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Effects of nutrient (N, P, K) fertilization on the dynamics of fine roots in tropical rain forests with different soil texture in the Colombian Pacific region

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ABSTRACT

Introduction: Fine root dynamics include production, turnover and decomposition; they are crucial to forest health, affect the entire biogeochemical complex of the ecosystem, and consequently, they substantially affect carbon balance. However, the influence of environmental factors and soil nutrient limitation on fine roots presents considerable uncertainties and has not been studied in tropical forests with more than 7 000 mm annual rainfall.

Objective: To measure the effect of fertilization on fine roots in the high precipitation Chocó forest.

Methods: We worked in two sites of the Chocó region, Colombia (August 2014-May 2015), where rainfall exceeds 10 000 mm per year. We applied five fertilization treatments (N, P, K, NPK and Control) to two soil type plots. Soil cylinders were removed at pre-established intervals to measure roots.

Results: Phosphorus applications increased fine roots; and more fine roots were produced in sandy than in loam soil. The effects of fertilization were related, but not clearly determined by edaphic conditions.

Conclusions: In this Chocó forest, the production of fine roots was higher in sandy and nutrient-rich soils but belowground net primary productivity was limited by the content of edaphic Phosphorus.

Key words: nutrient limitation; fine root production; fine root decomposition; fine root residence time; tropical soils.

Fine roots are a fundamental component of forest ecosystems because they are necessary for the acquisition of water and nutrients from soil (Jackson et al., 1997). Fine root dynamics include processes such as the production, turnover, and decomposition of fine roots (Green et al., 2005; Jiménez et al., 2009; Violita et al., 2016; Wang et al., 2019a). They are crucial to forest health, affect the entire biogeochemical

complex of the ecosystem, and consequently, they substantially affect the carbon balance of forests (Jiménez et al., 2009). Particularly, fine root production represents between 30 and 40 % of net primary productivity (NPP) in tropical forests (Aragão et al., 2009; Jackson et al., 1997; Saugier et al., 2001). For this reason, fine root production plays an important role in global carbon dynamics, in the biogeochemical

cycle of nutrients, and in mitigating climate change (Jackson et al., 1997; Vitousek & Sanford, 1986); it is strongly influenced by the conditions of the site, both biological (i.e. biome and species), atmospheric (temperature, humidity, and rainfall), and edaphic (soil pH, texture, and nutrient content) (Finér et al., 2011; Metcalfe et al., 2008; Silver et al., 2005).

On the other hand, fine root decomposition is a key process for regulating carbon and nutrient cycling in soils; it is controlled by multiple factors, including climate, temperature, water availability, moisture, and soil properties, such as nutrients, biota (diversity and microbial activity), and oxygen (Chapin III et al., 2002; Zhang & Wang, 2015). If there were no decomposition, ecosystems would quickly accumulate large quantities of detritus, leading to sequestration of nutrients in forms unavailable to plants (Chapin III et al., 2002); therefore, fine root turnover is a critical component of ecosystem nutrient dynamics and carbon sequestration (Gill & Jackson, 2000; Matamala et al., 2003). Different studies have demonstrated that fine root residence time is controlled mainly by soil temperature, moisture status, and nutrient availability (Cordeiro et al., 2020; Hendrick & Pregitzer, 1997; Nadelhoffer, 2000). Despite the importance of fine root dynamics in tropical ecosystems, most of the studies have been done in the temperate regions; therefore, the influence of environmental factors, and specifically the soil nutrients, on the functioning of fine roots in tropical forests is debated and presents considerable uncertainties. This study aims to help filling that knowledge gap.

The availability and release rate of nutrients from the soil limit fine root dynamics of tropical forests (Kochsiek et al., 2013; Yuan & Chen 2012); therefore, evaluating its nutrient limitation is essential to understand the role of these forests as carbon sinks; it is also important to predict how they will respond to various anticipated environmental changes, including increasing N deposition, atmospheric CO₂, drought, and warming (Alvarez-Clare & Mack, 2015; Thornton et al., 2007). It has been hypothesized that lowland tropical rainforests

are limited mainly by the low availability of soil P, due to the high rates of parent material weathering that facilitate mineral losses by leaching, and by its fixation, e.g. in oxides of Fe and Al (Miller et al., 2001; Vitousek, 1984). In contrast, soil N, when biologically fixed, is usually less limiting than P in old soils (Vitousek, 1984; Walker & Syers 1976).

To determine how soil nutrients limit fine root dynamics in tropical forest ecosystems, various methodological approaches have been used. Fertilization with minerals (N, P, K) has been considered as one of the most effective and reliable ways to determine nutritional limitation in tropical forests (Sullivan et al., 2014). Even though, plants develop more fine roots to increase nutrient uptake when nutrients are scarce, the response to the addition of nutrients needed by plants is the increase of fine root growth (Yuan & Chen, 2012); in areas enriched with nutrients whose availability is adequate or excessive, the growth response should be null or even negative (Sullivan et al., 2014). Consequently, higher fine root dynamics are expected when limiting nutrients are added in infertile soils.

However, research evaluating the effects of soil fertilization on fine root production in tropical forests shows contrasting patterns. For example, Cuevas and Medina (1988) observed increases in fine root production with the addition of NH₄Cl in Amazonian forests of Tall Caatinga and Low Bana (spodosols poor in N), and with KH₂PO₄ in forests of Tierra Firme (oxisols) and Low Bana. Yuan and Chen (2012), showed in a meta-analysis that fine root production increased with the application of N and P in low altitude tropical forests, whereas in acrisols (ultisols and oxisols) the fine root production responded negatively to the application of N and positively to the addition of P. Alvarez-Clare et al. (2013) did not find effects of the addition of N and P on fine root production in clayey tropical soils, poor in P and rich in N. The application of N and P had little effect on the dynamics of fine roots in young, N-limited soils, while conversely, the application of N and P in old, P-poor soils increased



the decomposition and turnover of fine roots (Ostertag, 2001). Guo et al. (2020) found that N addition largely increased shoot growth but had a limited effect in root growth in two tree species in China and root mass fraction decreased significantly with high N fertilization. Wurzburger and Wright (2015) reported that the addition of N, P, and K together reduced fine-root biomass in a lowland forest in Panama. Yavitt et al. (2011) reported that fine root production and turnover responded to the addition of K rather than P, and that after 2 years, the K added increased the turnover of fine roots in moderately fertile soils. The addition of N, P, and K together reduced fine-root biomass in a lowland forest in Panama (Wurzburger & Wright, 2015). These results show that the response of fine root dynamics to fertilization is variable and seems to be significantly determined by other edaphic factors, including topography, soil type, texture, and nutrient content.

Evaluations of fertilization effects on fine root dynamics in the tropics have been carried out in forests with average annual rainfall less than 7 000 mm (Alvarez-Clare et al., 2013; Cuevas & Medina, 1988; Yuan & Chen, 2012). As a consequence of global climate change significant increases of rainfall are expected in different tropical regions (Intergovernmental Panel on Climate Change, 2014), which could affect the availability of nutrients and the function of these ecosystems as CO₂ sinks. Consequently, it is crucial to understand how fine root dynamics are affected by nutrient limitation in highly rainy tropical forests, which has not been studied before. Likewise, it is also important answering to which extent edaphic conditions, such as texture and nutrient availability, affect the response of fine root dynamics to fertilization.

The objective of this study is to evaluate the effects of soil fertilization on fine root dynamics in tropical rain forests with topographies and soils of different textures (sandy and loam) in the Chocó biogeographic region, where rainfall exceeds 10 000 mm per year (Poveda et al., 2004). We expect that responses

of fine root dynamics to fertilization (N, P, K) vary with edaphic conditions, such as texture and nutrient content in these forests. In particular, the application of N, P, K and NPK is expected to increase fine root dynamics (production and turnover), especially in soils with sandy textures because their lower capacity of nutrient retention in the soil matrix by their coarse particles makes them more prone to nutrient limitation; contrarily, in loam soils the response to nutrient application is expected to be lower. We also expect that the responses to each nutrient (N, P, K, NPK) applied is different, with a greater influence of P application on fine root dynamics because of the low P contents of soil in these forests (Quinto & Moreno, 2016).

MATERIALS AND METHODS

Study area: the present study was conducted in tropical rain forests of the towns of Pacurita (municipality of Quibdó) and Opopodó (municipality of Condoto), department of Chocó, Colombia. These two forest sites are part of the Chocó region located in the Central North ecogeographic subregion, which includes the upper basins of the Atrato and San Juan rivers (Poveda et al., 2004); the mean temperature is 26 °C and annual precipitation is 8 000 mm. The localities are within the geomorphological unit of Sedimentary Hills of the Tertiary, which are formed by sedimentary rocks of low altitude, composed of sandy claystones, sandstones and limestones. The soils of both sites are ultisols, extremely acidic (pH between 3.7 and 5.5), with very low values of P (0.5-3.5 ppm), Mg (0.06-1.85 cmol kg⁻¹), Ca (0.06-0.96 cmol kg⁻¹) and ECEC (0.56-2.64 cmol kg⁻¹), and intermediate values of K (0.03-0.48 cmol kg⁻¹). Particularly in Opopodó, soils are less steep, with higher contents of sand (62-96 %), organic matter, and total N; while in Pacurita they have greater Al saturation and are loam, with lower contents of sand and higher of clay (Table 1).

In both locations the sampling was carried out in well-conserved primary forests; in

TABLE 1
Parameters of edaphic fertility in the studied forests. Data are means \pm standard deviation

Parameters	Opogodó	Range	Pacurita	Range	Mann-Whitney test
pH	4.97	4.22-5.51	4.03	3.68-4.37	-1 869.0*
Aluminum (Al cmol kg ⁻¹)	0.12 \pm 0.05	0.1-0.3	0.94 \pm 0.21	0.2-1.4	1 790.0*
Al saturation (%)	12.65 \pm 5.25	3.78-31.57	57.21 \pm 9.61	15.6-71.06	1 786.0*
Organic matter (OM %)	11.94 \pm 3.85	4.61-24.74	4.06 \pm 1.27	1.95-5.85	-1 816.0*
Nitrogen (N %)	0.61 \pm 0.22	0.23-1.68	0.20 \pm 0.06	0.1-0.29	-1 815.0*
Phosphorous (P ppm)	1.32 \pm 0.60	0.63-3.5	1.36 \pm 0.64	0.49-3.2	43.5 NS
Potassium (K cmol kg ⁻¹)	0.23 \pm 0.08	0.06-0.48	0.17 \pm 0.09	0.03-0.47	-796.0*
Magnesium (Mg cmol kg ⁻¹)	0.28 \pm 0.21	0.12-1.85	0.18 \pm 0.05	0.06-0.35	-964.0*
Calcium (Ca cmol kg ⁻¹)	0.38 \pm 0.22	0.06-0.96	0.35 \pm 0.10	0.17-0.79	-89.0 NS
ECEC ¹ (cmol kg ⁻¹)	1.03 \pm 0.38	0.56-2.64	1.64 \pm 0.26	0.77-2.19	1 474.5*
Clay (%)	1.04 \pm 2.31	0.0-12.0	18.52 \pm 3.69	10.0-28.0	1 772.5*
Silt (%)	13.23 \pm 4.97	4.0-28.0	28.12 \pm 6.21	8.0-40.0	1 626.0*
Sand (%)	85.71 \pm 6.57	62.0-96.0	53.36 \pm 6.73	42.0-70.0	-1 763.5*
Carbon (C %)	6.93	2.65-14.35	2.35	1.13-3.39	-1 816.0*
C/N	11.35	2.49-11.7	11.77	11.17-11.98	35.0 NS
N/P	0.46	0.10-2.0	0.15	0.03-0.59	-1 541.0*
Number of samples	75		50		

¹ Effective cation exchange capacity. The asterisks (*) indicate significant differences $P < 0.05$. NS: Non-Significant.

Opogodó, three permanent plots of one hectare were established inside the facility of the Universidad Tecnológica del Chocó “Diego Luis Córdoba” in 2 013. In Pacurita, two permanent plots were established in the forest reserve area called Estación Biológica Pacurita.

Methods: o evaluate the effect of fertilization on the dynamics of fine roots, a randomized complete block design was established (Shieh & Jan, 2004) with five fertilization treatments (N, P, K, NPK and Control) and five repetitions (blocks), three of them in Opogodó and two in Pacurita. The blocks consisted of permanent plots of 1 ha. For the application of the fertilization treatments, each plot was divided into five experimental units of 20 x 100 m (0.2 ha), where the fertilization treatments were applied randomly. Likewise, to evaluate the variability within each experimental unit, they were divided into 20 x 20 m recording units, where the dynamics of fine roots were monitored.

The fertilizers were applied to each experimental unit by broadcast; two-meter perimetric

strips were left unfertilized inside each experimental unit to reduce the risk of nutrient contamination from adjacent plots due to the effects of runoff and leaching. In order to reduce the influence of topography on the contamination and losses of nutrients of neighboring units, the longest side of the experimental units in Pacurita was arranged parallel to the slope of the terrain.

The doses and timing of fertilizer application were similar to those reported in experiments carried out in other low altitude tropical forests (Mirmanto et al., 1999; Wright et al., 2011). Thus, along one year, four equal doses were applied starting in August 2014 and finishing in May 2015 (in the months of August, November, February and May) in the following amounts and formulations: for the N treatment, 125 kg N ha⁻¹ year⁻¹ were applied in the form of urea ((NH₂)₂CO), distributed in four doses, each one of 2.72 kg of Urea per recording unit; for the P treatment, 50 kg P ha⁻¹ year⁻¹ were added in the form of phosphoric rock (H₃PO₄) distributed in four doses of 1 kg of H₃PO₄ per recording unit; for the K treatment, 50 kg K



ha⁻¹ year⁻¹ were applied in the form of potassium chloride (KCl) distributed in four doses of 1 kg of KCl per recording unit; for the NPK treatment, each of the doses mentioned in the previous treatments were applied together; and for the control no fertilizers were applied.

Measurement of the production and residence time of fine roots: to measure the production of fine roots, a modification of the growth cylinder method (ingrowth cores) was used (Moreno, 2004). In essence, the method consists of extracting a soil core from which roots are removed; then, the soil is returned to the same hole and left for a time period to allow the growth of fine roots. Soil cylinders are removed at pre-established intervals, roots are extracted, and fine root production are determined (Hendricks et al., 2006). To control that the volume of soil deposited and removed was the same, three thick metal wires were vertically installed in the walls and left in each hole (Moreno, 2004); these wires were used as guides to fill the hole with soil and to align the core during subsequent sample collection. Another advantage of this modification is that the soil deposited back into the hole is not packed in any container, in such a way that it is completely in contact with the surrounding environment and there are no obstacles that could limit the root growth as happens with the traditional method, in which the deposited soil is packed in a mesh-made container.

Each 20 x 20 m recording unit was subdivided into 4 (10 x 10 m squares). Then, the modified growth cylinders were placed in the center of each 10 x 10 m square, where two samples were extracted (0-10 cm and 10-20 cm deep) with an Eijkelkamp® soil core sampler (8 cm in diameter and 15 cm deep). Standing stocks of fine roots were sampled in the first sampling campaign before the application of fertilization treatments, and fine root production were sampled every three months in all the holes, which were filled again with root-free soil previously collected and prepared of the respective soil depth. Subsequently, the separation and manual extraction of fine roots (with

diameters ≤ 5 mm) was carried out using plastic trays and sieves of different calibers. After extracting fine roots, the soil was introduced back into the respective hole, while roots were transported to the Botany and Ecology laboratory of the Technological University of Chocó for processing. This procedure was performed quarterly for one year. In each sampling campaign, 100 soil cylinders were evaluated at each of the two depths per plot; therefore, a total of 1 000 fine root samples were taken in each sampling in the five plots evaluated. Fine-root sampling began six months after the first application of fertilization treatments to allow time for their effects.

In the laboratory, a final cleaning of fine roots was made with sieves of different calibers and water under pressure. Subsequently, fine root biomass was obtained by weighing in an analytical balance (0.001 g) after drying at 70 °C in a forced ventilation oven for 72 h (Acequilab Ltda®); the fine root production was determined as the accumulated value over time of fine root biomass in the ingrowth cores. By using appropriate expansion factors, the values obtained for fine root biomass (standing stock as measured in the first sampling campaign) and fine root production in the first 20 cm of soil (as measured through the procedure described above in the ingrowth cores and after adding values found in 0-10 and 10-20 cm) were expressed in t ha⁻¹ and t ha⁻¹ year⁻¹, respectively. The residence time of fine roots (years) was estimated as the division of fine root biomass by its production; the above, based on the fact that ecosystems are in a stable dynamic state (Olson, 1963).

Data analysis: to evaluate the effect of soil fertilization on the dynamics of fine roots, first, the assumptions of normality and homogeneity of variances were evaluated with the Bartlett, Hartley and Kurtosis statistics. Initially, mean values of root biomass, production and residence time were compared between soil types (sandy and loam) with the *T-student* test when data had normal statistical distribution; otherwise, we used the Mann-Whitney

(W) test (Hoshmand, 1998). When possible, data were log transformed to reach normal distribution. Subsequently, the variation of the dynamics (production and residence time) of fine roots as a function of the fertilization treatments, localities, and their interactions (localities x treatments) were evaluated using a two-way analysis of variance (ANOVA) with mixed effects, Tukey's Multiple Range Test, and General Linear Models (Hoshmand, 1998). Statistical analyses were performed in the R programming environment (R Core Team, 2017).

RESULTS

The production of fine roots in these tropical rain forests in the 0-20 cm layer was (mean \pm standard deviation) $4.16 \pm 1.38 \text{ t ha}^{-1} \text{ year}^{-1}$ in sandy-textured soils in forests of Opogodó, and $3.45 \pm 1.05 \text{ t ha}^{-1} \text{ year}^{-1}$ in loam-textured soils in forests of Pacurita (Table 2); with significant differences between them. Values of fine root biomass and production were higher in the 0-10 cm than in the 10-20 cm soil layer (Table 3). The interaction between factors (texture type * fertilization treatment) was also significant (Table 4), which means that at least one fertilization treatment had different effect between locations. Indeed, the production of

fine roots was significantly higher in sandy soils (but not in loamy soils) in response to the application of P, with respect to the Control (Fig. 1). Results of fine root production in each soil layer show that the effects described above occurred only in the 0-10 cm layer, while the effect of soil texture, fertilization treatment and interactions were not significant in the 10-20 cm layer (Table 5). The residence time of fine roots was 1.56 ± 0.76 years in soils with a sandy texture, and 1.96 ± 0.76 years in soils with a loam texture (Table 2); with significant differences between localities (Table 4). The interaction between factors also showed significant effects on the residence time of fine roots (Table 4, Fig. 1), which means that fertilization treatments did not have the same effect in the two texture types (Fig. 1).

DISCUSSION

Fine root dynamics of tropical forests of Chocó in soils of different texture: In the tropical rainforests of the biogeographic Chocó region, the dynamics (productivity and residence time) of fine roots were greater in sandy textured soils, compared to soils with loam texture; i.e., in sandy soils, fine roots grew faster and had shorter life span. These results are in line with Aragão et al. (2009), who found

TABLE 2
Production and residence time of fine roots in tropical rain forests with different soil texture of Chocó, Colombia

		Fine root biomass (t ha^{-1})							
Soil texture	Mean	S.D.	C.V. (%)	S.E.	Min.	Max.	Kurtosis	Mann-Whitney	
Sandy	5.90	1.84	31.19	0.21	2.22	12.07	0.97	1.1676 ns	
Loam	6.28	1.65	26.37	0.23	2.52	11.53	1.36		
		Fine root production ($\text{t ha}^{-1} \text{ year}^{-1}$)							
Soil texture	Mean	S.D.	C.V. (%)	S.E.	Min.	Max.	Kurtosis	Mann-Whitney	
Sandy	4.16	1.38	33.09	0.16	1.81	9.27	1.12	1.283**	
Loam	3.45	1.05	30.56	0.15	2.10	6.90	2.62		
		Fine root residence time (years)							
Soil texture	Mean	S.D.	C.V. (%)	S.E.	Min.	Max.	Kurtosis	Mann-Whitney	
Sandy	1.56	0.72	45.86	0.08	0.44	4.32	3.69	1.222***	
Loam	1.96	0.76	38.65	0.11	0.96	3.79	0.03		

S.D. standard deviation, C.V. coefficient of variation, E.E. standard error, Min minimum value, Max maximum value. In the Mann-Whitney test, asterisks indicate significant differences (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.001$; ns $P > 0.05$.



TABLE 3
Fine root biomass and production in tropical rain forests with different soil texture and fertilization treatments of Chocó, Colombia

Fine Root Biomass (0-10 cm)		Texture soil	N	Min	Max	Mean	S.E.	Variance	S.D.	Median	Kurtosis	C.V.	t-student tests
	Sandy		75	1.08	7.97	3.53	0.17	2.04	1.43	3.21	0.98	40.44	1.601 ns
	Loam		50	1.19	9.13	3.96	0.21	2.24	1.50	4.07	1.48	37.75	
Fine Root Biomass (10-20 cm)		Texture soil	N	Min	Max	Mean	S.E.	Variance	S.D.	Median	Kurtosis	C.V.	Mann-Whitney tests
	Sandy		75	0.79	6.54	2.37	0.11	0.94	0.97	2.32	3.52	41.01	0.047 ns
	Loam		50	1.07	4.37	2.32	0.11	0.63	0.79	2.33	-0.08	34.08	
Fine Root Production (0-10 cm)		Texture soil	N	Min	Max	Mean	S.E.	Variance	S.D.	Median	Kurtosis	C.V.	Mann-Whitney tests
	Sandy		75	1.03	5.29	2.65 a	0.10	0.82	0.91	2.59	-0.15	34.13	3.4145***
	Loam		50	1.09	5.32	2.13 b	0.11	0.58	0.76	2.07	5.70	35.64	
Fine Root Production (10-20 cm)		Texture soil	N	Min	Max	Mean	S.E.	Variance	S.D.	Median	Kurtosis	C.V.	Mann-Whitney tests
	Sandy		75	0.58	6.15	1.51	0.09	0.65	0.81	1.28	14.00	53.52	0.816 ns
	Loam		50	0.50	2.50	1.31	0.06	0.20	0.45	1.33	0.24	34.36	

N: number of subplots, S.D.: standard deviation, C.V.: coefficient of variation, S.E.: standard error, Min is the minimum value, Max is the maximum value. In the Mann-Whitney test, asterisks indicate significant differences (*): $P < 0.05$; (**): $P < 0.01$; (***): $P < 0.001$; ns $P > 0.05$.

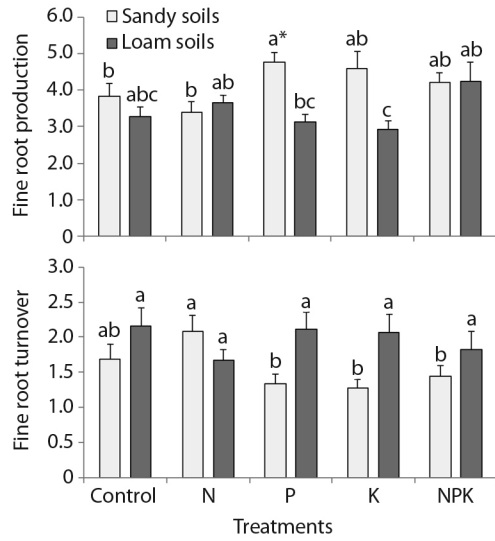


Fig. 1. Effect of soil fertilization treatments with N, P, K and NPK on the rates of production ($t\ ha^{-1}\ year^{-1}$), and residence time (years) of fine roots in two tropical rain forests with differences in soil texture (sandy and loam) in Chocó, Colombia. The asterisks (*) indicate significant differences between the fertilization treatments and the Control. The letters (a, b, c) indicate significant differences between fertilization treatments.

that allocation of NPP to below-ground shows no relationship to soil fertility but appears to decrease with the increase of soil clay content. Higher sand content favors soil aeration (oxygen content) and macroporosity, and promotes growth and productivity of fine roots, as has been evidenced in previous research carried out in tropical rainforests (Jiménez et al., 2009; Kochsiek et al., 2013; Metcalfe et al., 2008; Quinto et al., 2016). In summary, these results bring strong evidence that differences of edaphic conditions generate significant effects on the dynamics of fine roots in low altitude tropical rainforests.

Effect of soil fertilization on the dynamics of fine roots: In these tropical rain forests of the biogeographical Chocó, the effect of soil fertilization on the dynamics of fine roots apparently was determined by the edaphic conditions, in terms of texture, specific to each locality. In particular, it was found that fine

TABLE 4

Two-way ANOVA with interactions and fixed effects of soil texture (sandy and loam) and fertilization treatments (control, N, P, K and NPK) on the production and residence time of fine roots in tropical rain forests of Chocó, Colombia

Fine root production (t ha ⁻¹ year ⁻¹)					
	Sum of squares	Degrees of freedom	Mean square	F	P - value
Texture type	15.28	1	15.28	10.64	0.00145
Treatments	10.16	4	2.54	1.769	0.139
Interaction	19.43	4	4.86	3.383	0.0117
within	165.12	115	1.44		
Total	210.00	124			
Fine root residence time (years)					
	Sum of squares	Degrees of freedom	Mean square	F	P - value
Texture type	4.75	1	4.75	9.44	0.0026
Treatments	2.55	4	0.64	1.27	0.287
Interaction	5.89	4	1.47	2.93	0.0238
within	57.83	115	0.50		
Total	71.02	124			

TABLE 5

Two-way ANOVA with interactions and fixed effects of soil texture (sandy and loam) and fertilization treatments (control, N, P, K and NPK) on fine root production at 0-10 and 10-20 cm-depth in tropical rain forests of Chocó, Colombia

Fine root production (t ha ⁻¹ year ⁻¹) (0-10 cm)					
	Sum of squares	Degrees of freedom	Mean square	F	P - value
Texture	8.02	1	8.019	12.33	0.0006373
Treatment	7.77	4	1.941	2.986	0.02185
Interaction	6.62	4	1.656	2.547	0.04313
Within	74.78	115	0.650		
Total	97.19	124			
Fine root production (t ha ⁻¹ year ⁻¹) (10-20 cm)					
	Sum of squares	Degrees of freedom	Mean square	F	P - value
Texture	1.15	1	1.150	2.457	0.1197
Treatment	0.58	4	0.145	0.3103	0.8706
Interaction	3.66	4	0.915	1.955	0.1061
Within	53.82	115	0.468		
Total	59.21	124			

root production increased with the application of P in sandy soils. Therefore, a limitation of the underground net primary productivity was evidenced by the edaphic availability of P in these soils, which is in line with the hypothesis of P limitation proposed by Vitousek (1984), Vitousek et al. (2010), Yuan and Chen (2012), and Dalling et al. (2016), among others. However, the addition of N, P, and K did not have the same effect in promoting fine root

production, which is in line with results reported by Wurzbürger and Wright (2015), who found that the addition of these three nutrients actually reduced standing fine-root biomass and mycorrhizal colonization of fine roots; they also found that fertilization with these three nutrients shifted allocation away from fine roots to aboveground biomass. It seems that the effect of nutrient application varies depending on complex interactions among nutrients



applied, mycorrhizae, and allocation responses of plants. On the other hand, fertilization did not have significant effects on residence time; it appears that the effects of soil fertilization on the dynamics of fine roots are more evident in the production than in the residence time.

However, the results of fine root production described above for the 0-20 cm soil-layer were not recorded in the 10-20 layer, where the effect of soil texture or fertilization treatments were not significant. It has been widely reported that fine root biomass, production, decomposition, and turnover are all higher in the superficial layers of soil than in the deeper ones (Cordeiro et al., 2020; Cusack & Turner, 2021; Pries et al., 2018), which also was found in this study. Although the nutrient addition has been less studied, the effect of nutrient application also has been more pronounced in the surface than in the deeper soil layers (Wang et al., 2019b), in line with our results.

The fact that the responses to fertilization were so different between localities differing in edaphic and topographic characteristics, suggests that the particular conditions of the site explain such variation. Other authors reported similar results to ours in the sandy soils and flat topography of Opogodó, where fertilization with P increased the production of fine roots; for example, Cuevas and Medina (1988) in Amazonian forests of Tierra Firme (Oxisols) and Low Bana, with sandy soils. In a meta-analysis, Yuan and Chen (2012), also found that fine root production increased with the application of P in low altitude tropical forests. Based on these observations, it seems that in tropical sandy soils, the greater availability (or addition) of edaphic P increases the production of fine roots.

Likewise, results of the present study for the sandy soils of Opogodó are similar to those reported by Jiménez et al. (2009) and Kochsiek et al. (2013), who found higher production of fine roots in tropical sandy soils, which could be attributed to at least two causes: 1) given that sandy soils have lower mineral retention capacity (P, K, Ca, Mg) than loam soils (Jiménez et al., 2009; Silver et al., 2000), as well

as higher release rate of NH_4^+ , PO_4^{3-} and K^+ (Kochsiek et al., 2013), the higher production of fine roots probably constitutes a response of plants to capture more nutrients and reduce their losses due to leaching and runoff, especially in high-rainfall forests, such as these of Chocó; 2) in fine-textured tropical soils, the higher nutrient fixation in addition to the lower volume of macropores probably limits the production of fine roots.

In this study, soil fertilization with N, P, K and NPK had little effect in loam soils. Apparently, the greater fixation of mineral ions that occurs in these tropical soils tends to cause immobilization of multiple nutrients, which probably makes it difficult to show the limitation of each particular mineral nutrient (Alvarez-Clare et al., 2013). In addition to the fixation and occlusion of cations, other factors may have contributed to the lack of response of fine root production to treatments of N, P and K application; among them, the lower porosity that reduces the penetration of nutrients applied through fertilization, the high rainfall, and the steep topography, which cause easy washing by runoff and leaching of added ions (Quinto & Moreno, 2016; Silver et al., 2000). In addition to the above reasons, Sayer and Banin (2016), in an analysis of fertilization experiments found that one of the main effects of nutrient application to the soil in tropical forests is the increase of added nutrients in plant tissues such as leaves and fine roots, without affecting other parameters such as the variables of fine root dynamics measured in the present study.

Another reason that would explain the little effect of the N and K addition on fine root dynamics in the studied forests is the fact that these forests have soils rich in N with moderate K contents (Table 1), which would have prevented significant effects of the application of these nutrients on the fine root dynamics. Apparently, the high levels of total edaphic N, added to the high rates of biological fixation of N that regularly occur in this type of ecosystems (Cleveland et al., 1999), generate an adequate supply of N and therefore, no limitation of underground net primary productivity

by this nutrient (Vitousek, 1984; Vitousek et al., 2010; Walker & Syers 1976). Likewise, K may not be limiting the dynamics of fine roots because it is a highly mobile nutrient, and its concentrations remain high due to the input to the soil from forest canopy (Osorio, 2014), which would explain the little effect of its application on the dynamics of fine roots.

In the tropical rain forests of the biogeographic Chocó, the production of fine roots was higher in sandy and nutrient-rich soils. The effects of soil fertilization on the production of fine roots were associated with the particular edaphic conditions of each locality. Likewise, the production of fine roots increased with the application of P in sandy soils; therefore, a limitation of underground net primary productivity was evidenced by the content of edaphic P in such soils.

Ethical statement: the authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgements section. A signed document has been filed in the journal archives.

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RESUMEN

Efectos de la fertilización con nutrientes (N, P, K) sobre la dinámica de raíces finas en bosques húmedos tropicales con diferente textura del suelo en la región del Pacífico colombiano

Introducción: La dinámica de las raíces finas incluye producción, rotación y descomposición; son cruciales para la salud de los bosques, afectan todo el complejo biogeoquímico del ecosistema y, en consecuencia, afectan sustancialmente el balance de carbono. Sin embargo, la influencia de los factores ambientales y la limitación de nutrientes del suelo en las raíces finas presenta incertidumbres considerables y no se ha estudiado en bosques tropicales con más de 7 000 mm de precipitación anual.

Objetivo: Medir el efecto de la fertilización en las raíces finas en el bosque chocoano de alta precipitación.

Métodos: Se trabajó en dos sitios de la región del Chocó, Colombia (agosto 2014-mayo 2015), donde las precipitaciones superan los 10 000 mm anuales. Se aplicaron cinco tratamientos de fertilización (N, P, K, NPK y Control) a dos parcelas por tipo de suelo. Los cilindros de suelo se retiraron a intervalos preestablecidos para medir las raíces.

Resultados: Las aplicaciones de fósforo aumentaron las raíces finas; y se produjeron más raíces finas en suelos arenosos que en francos. Los efectos de la fertilización estuvieron relacionados, pero no claramente determinados por las condiciones edáficas.

Conclusiones: En este bosque chocoano, la producción de raíces finas fue mayor en suelos arenosos y ricos en nutrientes, pero la productividad primaria neta subterránea estuvo limitada por el contenido de fósforo edáfico.

Palabras clave: limitación de nutrientes; producción de raíces finas; descomposición de raíces finas; recambio de raíces finas; suelos tropicales.

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