

Research Article

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Effects of soil fertilization on the allocation of net primary productivity in tropical rainforests of Chocó, Colombia

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Abstract

Tropical rainforests exhibit some of the highest net primary production (NPP) rates in the world. It is widely hypothesized that soil nutrient availability, particularly phosphorus (P), limits NPP and influences the allocation of productivity between above- and below-ground components in tropical forests. However, these hypotheses have rarely been tested experimentally in extremely wet tropical rainforests. Here, we evaluated the effects of soil fertilization on above- and below-ground NPP in two localities in the Chocó region (Colombia), among the rainiest forests in the world, using five fertilization treatments (N, P, K, NPK, and control) applied in permanent plots. Contrary to expectations, total NPP did not respond to the addition of N, P, or K, despite the very high rainfall and extremely nutrient-poor soils. While total NPP remained unchanged, N fertilization significantly increased canopy NPP, measured as litterfall biomass. In addition, P fertilization induced a redistribution of NPP between above- and below-ground compartments, increasing the relative contribution of fine roots and litterfall while decreasing allocation to woody biomass. These shifts in carbon allocation likely represent an ecological strategy to enhance nutrient acquisition in soils with extremely low phosphorus availability.

Introduction

Lowland tropical rainforests (TRF) are considered the terrestrial ecosystems with the highest net primary productivity (NPP, defined as the total new organic matter produced during a specified time interval) in the world (Clark *et al.* 2001a; Pan *et al.* 2011; Saugier *et al.* 2001). However, most of them are located on poor soils, with extreme acidity and aluminum (Al) toxicity (Baillie *et al.* 1996; Chapin III *et al.* 1986). Therefore, soil fertility, especially nitrogen (N), phosphorus (P), and potassium (K) concentrations (Wieder *et al.* 2015), is considered among the main factors that determine the NPP of TRF (Cleveland *et al.* 2011, Jiménez *et al.* 2014; Vitousek 1984).

Although the availability of nutrients limits NPP in TRF (Wieder *et al.* 2015), each nutrient generates different effects on the above- and below-ground components of NPP (Aragão *et al.* 2009; Cleveland *et al.* 2011; Paoli and Curran 2007; Quinto-Mosquera and Moreno-Hurtado 2017). In this regard, Vitousek (1984) hypothesized that the edaphic content of available P is the main limiting factor of above-ground NPP in these ecosystems, because P loss by leaching and its immobilization in Fe and Al oxides reduce its availability for plants (Vitousek *et al.* 2010; Walker 1976). Contrary to this, the availability of soil N in TRF tends to be high, for which it has been described as less limiting (Cleveland *et al.* 2011; Vitousek 1984; Vitousek *et al.* 2010). Likewise, soil availability of K has been considered a limiting factor for NPP at a global scale, but it has been little evaluated in tropical forests (Sardans and Peñuelas 2015; Tripler 2006). In summary, the nutrient limitation of NPP in TRF has been poorly tested through field experiments; for this reason, the current debate about this issue requires further studies.

To experimentally test the hypothesis of nutrient limitation, it is necessary to add fertilizers or organic amendments and evaluate their effects on the above- and below-ground components of NPP (Sullivan 2014). The few studies that have evaluated this limitation in TRF show that the factorial application of N, P, and K has positive, null, and/or even negative effects on the components of NPP (Sayer and Banin 2016). However, only a limited number of long-term fertilization experiments in lowland tropical rainforests have simultaneously evaluated above- and below-ground components of NPP, and results remain variable and context-dependent (Wright *et al.* 2018, 2024). Consequently, the extent to which total NPP and its allocation are constrained by nutrient availability, particularly in extremely wet tropical forests, is still not fully resolved.

Most fertilization experiments in lowland tropical forests have been conducted in sites receiving less than 5000 mm of annual rainfall. Thus, empirical evidence from forests with

higher rainfall remains limited, and nutrient effects in these systems are still poorly constrained. For example, it is believed that above this level of precipitation, NPP tends to decrease drastically (Schuur 2003). Rains usually cause nutrient losses through leaching and runoff (Austin and Vitousek 1998; Posada and Schuur 2011; Quinto-Mosquera and Moreno-Hurtado 2016), lower foliar concentration of nutrients, and a decrease of N mineralization and nitrification rates [Alvarez-Clare and Mack 2011; Santiago *et al.* 2005; Schuur and Matson 2001]. Therefore, a greater nutritional limitation of the ecosystem NPP is expected under such conditions.

To test the hypothesis of nutritional limitation of NPP in high-rainfall tropical forests, two forest sites were selected in the biogeographic Chocó region, which has one of the highest rainfall levels in the world ($\approx 10,000$ mm annually) (Poveda *et al.* 2004). At these sites, a fertilization experiment with N, P, and K was conducted to test the following hypotheses regarding the effects of nutrient addition: (1) nutrient addition increases total NPP; and (2) nutrient addition alters NPP allocation patterns, leading to a decrease in below-ground NPP and an increase in above-ground NPP allocation. This study therefore addresses the following questions: (1) How does the addition of N, P, and K affect total NPP and its components, and does nutrient addition lead to a redistribution of NPP among plant components? (2) Is NPP limited by nutrient availability in these ecosystems, and if so, which nutrient is most limiting?

Materials and methods

Study area

The present study was conducted in a tropical rain forest located in the localities of Pacurita (municipality of Quibdó) and Opogodó (municipality of Condoto), department of Chocó, Colombia. The mean temperature is 26°C , and annual precipitation is about 8000 mm. These localities are within the geomorphological unit of Tertiary sedimentary hills, which are characterized by low altitudes and are composed of sedimentary rocks, including sandy argillolites, sandstones, and limestones (Quinto-Mosquera and Moreno-Hurtado 2017). The soils of both sites are strongly acidic (pH between 3.9 and 5.2), with very low P content (1.02–1.83 ppm) and low exchangeable base concentrations. In Opogodó, soils have higher contents of sand (85–87%), organic matter (10–14%), and total N (0.56–0.72%); whereas in Pacurita they have lower pH, greater Al saturation, and are loam, with lower contents of sand and higher of clay (Table 1). Soil chemical and physical properties reported in Table 1, where the analytical methods used for each variable are also specified, were obtained from Quinto-Mosquera and Moreno (2017). In Opogodó the sampling was carried out in three permanent plots—one ha each—installed in a primary forest located in the facilities of the Technological University of Chocó ‘Diego Luis Córdoba’. In Pacurita, the study was carried out in two permanent plots of a forest located on the left margin of the road between Quibdó and Pacurita (Table 1).

Methods

Experimental design

We used a randomized complete block design with five fertilization treatments (N, P, K, NPK, and control) and five replicates (Shieh and Jan 2004). At each site, a 100×100 m forest area was established in 2013. Within this area, five parallel strips of 20×100 m

(0.2 ha) were established. Each strip was subdivided into five experimental units of 20×20 m, to which the five fertilization treatments were randomly assigned. A 2 m buffer zone was established within each experimental unit, resulting in an effective treated area of 18×18 m. Understory vegetation within the buffer zones was not removed, and thus potential lateral root uptake between adjacent experimental units cannot be entirely ruled out. Each experimental unit was further subdivided into four 9×9 m subplots to facilitate fertilizer application, soil sampling, and subsequent NPP measurements.

Fertilizers were applied by broadcast application, that is, evenly distributed over the soil surface of each experimental unit without soil incorporation (Mirmanto *et al.* 1999; Wright *et al.* 2011). The annual dose of fertilizer was applied in four equal doses throughout the year 2014, in the months of February, May, August, and November. Thus, in the treatment of N, $125 \text{ kg N ha}^{-1} \text{ year}^{-1}$ was applied in the form of urea $[(\text{NH}_2)_2\text{CO}]$; in the treatment of P, $50 \text{ kg P ha}^{-1} \text{ year}^{-1}$ was applied in the form of phosphate rock; in the treatment of K, $50 \text{ kg K ha}^{-1} \text{ year}^{-1}$ was applied in the form of potassium chloride (KCl); in the treatment of NPK, each of the doses mentioned in the previous treatments was applied together; and in the control, no fertilizers were applied.

Measurement of tree diameters and heights

Two censuses of the plots were carried out in the months of August of 2013 and 2014 on individuals with diameter at breast height (DBH) ≥ 10 cm. In each census the living, dead, and recruited individuals (i.e., those that reached the DAP ≥ 10 cm) were recorded. For all trees measured, the morpho species were identified up to the maximum taxonomic level possible (NN ‘unidentified specimens’, species, genus, botanical family) in the Herbarium of the Technological University of Chocó ‘D.L.C.’ ‘Herbario Choco’. This identification was made using the specialized keys of Gentry (1993).

We marked the perimeter of the tree trunk where the diameter was measured with yellow paint in order to ensure that subsequent measurements were made in the same area of the first measurement. All measurements were made in areas free of knots, buttresses, or branches. In addition, the location of each individual in the grid was recorded. All trees measured were also marked with aluminum tags. Heights were measured in 40% of the trees with a Suunto clinometer at fixed distances of 15 and 20 m from the tree; likewise, the heights of the smallest trees (heights less than 10–15 m) were measured with a graduated rod. For the remaining 60% of trees, Equations (1) and (2) (Quinto-Mosquera and Moreno-Hurtado 2011) were used to estimate the height of the trees based on the ecological groups of species.

$$\begin{aligned} \text{Total height of non – pioneer species (m)} \\ = 6.28 + 0.607 \times \text{DBH} \end{aligned} \quad (1)$$

$$\begin{aligned} \text{Total height of pioneer species (m)} = 7.422 + 0.411 \times \text{DBH} \end{aligned} \quad (2)$$

Measurement of litter and fine-root production: a litter trap (1×0.5 m) was installed 1 m above ground at the center of the 20×20 m sampling subplot. In total, 125 traps were installed for litterfall sampling. The litter accumulated in the collectors was collected every month for one year in plastic bags. Given the warm and humid conditions of the study sites, some decomposition of

Table 1. Edaphic (mean $\pm$ SE) and structural parameters of five permanent plots in the Chocó region, Colombia. Soil data (replicates per site collected from the 0–20 cm soil layer) and forest structural parameters (e.g., tree density and above-ground biomass) were obtained from the supplementary material of Quinto-Mosquera and Moreno-Hurtado (2017). Soil analyses were conducted using standard procedures: the Bouyoucos method for soil texture, potentiometric determination in water solution (1:2) for pH, the Walkley and Black method for organic matter, Micro-Kjeldahl for total N, available P determined by the ascorbic acid method after Bray II extraction using a UV–VIS spectrophotometer, and Ca, mg, and K determined by atomic absorption after extraction with ammonium acetate

Edaphic parameters	Unid	Opogodó I (n = 25)	Opogodó II (n = 25)	Opogodó III (n = 25)	Pacurita I (n = 25)	Pacurita II (n = 25)
pH		4.73 $\pm$ 0.04	5.14 $\pm$ 0.05	5.01 $\pm$ 0.05	3.90 $\pm$ 0.02	4.16 $\pm$ 0.02
Aluminum (Al)	cmol kg ⁻¹	0.13 $\pm$ 0.01	0.13 $\pm$ 0.01	0.11 $\pm$ 0.01	0.94 $\pm$ 0.03	0.95 $\pm$ 0.05
Organic matter (OM)	%	14.0 $\pm$ 0.82	9.95 $\pm$ 0.42	11.1 $\pm$ 0.87	4.93 $\pm$ 0.22	3.21 $\pm$ 0.15
Total Nitrogen (N)	%	0.70 $\pm$ 0.04	0.55 $\pm$ 0.05	0.55 $\pm$ 0.04	0.25 $\pm$ 0.01	0.16 $\pm$ 0.01
Phosphorus (P)	ppm	1.86 $\pm$ 0.15	1.09 $\pm$ 0.06	1.06 $\pm$ 0.06	1.02 $\pm$ 0.05	1.71 $\pm$ 0.15
Potassium (K)	cmol kg ⁻¹	0.20 $\pm$ 0.02	0.27 $\pm$ 0.01	0.25 $\pm$ 0.02	0.15 $\pm$ 0.02	0.20 $\pm$ 0.02
Calcium (Ca)	cmol kg ⁻¹	0.24 $\pm$ 0.05	0.39 $\pm$ 0.01	0.52 $\pm$ 0.05	0.35 $\pm$ 0.02	0.36 $\pm$ 0.02
Magnesium (Mg)	cmol kg ⁻¹	0.33 $\pm$ 0.03	0.27 $\pm$ 0.07	0.25 $\pm$ 0.02	0.19 $\pm$ 0.01	0.16 $\pm$ 0.01
Cation exchange capacity	cmol kg ⁻¹	0.90 $\pm$ 0.08	1.05 $\pm$ 0.08	1.13 $\pm$ 0.08	1.62 $\pm$ 0.05	1.67 $\pm$ 0.06
Clay	%	0.52 $\pm$ 0.26	1.00 $\pm$ 0.29	1.81 $\pm$ 0.80	20.0 $\pm$ 0.61	17.0 $\pm$ 0.75
Silt	%	13.0 $\pm$ 1.10	13.6 $\pm$ 0.93	14.0 $\pm$ 1.09	28.2 $\pm$ 1.33	28.0 $\pm$ 1.18
Sand	%	86.5 $\pm$ 1.25	85.4 $\pm$ 1.07	84.2 $\pm$ 1.81	51.8 $\pm$ 1.22	55.0 $\pm$ 1.41
Abundance	ind. ha ⁻¹	954	705	635	913	979
Above-ground biomass	t ha ⁻¹	305	166	175	335	201
Mean diameter	cm/ind	15.5	17.1	17.9	16.9	15.0
Mean height	m/ind	15.1	16.0	16.3	15.9	14.9

In both locations, sampling was carried out in well-preserved primary forests. Although tree density, above-ground biomass, mean diameter, and height varied among plots, values were within the range reported for mature tropical rainforests in the region (Quinto-Mosquera and Moreno-Hurtado 2017).

leaf litter may have occurred between monthly collections. To measure the NPP of fine roots, we used the ingrowth core method (Cuevas & Medina 1988) modified by Moreno-Hurtado (2004). In this method, a volume of soil is extracted and the soil removed; then, this volume of root-free soil is returned back to the orifice previously left on the forest floor. Cores are left in the soil for a period of two months to allow fine-root growth; subsequently, the cores are extracted, roots are removed, and fine-root NPP is determined (Cuevas & Medina 1988, Hendricks *et al.* 2006).

The modified ingrowth cores were located in the center of each 10 $\times$ 10 m subplot; for this purpose, two soil samples (0–10 cm and 10–20 cm deep) were extracted with an Eijkkelkamp® soil auger (8 cm diameter and 15 cm long). Fine roots (FR) (with diameters $\leq$ 5 mm) were manually separated in the field using plastic trays and sieves (0.5 and 1.0 mm). After extracting FR, the soil was introduced again into the holes, while roots were transported to the laboratory for processing. This procedure was performed every three months for one year; in each sampling, 100 soil cores were evaluated at two depths per plot, which resulted in a total of 1000 FR samples per field campaign. In the laboratory, the FR sampled quarterly were washed and sieved (0.5 and 1 mm) to remove the remaining soil. Subsequently, the FR were oven-dried (70°C for 48 hours) and weighed in an analytical balance (accuracy $\pm$ 0.0001 g). The NPP of fine roots was determined as the value accumulated over time and expressed in t ha⁻¹ year⁻¹.

Data analysis

For the estimation of tree above-ground biomass (AB), we reviewed seven models generated with information from tropical

wet forests of different areas of the world (Bake *et al.* 2004; Brown 1997; Chave *et al.* 2005); the model from Chave *et al.* (2005; Equation 3) was chosen because it had a higher average correlation coefficient with the AB estimates of the other models, according to the evaluation made by Quinto-Mosquera and Moreno-Hurtado (2011); in addition, the model was chosen because it includes as predictors three key variables of wood biomass (DBH, total height, and wood density) (Quinto-Mosquera and Moreno-Hurtado (2011). The below-ground biomass in coarse roots (BB, Equation 8) was estimated as 21% of AB (Aragão *et al.* 2009).

$$AB \text{ (kg)} = \exp[-2.557 + 0.94 \times \ln(\rho_i \times DBH^2 \times H)]. \quad (3)$$

$$BB \text{ (kg)} = 0.21 \times AB \quad (4)$$

Where $\ln$ is the natural logarithm, H is the total height, and ρ_i is the wood density. The increase in forest biomass was calculated from the information of AB and BB of each sample and measurement. For the estimation of wood density, we used the values published in two databases, generated mainly in forests of the Amazon (Baker *et al.* 2004) and in tropical forests of different regions of the world (Brown 1997). If any species or genus found in the plots was not reported in these databases, the average wood density of the respective genus or family was used; for the taxonomically undetermined individuals, we used the average wood density of the plot.

The total NPP and its components were determined with Equations (5) – (8) (Chapin III 2006; Clark 201b):

$$NPP = NPP_{\text{above-ground}} + NPP_{\text{below-ground}} \quad (5)$$

Table 2. Effects of the localities and fertilization treatments on NPP and its components in tropical rain forests of the Chocó region, Colombia

Factors	Net primary productivity (t ha ⁻¹ yr ⁻¹)								
	Above-ground wood	Coarse roots	Total wood	Litterfall	Fine roots	Total Above-ground	Total Below-ground	Total labile	NPP total
Localities									
Opogoó	9.07 ± 0.64	1.49 ± 0.14	10.6 ± 0.78	4.83 ± 0.14	4.15 ± 0.16	13.9 ± 0.69	5.64 ± 0.21	8.98 ± 0.22	19.5 ± 0.82
Pacurita	8.84 ± 0.74	1.33 ± 0.15	10.2 ± 0.89	3.10 ± 0.10	3.46 ± 0.15	11.9 ± 0.73	4.79 ± 0.21	6.56 ± 0.18	16.7 ± 0.89
LME (F _{1,112})	0.006	0.515	0.0004	112.2***	9.425**	3.592	8.181*	70.92***	5.625*
Treatments									
N (%)	9.55 ± 1.00 ^a	1.53 ± 0.20 ^a	11.1 ± 1.19 ^a	4.56 ± 0.31 ^a	3.49 ± 0.20	14.1 ± 1.08	5.02 ± 0.28	8.06 ± 0.38 ^{ab}	19.1 ± 1.26
P (ppm)	6.21 ± 0.65 ^b	0.88 ± 0.31 ^b	7.09 ± 0.77 ^b	4.28 ± 0.27 ^{ab}	4.18 ± 0.25	10.5 ± 0.79	5.06 ± 0.31	8.46 ± 0.43 ^{ab}	15.5 ± 1.00
K (cmol kg ⁻¹)	10.9 ± 1.51 ^a	1.87 ± 0.33 ^a	12.8 ± 1.84 ^a	3.79 ± 0.24 ^b	3.94 ± 0.35	14.7 ± 1.55	5.82 ± 0.49	7.73 ± 0.52 ^{ab}	22.5 ± 1.90
NPK	8.72 ± 1.04 ^a	1.34 ± 0.24 ^{ab}	10.1 ± 1.28 ^a	4.20 ± 0.29 ^{ab}	4.24 ± 0.25	12.9 ± 1.11	5.58 ± 0.32	8.44 ± 0.38 ^a	18.5 ± 1.35
Control	9.37 ± 0.84 ^a	1.47 ± 0.16 ^a	10.8 ± 0.99 ^a	3.79 ± 0.20 ^b	3.51 ± 0.23	13.2 ± 0.89	4.98 ± 0.29	7.31 ± 0.34 ^b	18.1 ± 1.08
LME (F _{4,112})	3.042*	2.419*	2.961*	2.914*	2.128	2.321	1.080	2.615*	1.830
Localities × Treatments									
LME (F _{4,112})	1.077	1.187	1.107	1.154	3.483*	1.478	2.916*	2.056	1.642

LME is the Linear Mixed-Effects Model. *F* values with asterisks indicate statistically significant differences **P* < 0.05. ***P* < 0.01. ****P* < 0.0001. Different letters indicate statistically significant differences between treatment levels. Total wood = above-ground wood + coarse roots; total labile = litterfall + fine roots. Total above-ground = above-ground wood + litterfall; total below-ground = coarse roots + fine roots.

$$NPP_{\text{above-ground}} = \Delta AB_{\text{survivors}} + \Delta AB_{\text{recruited}} + NPP_{\text{litterfall}} \quad (6)$$

$$NPP_{\text{above-ground wood}} = \Delta AB_{\text{survivors}} + \Delta AB_{\text{recruited}} \quad (7)$$

$$NPP_{\text{below-ground}} = \Delta BB_{\text{survivors}} + \Delta BB_{\text{recruited}} + NPP_{\text{fine roots}} \quad (8)$$

Where $\Delta AB_{\text{survivors}}$ is the increase in aerial biomass (AB) of surviving trees, determined as the final AB (second measurement) minus the initial AB (first measurement) of each surviving tree; $\Delta AB_{\text{recruited}}$ is the increase in AB of trees recruited between samplings, calculated as the AB of the recruited trees (new individuals that reached DBH ≥ 10 cm) recorded in the second measurement minus the AB of an individual of 10 cm of DBH. Trees that died between censuses were recorded as mortality and were excluded from aboveground biomass increment calculations. The increase of coarse root biomass (ΔBB , Equation 8) was determined similarly to the increase of AB of Equation (6). NPP fine roots is the production of fine roots determined by the ingrowth core technique described above (Clark *et al.* 2001b).

A linear mixed-effects model was used to evaluate the effect of soil fertilization treatments and the locality on total NPP and its components, including the interaction between fertilization and locality. Fertilization treatment and locality were treated as fixed effects, while the experimental plot was included as a random effect to account for spatial dependence among experimental units. Models were fitted assuming independent residuals within plots. Model assumptions were evaluated by inspecting residuals, and normality and homoscedasticity were assessed using the Shapiro-Wilk test and Levene's test, respectively. When assumptions were violated, data were log-transformed [$\log(x + 1)$] prior to analysis. For clarity of presentation, untransformed data (mean ± 2 standard errors) are shown in the text, tables, and figures. When significant main effects or interactions were detected, Fisher's least significant difference (LSD) test was used for post hoc comparisons. Given the

number of response variables and derived ratios analyzed, marginally significant results were interpreted with caution to minimize potential inflation of Type-I error. All statistical analyses were performed in the R statistical computing environment version 4.4.3 (R Core Team 2025), using the package 'nlme' version 3.1–137 (Pinheiro *et al.* 2018). All raw data and R scripts used in the analyses are made available as Supplementary material (dataset S1).

Results

Opogodó had values of total NPP significantly higher than Pacurita, with several components of NPP accounting for this result, particularly higher NPP of labile components (litterfall NPP and fine-root NPP). Below-ground NPP was also higher, mostly as a result of higher fine-root NPP (Table 2). Fertilization treatments had variable and even contrasting effects on different components of NPP, so the effect on total NPP was not significant. Fertilization treatments had a significant effect on the following components of NPP: above-ground wood, coarse roots, total wood, litterfall, and total labile (Table 2). In particular, P-fertilization decreased the production of woody tissue (above-ground wood, coarse roots, and total wood). N-fertilization increased the litterfall production, and the NPK-fertilization increased the total labile NPP; no other significant effects of treatments were found (Table 2).

The fertilization treatment $\times$ location interaction was significant for fine roots and total below-ground NPP (Table 2, Figure 1). In Opogodó, the P-fertilization treatment increased the production of these two components, which were higher than for the control and N-fertilization treatments. Similarly, the K treatment also produced higher values for these two variables as compared to the N treatment in Opogodó, which showed the lowest values among all fertilization treatments in this location (Figure 1). In Pacurita, the NPK treatment produced higher values than K for these two variables; no other significant effect was detected.

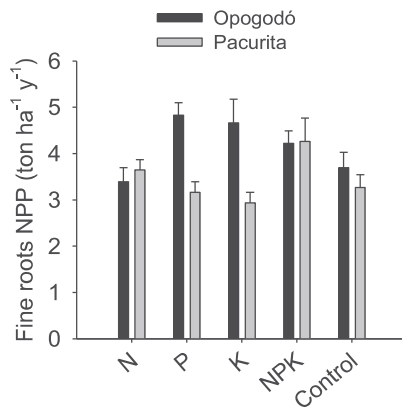


Figure 1. Locality $\times$ fertilization interaction on fine-root NPP in tropical rain forests of the Chocó region, Colombia. Different letters indicate statistically significant differences between treatment levels ($P < 0.05$).

Several ratios among components of NPP were significantly different between locations; particularly, labile/total wood, litterfall/fine roots, and litterfall/above-ground wood were higher in Opogodó. Likewise, the percentages of labile NPP and litterfall NPP were higher in Opogodó than in Pacurita (Table 3).

Fertilization treatments did not have significant effects on labile/total wood NPP and litterfall/above-ground wood NPP. They were significant on other ratios, particularly on above-ground/below-ground NPP and litterfall/fine roots NPP; however, the effects varied between locations (the interactions localities $\times$ fertilization treatments were significant for both variables Table 3). In Opogodó, the above-ground/below-ground NPP was significantly higher under N fertilization as compared to all other treatments, while P fertilization decreased this ratio as compared to the control (Figure 2). In Pacurita, the NPK treatment decreased this ratio as compared to the control. Similarly, in Opogodó the litterfall/fine-root NPP ratio was higher under N fertilization than under the other treatments. In Pacurita, the lowest value of this ratio was observed under the NPK treatment; however, differences among fertilization treatments at this site were not statistically significant (Figure 2).

Fertilization treatments also had significant effects on the allocation of NPP to different compartments, measured as percentages, particularly on below-ground NPP, above-ground NPP, labile NPP, fine-root NPP, and litterfall NPP (Table 3). The percentage of NPP allocated to labile, fine roots, and litterfall NPP increased significantly under the treatment of P fertilization as compared to the control (Table 3). The effects of fertilization treatments on the percentages of above-ground and below-ground NPP varied between localities. The percentage of above-ground NPP in Opogodó decreased with P fertilization as compared to the control and N, while in Pacurita, this variable was lower with the NPK treatment as compared to the control (Figure 3). In Opogodó, the percentage of below-ground NPP increased with P-fertilization as compared to treatments with control and N; likewise, this variable was lower under N fertilization as compared to all other treatments. In Pacurita, below-ground NPP was higher under the NPK treatment as compared to the control.

Discussion

Effects of fertilization on total forest NPP. None of the soil fertilization treatments applied had significant effects on total NPP of the tropical rainforests evaluated. This result does not support the

hypothesis of P limitation of NPP (Aragão *et al.* 2009; Cleveland *et al.* 2011; Vitousek 1984), as well as the N limitation of NPP of this forest, as suggested by several investigations (Lebauer and Treseder 2008, Mirmanto 1999). Nevertheless, it should be noted that NPP components were measured over a single year following fertilization, and longer-term observations may reveal delayed, cumulative, or transient responses that are not captured at short temporal scales, as documented in long-term fertilization experiments in other tropical forests (Wright *et al.* 2018, 2024). Consistent with these findings and with the limited number of published studies, total NPP in mature tropical forests appears to be only weakly influenced by nutrient addition or by unforeseen increases in nutrient availability, even after fertilization periods longer than ten years (Wright *et al.* 2011, 2024). Accordingly, total NPP in the studied rainforests does not seem to be limited by the addition of N, P, or K. Several reasons might explain the unresponsiveness of total NPP to the addition of fertilizers:

1) Structure and diversity of vegetation: these old-growth rainforests of the biogeographic Chocó have high diversity of tree species (Faber-Langendoen 1991; Quinto-Mosquera and Moreno-Hurtado 2014), with different ages, sizes, wood densities, nutrient contents, light requirements, photosynthetic capacity, and growth rates; that enormous variability might produce differences in the amount of the most limiting nutrients required for the production of organic matter (Alvarez-Clare *et al.* 2013; Quinto-Mosquera and Moreno-Hurtado 2017). In particular, differences in life histories of plants lead to differences in the nutritional requirements and therefore, in the responses to fertilization (Santiago 2015; Sullivan *et al.* 2014); for example, it is known that small trees respond to fertilization differently from large trees (Alvarez-Clare & Mack 2013; Quinto-Mosquera and Moreno-Hurtado 2017; Santiago *et al.* 2012; Wright *et al.* 2011). This situation would make it difficult to prove effects of the application of nutrients on NPP at the ecosystem level in low-altitude tropical forests (Chapin III 1986; Wright *et al.* 2018). Additionally, the presence of species adapted to nutrient-poor soils may contribute to limited responses to nutrient addition, as such species may have relatively low nutrient requirements and growth rates (Wright *et al.* 2018).

2) Chemical, physical, and biological processes: The added nutrients can be fixed and immobilized by soil microorganisms (Richardson and Simpson 2011), by inorganic absorption processes, and/or chemical solubility phenomena in the soil (Chapin III 1986; Gyaneshwar *et al.* 2002; Olander and Vitousek 2004); particularly, the edaphic P can react with oxides of Fe and Al, making it not available for plants (Dalling *et al.* 2016; Walker and Syers 1976). The applied nutrients can also be leached by frequent rains (Austin and Vitousek 1998; Quinto-Mosquera and Moreno-Hurtado 2016; Santiago *et al.* 2005), which in the study area range between 8000 and 10000 mm per year (Poveda *et al.* 2004); in these sites, leaching may be further enhanced by the low pH of soil, with high saturation of Al in the exchange complex. Furthermore, added nutrients can be absorbed and stored in labile plant tissues, such as leaves and fine roots (Alvarez-Clare and Mack 2015; Mayor *et al.* 2014; Mirmanto *et al.* 1999; Newbery *et al.* 2002; Wright *et al.* 2018), with little effect on tissue production due to the low availability of other nutrients not included in the fertilization treatments, such as Ca and Mg. Although nutrient leaching is proposed as a plausible mechanism contributing to the weak NPP response, leachate chemistry was not measured in this study, and therefore direct evidence of nutrient losses is not available.

The high concentration of total N in these soils (Table 1) (Quinto-Mosquera and Moreno-Hurtado 2016) and the high

Table 3. Effects of the localities and fertilization treatments on the ratios among components of NPP in tropical rain forests of the Chocó region, Colombia

Factors	Net primary productivity ($\text{t ha}^{-1} \text{yr}^{-1}$)								
	Above-ground / below-ground	Labile/ total wood	Litterfall/ fine roots	Litterfall / above-ground wood	Below-ground (%)	Above-ground (%)	Labile (%)	Fine roots (%)	Litterfall (%)
Localities									
Opogodo	2.53 ± 0.10	1.25 ± 0.10	1.28 ± 0.06	0.73 ± 0.05	30.2 ± 0.90	69.8 ± 0.90	50.3 ± 1.80	23.5 ± 1.17	26.8 ± 0.91
Pacurita	2.49 ± 0.09	0.95 ± 0.10	0.96 ± 0.04	0.51 ± 0.06	29.7 ± 0.78	70.3 ± 0.78	43.8 ± 2.15	22.8 ± 1.16	21.0 ± 1.28
LME ($F_{1,112}$)	0.013	4.011*	18.68***	8.875**	0.02	0.43	5.825*	0.384	17.94***
Treatments									
N (%)	2.86 ± 0.19^a	1.05 ± 0.18	1.42 ± 0.13^a	0.65 ± 0.11	27.4 ± 1.34^c	72.6 ± 1.34^a	45.6 ± 2.97^b	20.2 ± 1.71^b	25.4 ± 1.83^{ab}
P (ppm)	2.13 ± 0.13^c	1.48 ± 0.16	1.07 ± 0.07^b	0.82 ± 0.08	33.2 ± 1.36^a	66.8 ± 1.36^b	56.4 ± 2.46^a	28.1 ± 1.68^a	28.3 ± 1.34^a
K (cmol kg^{-1})	2.55 ± 0.18^{ab}	1.00 ± 0.15	1.04 ± 0.07^b	0.54 ± 0.08	29.9 ± 1.51^{bc}	70.1 ± 1.51^{ab}	44.0 ± 3.70^b	22.3 ± 2.10^b	21.6 ± 1.85^b
NPK	2.32 ± 0.13^{bc}	1.20 ± 0.16	1.06 ± 0.09^b	0.67 ± 0.10	31.2 ± 1.15^{ab}	68.8 ± 1.15^{ab}	49.6 ± 3.03^{ab}	24.9 ± 1.72^{ab}	24.7 ± 1.95^b
Control	2.70 ± 0.15^{ab}	0.94 ± 0.17	1.17 ± 0.08^{ab}	0.53 ± 0.08	28.1 ± 1.37^{ab}	71.7 ± 1.37^a	43.1 ± 2.84^b	20.8 ± 1.80^b	22.3 ± 1.51^b
LME ($F_{4,112}$)	3.767*	1.932	3.038*	1.796	3.76**	3.26*	4.006**	3.854**	3.711**
Localities $\times$ Treatments									
LME ($F_{4,112}$)	2.986*	1.320	3.673**	1.144	2.97*	2.56*	0.880	2.113	0.743

LME is the Linear Mixed-Effects Model. *F* values with asterisks indicate statistically significant differences * $P < 0.05$. ** $P < 0.01$. *** $P < 0.0001$. Different letters indicate statistically significant differences between treatment levels ($P < 0.05$). Above-ground (%) and below-ground (%) represent the proportional contributions of these compartments to total NPP and are complementary measures.

expected rates of biological fixation of N resulting from the abundance of legumes in these forests (Cleveland *et al.* 1999; Posada and Schuur 2011) could explain the unresponsiveness of total NPP to the application of N. Despite the low stores of available P in these soils (Quinto-Mosquera and Moreno-Hurtado 2016), its application did not affect the total NPP, probably due to the adaptive strategies that allow plants to obtain the required P from soil. Such strategies include the development of mycorrhizal associations that increase the surface area for P uptake, the solubilization of P retained in Fe and Al sesquioxides in the soil (Lambers *et al.* 2008; Smith and Read 2008), and the formation of cluster roots that release carboxylates into the rhizosphere, thereby mobilizing poorly available edaphic P (Finlay 2008; Smith *et al.* 2008). Likewise, the increased activity of phosphatase enzymes, released by plants and microorganisms, allows the absorption of P from soil organic matter (Vitousek *et al.* 2010). These strategies could explain the effect of P fertilization on the increased below-ground NPP, which will be further discussed. K is a highly soluble nutrient, easily leached from the soil, even more than other macronutrients such as N or P (Boxman *et al.* 1985; Sardans and Peñuelas 2015); therefore, its edaphic availability decreases with high rainfall (Austin and Vitousek 1998). For these reasons, K also shows large deposition rates to the soil by foliar leaching (Duchesne *et al.* 2001; Kopacek *et al.* 2009; Santiago *et al.* 2005). Consequently, despite the low content of K in the soils (Table 1), it should not be limiting NPP in these forests and consequently its unresponsiveness to K application.

The application of N, P, and K produces eco-physiological responses in tropical trees, such as the increase in foliar content of nutrients, maximum photosynthetic rate, stomatal conductance, transpiration, water use efficiency, and tree growth and production, among others (Santiago 2015). However, these responses

could be modified by other limiting factors, such as light, temperature, soil aeration, etc. (Alvarez-Clare and Mack 2011; Santiago *et al.* 2005; Schuur and Matson 2001). In particular, the cloudy skies typical of this rainy region could be an important factor in decreasing the solar radiation incident, limiting the total photosynthesis of the forest. Consequently, this combination of factors would explain that the effects of nutrient application at the forest community level are more difficult to detect even in experiments longer than a few years (Chapin III *et al.* 1986; Santiago *et al.* 2012; Wright *et al.* 2018). The effects would be even more diluted when considering that NPP limitation for each nutrient can be different (Lambers *et al.* 2008; Sayer and Banin 2016; Sullivan *et al.* 2014), and that the ecosystem could be limited by more than one factor (Alvarez-Clare *et al.* 2013; Kaspari *et al.* 2008; Mirmanto *et al.* 1999). In this context, although soil chemistry was not re-evaluated after fertilization, the randomized assignment of treatments within each locality, together with the strong baseline edaphic contrasts between sites, supports the interpretation that the observed NPP responses primarily reflect treatment effects interacting with site-level soil constraints.

Effects of fertilization on the above- and below-ground allocation of forest NPP. It is known that the availability of resources such as water, nutrients, or solar radiation stimulates a redistribution of NPP between the above- and below-ground components of vegetation (Malhi *et al.* 2011; Thornley 1972). Plants allocate biomass and NPP according to the most limiting resource; consequently, a greater proportion of NPP and biomass is allocated to fine roots in soils with limited availability of water and nutrients. However, when solar radiation is a limiting factor, higher NPP is allocated to aerial structures, such as stems and canopy (Aerts & Chapin III 2000; Bloom *et al.* 1985; Malhi *et al.* 2011; Poorter *et al.* 2012; Portsmouth & Niinemets 2007). The differential allocation

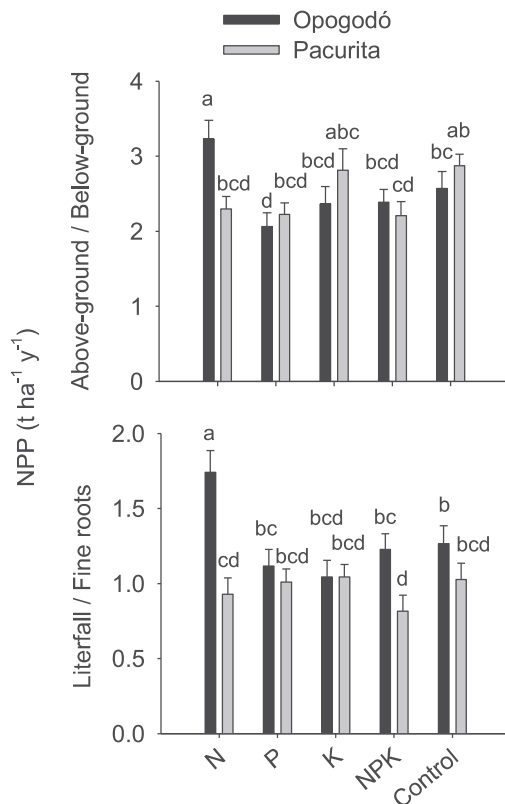


Figure 2. Locality $\times$ fertilization treatments interaction on the ratios above-ground/below-ground and litterfall/fine-root NPP in tropical rain forests of the Chocó region, Colombia. Different letters indicate statistically significant differences between treatment levels ($P < 0.05$).

can profoundly affect the ecosystem functioning; for example, a greater proportion of canopy NPP influences the photosynthetic capacity and the production of flowers and fruits; the wood NPP represents the long-term carbon storage in the ecosystem; and the fine-root NPP determines the acquisition of water and nutrients from the soil (Malhi *et al.* 2011).

This hypothesis has received different names, among them optimal partitioning theory (Thornley 1972), hypothesis of differential allocation (Hendricks *et al.* 2006), hypothesis of balanced growth, and functional balance of biomass allocation (Poorter *et al.* 2012). Few studies have evaluated the relation between the above- and below-ground components of NPP and the edaphic availability of nutrients in tropical rainforests (Aragão *et al.* 2009; Jiménez *et al.* 2014; Quinto-Mosquera and Moreno-Hurtado 2017), with variable results. Araújo *et al.* (2009) found that total and root NPP increased with the available soil P, in accordance with this hypothesis, in the sense that edaphic P limits the below-ground NPP (Vitousek 1984). Quinto-Mosquera and Moreno-Hurtado (2017), working in the same forests studied here, found correlations explaining variation in both above- and below-ground NPP components in relation to nutrient availability, except for available P, likely because P concentrations were low and showed little variability in that study; however, the relationship between the availability of nutrients and total NPP was not significant. The higher total NPP and below-ground NPP, as well as the labile components of NPP (litterfall and fine roots) in forests of Opogodó in this study, which have higher sand content as well as higher availability of several nutrients (organic matter, N, K, and Mg),

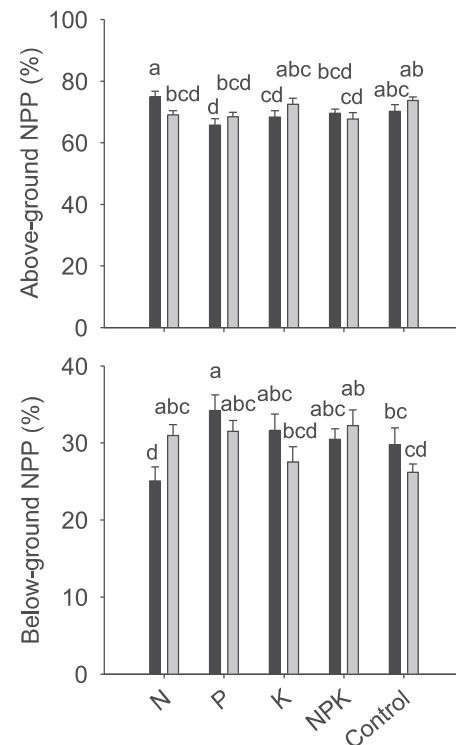


Figure 3. Locality $\times$ fertilization treatment interaction on the allocation percentage of NPP to above- and below-ground components in tropical rain forests of the Chocó region, Colombia. Different letters indicate statistically significant differences between treatment levels ($P < 0.05$).

support the well-established idea that total NPP is affected by soil fertility (Quinto-Mosquera *et al.* 2024); these results show additional evidence of differential allocation to components of NPP as a result of variation of soil fertility, probably as a mechanism to capture resources in oligotrophic soils (Quinto-Mosquera and Moreno-Hurtado 2017), according to the differential allocation hypothesis mentioned above. Our results with the application of P are similar in the sense that it increased the below-ground and the percentage of labile components of NPP (litterfall and fine roots) in these forests whose soils have very low contents of P (Table 1). Although this pattern is consistent with an ecophysiological reallocation of carbon aimed at improving P acquisition, alternative, non-mutually exclusive mechanisms should also be considered. P addition may have promoted changes in species composition or relative growth rates, favoring fast-growing species or functional groups characterized by higher fine-root turnover and litter production. Such community-level responses could contribute to the observed shifts in NPP allocation without necessarily implying direct physiological reallocation within individual plants. Disentangling these mechanisms would require species-specific and trait-based analyses that were beyond the scope of the present study.

Based on the differential allocation hypothesis, the response to the application of nutrients should be a redistribution of NPP among its components (Chapin III *et al.* 1986). This was the response evidenced in the present study, where the application of N increased the litterfall NPP, the addition of P decreased the NPP of woody tissue, while NPK increased the total labile NPP (Table 2). P-fertilization also increased the percentage of NPP allocated to leaf litter, fine roots, and total labile (Table 3). The significant

Table 4. Summary of nutrient-addition experiments conducted in lowland tropical rainforests evaluating total net primary production (NPP) and/or its main components. Studies were selected based on the availability of ecosystem-level NPP measurements and comparable experimental designs. The table includes representative studies from different tropical regions and is not intended to be an exhaustive review of all fertilization experiments

Sites	Nutrients applied	Litterfall	Above-ground biomass	Coarse roots	Fine roots	Total NPP	References
Tierra Firme. Amazonia. Brasil	NH ₄ Cl	ND ¹	ND	ND	No effect	ND	Cuevas and Medina (1988)
	KH ₂ PO ₄	ND	ND	ND	Positive	ND	
	CaCl ₂	ND	ND	ND	Positive	ND	
Tall Caatinga. Amazonia. Brasil	NH ₄ Cl	ND	ND	ND	Positive	ND	
	KH ₂ PO ₄	ND	ND	ND	No effect	ND	
	CaCl ₂	ND	ND	ND	No effect	ND	
Low Bana. Amazonia. Brasil	NH ₄ Cl	ND	ND	ND	Positive	ND	
	KH ₂ PO ₄	ND	ND	ND	Positive	ND	
	CaCl ₂	ND	ND	ND	No effect	ND	
Dipterocarpaceae forest. Indonesia	N	Positive	No effect	ND	ND	ND	Mirmanto <i>et al.</i> (1999)
	P	Positive	No effect	ND	ND	ND	
	NP	Positive	No effect	ND	ND	ND	
Luquillo Forest. Puerto Rico	N	No effect	No effect	ND	ND	ND	Cusack <i>et al.</i> (2011)
Barro Colorado Panama	N	No effect	No effect	ND	ND	ND	Wright <i>et al.</i> (2011, Wright <i>et al.</i> 2018; 2024)
	P	Positive	No effect	ND	ND	ND	
	K	No effect	No effect	ND	ND	ND	
	NPK	No effect	No effect	ND	ND	ND	
	NP	No effect	No effect	ND	ND	ND	
	NK	No effect	Positive	ND	ND	ND	
	PK	No effect	No effect	ND	ND	ND	
Lowland tropical wet forest Costa Rica	N	No effect	No effect	ND	No effect	ND	Alvarez-Clare <i>et al.</i> (2013)
	P	No effect	Positive	ND	No effect	ND	
	NP	No effect	Positive	ND	No effect	ND	
Tambopata, Amazon Perú	N	ND	No effect	ND	ND	ND	Fisher <i>et al.</i> (2013)
	P	ND	No effect	ND	ND	ND	
	NP	ND	Positive	ND	ND	ND	

¹ND: undetermined.

interactions of fertilization treatments $\times$ localities for several variables show the differential effect of fertilization treatments on components of NPP depending on local soil conditions. In Opogodó, N-fertilization increased the ratios of litterfall/fine root as well as above-ground/below-ground NPP; P application had the opposite effect, with a lower percentage of above-ground NPP and, consequently, higher allocation to below-ground NPP. Although fertilization responses in Pacurita were lower, it is remarkable the higher allocation to below-ground NPP in response to NPK application; this lower response to fertilization treatments in

Pacurita could be related to the lower contents of most nutrients, and more importantly, lower pH and higher Al saturation in their soils; Al has toxic effects on plants and affects the absorption of other nutrients (Sharma *et al.* 2025). For this reason, future fertilization studies in tropical forests with acidic soils would benefit from including an acidity neutralization treatment.

Studies on the effects of fertilization in tropical rainforests show that NPP responses can be differential according to the NPP component measured and the nutrients evaluated (Table 4). In this regard, Mirmanto *et al.* (1999) and Wright *et al.* (2011), in forests

of Indonesia and Panama, respectively, showed increases in litterfall NPP with the application of nutrients (N, P, and N + P) but did not show significant changes in tree diameter growth rates. Similarly, Sayer *et al.* (2012) observed an increase in litterfall NPP with the application of N, P, and organic matter. Contrarily, other investigations did not detect changes in litterfall NPP with the application of nutrients (Alvarez-Clare *et al.* 2013; Cusack *et al.* 2011; Newbery *et al.* 2002). On the other hand, increases in growth rates of small trees (5–10 cm of DBH) with the application of P were reported, but effects on fine roots or litterfall NPP were not identified (Alvarez-Clare and Mack 2015; Alvarez-Clare *et al.* 2013). Despite these results showing the variability and complexity of NPP responses to fertilization, the present study experimentally proves that fertilization generated a redistribution of the above- and below-ground components of NPP.

Final remarks

Most tropical forests are characterized by high NPP rates (Lu *et al.* 2025; Pan *et al.* 2011; Saugier *et al.* 2001) despite growing on nutrient-poor soils with low nutrient concentrations (Chapin III *et al.* 1986). This apparent paradox has led to the hypothesis that these ecosystems are limited by key nutrients such as N, P, and K (Aragão *et al.* 2009; Cleveland *et al.* 2011; Fisher 2013; Paoli and Curran 2007; Vitousek 1984). However, the results of the present study experimentally demonstrated that total NPP in extremely pluvial tropical forests of the biogeographic Chocó is not limited by the availability of N, P, or K, at least over the time scale evaluated. The rejection of this first hypothesis constitutes an important finding, as it indicates that total NPP can be remarkably insensitive to nutrient addition even under conditions of severe soil nutrient limitation.

Instead of increasing total productivity, nutrient addition primarily promoted a redistribution of NPP between above- and below-ground compartments, with particularly strong effects of phosphorus addition, thereby supporting the second hypothesis. Phosphorus fertilization increased the relative contribution of below-ground and labile components (fine roots and litterfall) while reducing allocation to woody biomass. This shift in allocation may represent an adaptive strategy to enhance nutrient acquisition and retention in soils where phosphorus is scarce and strongly immobilized (Finlay 2008; Lambers *et al.* 2008; Smith 2008).

These findings suggest that fertilization effects in highly pluvial tropical forests may be better detected through changes in carbon allocation patterns rather than through responses of total NPP. Future fertilization experiments in these ecosystems should therefore prioritize long-term designs and integrative approaches that include nutrient cycling, fine-root dynamics, plant–microbial interactions, and hydrological constraints in order to improve understanding of the mechanisms regulating productivity and carbon allocation under conditions of extreme rainfall.

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