack of change in soil extractable P pools in the double-litter plots suggests that most of the plant demands for P were met by direct cycling from the forest floor.

As P is thought to be the main process-limiting element at our study site, we expected a sizeable effect of litter removal on soil and litter P concentrations. However, the reductions in the soil and litter P pools observed after 7 years of litter removal were minor and not statistically significant. Previous work at our study site has shown decreased organic P levels at the soil surface (0–2 cm) after several years of litter removal, which suggests that some organic P compounds may play a role as an alternative source of P to plants (Vincent and others 2010). On the other hand, as rocks are still present in the soil profile at our study site (Yavitt and others 2009), it is also conceivable that P is still entering the system through weathering and transport by deep roots.

Potassium

Throughfall is the main pathway for K inputs to tropical forests (Vitousek and Sanford 1986), nevertheless K-fertilization and litter addition increased annual K inputs by around 30% (Sayer and Tanner 2010). Potassium cycling follows a pattern more similar to N cycling than to other cations (Tripler and others 2006) and it is therefore

remarkable that in contrast to N, the amount of K in the soil increased greatly in response to K-fertilization but remained more or less unchanged in the double-litter plots (Figure 1).

Potassium is highly soluble and if not adsorbed onto cation exchange sites or assimilated by plants or soil organisms it is readily leached from the soil (Likens and others 1994). There appear to be strong biotic controls on K leaching (Tripler and others 2006) and K retention is thought to be principally achieved through rapid and efficient uptake by plants (Gosz and others 1976). We can only speculate that the increase in K in the mineral soil of the plots with added K may be a result of greater occupation of cation exchange sites by K^+, whereas in the double-litter plots it is possible that much of the K added with the litter resides in the forest floor rather than the mineral soil. A thick layer of litter can retain large amounts of nutrients, including K (Qualls and others 1991; Tobón and others 2004) and the release of K from decomposing litter was reduced in the double-litter plots (Sayer and others 2006b). Further, litter addition treatments can increase fungal abundance in the forest floor (Lodge and others 2008) and as fungi accumulate K (Tyler 2005) much of the K added with the litter may be immobilized in fungal biomass and would not be available to plants.

Although litter as a source of K is secondary to throughfall, its importance for K cycling and retention is demonstrated by the litter removal treatment—not only did soil K concentrations decrease in the no-litter plots (Figure 1) but litter K concentrations also declined substantially over 7 years of treatments (Figure 3). This could indicate either decreased K uptake or greater translocation of K before leaf abscission in response to dwindling availability in the soil (Likens and others 1994).

The soil K pool also decreased in the plots with added N, which, along with the trend towards decreased Ca in the soil in the N-fertilized plots (Figure 1) is indicative of cation leaching as a consequence of acidification (Vitousek and others 1997).

Calcium, Magnesium, and Zinc

There are large soil pools of Ca and Mg in the study forest because both the nutrients are present in the bedrock and in marine aerosol inputs at high concentrations (Yavitt and Wieder 1988; Cavelier 1992) and consequently we expected to see no treatment effects on these nutrients. Despite this, there was a trend towards lower concentrations of Ca in the soil and litter in the N-fertilized plots and increased soil Ca in litter-addition plots. Ca is mainly cycled in litterfall (Vitousek 1982) and annual litterfall can contribute 80–90% of the Ca needed for growth (Parker 1983). If the Ca requirements of plants were already being largely met by normal annual litterfall, then 7 years of litter addition probably added enough Ca to the system for Ca to accumulate in the topsoil. The decrease in litter Ca concentrations in the N-fertilized plots is more intriguing. Given the large soil Ca pool, it seems unlikely that the minor decrease in the soil Ca pool would affect foliar Ca concentrations and no other nutrient concentrations decreased significantly with N-fertilization. However, it is possible that the decrease in litter Ca is a sign of nutrient imbalance caused by excess N availability (Vitousek and others 1997) and this finding merits further attention in future studies.

The soil pool of extractable Zn increased in the N-fertilized and double-litter plots (Figure 1). In the plots with added N, we can attribute the greater availability of Zn to the decrease in soil pH as a consequence of N-fertilization. The concentrations of Zn in solution are inversely related to soil pH (Marschner 1993) and the sorption of Zn in clay soils increases rapidly above a pH of 5 (Cavallaro and McBride 1984). The decrease in soil pH of half a unit in the plots with added N (from 5.4 to 4.9) appears to have been sufficient to mobilize extra Zn.

On the other hand, Zn concentrations in the soil also increased in the double-litter plots, despite the trend towards increased soil pH (Figure 1), possibly through greater fluxes of DOC to the soil. The addition of organic matter can increase the solubility of Zn at pH above 5 by forming organo-metallic complexes; consequently, a large proportion of Zn in soil solution is bound to dissolved organic matter (Reddy and others 1995). Zinc complexed with organic carbon may not be as readily available to plants because of lower diffusivity but a larger amount would be detected by chemical extraction (Reddy and others 1995). It follows that what appears to be a similar effect of N-fertilization and litter addition on the extractable soil Zn pool can be attributed to two distinct processes with different consequences for plant Zn uptake. This conjecture is supported by the much smaller effect size of litter addition on Zn concentrations in litter compared to fertilization with N, despite a similar effect on the amount of Zn extracted from the soil (Figures 1, 3).

Litterfall and Fine Root Biomass

There was a trend towards increased rainy season litterfall in the plots with added P, added N, and litter addition (Figure 5) but there were no treatment effects on dry season litterfall, indicating that fertilization with N and P boosts leaf turnover during the main growth period (Wood and others 2009; Sayer and Tanner 2010). We can take this as a first sign of changes in total litter production because Wright and others (2011) showed increased annual litterfall after 11 years of P-fertilization. The trend towards increased rainy season litterfall in the double-litter plots provides strong evidence for improved nutrient uptake by plants through litter addition. Correspondingly, the withdrawal of nutrients with the litter removal treatment caused a sizeable (but non-significant) decrease in rainy season litterfall (Figure 5) and appeared to be affecting annual litterfall after 7 years of litter removal. We anticipate a significant decline in productivity in the no-litter plots within the next few years as the system becomes more nutrient-limited.

Potassium fertilization reduced fine root biomass in the mineral soil (Figure 4; Yavitt and others 2011). The source/sink theory postulates that trees should allocate more energy to root production on infertile sites (Bloom and others 1985); accordingly, if the supply of a limiting nutrient increases, root biomass should decline. This suggests that K is potentially limiting to plant growth in our study forest (Wright and others 2011; Yavitt and others 2011). The importance of K as a nutrient limiting productivity has been demonstrated for temperate forests (Tripler and others 2006) but until recently there was little evidence for K limitation in tropical forests (Kaspari and others 2008; Wright and others 2011; Yavitt and others 2011).

Fine root biomass in the mineral soil also decreased dramatically in the double-litter plots (Figure 4); although it is conceivable that this decrease was a result of greater availability of K in the forest floor, we found little evidence for increased plant uptake of K because litter K concentrations remained unchanged (Figure 3). It is more likely that fine roots responded to the overall greater nutrient availability in the thicker forest floor of the double-litter plots as the decline in fine root biomass in the mineral soil was accompanied by proliferation of fine roots into the litter layer (Sayer and others 2006a).

Co-limitation of N and K has been demonstrated in our study forest (Wright and others 2011), and increased availability of both of these nutrients in the forest floor may explain the changes in fine root biomass in the double-litter plots. Further evidence of co-limitation by N and K is provided in this study by the increase in litter N with K-fertilization (Figure 3).

CONCLUSIONS

We show marked differences in the responses of nutrient pools and plant nutrient uptake depending on whether nutrients were applied as inorganic fertilizer or in organic matter (litter). Many of these differences can be attributed to the combined addition of nutrients and carbon in the litter. Effective retention mechanisms through microbial processes and plant uptake may result in an overall positive impact of increased nutrient input via litterfall. Whereas large amounts of inorganic nitrogen inputs (for example, from atmospheric deposition) can cause nutrient imbalances and losses of nitrogen from the system, smaller nutrient inputs may be particularly important for replenishing pools of limiting nutrient elements. Once taken up by plants, atmospheric nutrient inputs are likely to be retained in the ecosystem through plant growth and recycling through litterfall.

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