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Precipitation effects on soil characteristics in tropical rain forests of the Chocó biogeographical region

UNIVERSIDAD NACIONAL DE COLOMBIA SEDE MEDELLÍN FACULTAD DE CIENCIAS AGRARIAS

Efectos de la precipitación sobre las características del suelo en bosques lluviosos tropicales de la región del Chocó biogeográfico

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ABSTRACT

Key words:
Lixiviation
Nutrient limitation
Tropical rainforest
Ultisol

Average annual precipitation (AAP) is one of the principal environmental factors that regulates processes in terrestrial ecosystems. The effect of AAP on the availability of edaphic nutrients is poorly understood, especially in tropical zones with high rainfall. In order to evaluate the effects of high AAP on the availability of soil N, P, and K, physicochemical parameters were measured in soils of three tropical rainforests in the Chocó biogeographical region with different AAPs (7,500, 8,000, and 10,000 mm yr^{-1}). Furthermore, a bibliographical review was carried out that including studies for distinct tropical Ultisols and AAP ranging from 1,800 to 10,000 mm yr^{-1}. The evaluated soils presented extreme acidity with high contents of Al, organic matter (OM) and total N, and low quantities of P, Mg, and Ca. The K concentrations were intermediate and the effective cation exchange capacity (ECEC) was low. On the other hand, in the evaluation of the influence of the AAP on the availability of N, P, and K in the soil, contrasting tendencies were observed. On one side, a positive curvilinear relationship was found between the availability of N and the increase in the AAP. On the other side, the available P content significantly decreased with increasing AAP. In conclusion, the excessive AAP resulted in increases in total N and low availability of P, thereby altering the dynamics of the nutrients and the carbon balance of the tropical forest.

RESUMEN

Palabras claves:
Lixiviación
Limitación de nutrientes
Bosques tropicales
Ultisoles

La precipitación promedio anual (PPA) es uno de los principales factores ambientales que regula el funcionamiento de los ecosistemas terrestres. El efecto del incremento de la PPA sobre la disponibilidad de los nutrientes edáficos es aun pobremente comprendido, principalmente en zonas tropicales de alta pluviosidad. Para evaluar la influencia de la alta PPA sobre la disponibilidad de N, P y K en el suelo, se midieron parámetros fisicoquímicos del suelo en tres bosques lluviosos tropicales de la región del Chocó biogeográfico con diferente PPA (7.500, 8.000 y 10.000 mm $año^{-1}$). Además, se realizó una revisión bibliográfica que incluyó datos de distintos Ultisoles tropicales en sitios con PPA entre 1.800 y 10.000 mm $año^{-1}$. Los suelos en el Chocó biogeográfico fueron extremadamente ácidos, con altos contenidos de Al, materia orgánica (MO) y N total, y cantidades bajas de P, Mg y Ca. Los valores de K fueron intermedios y la CICE fue baja. Por otra parte, al evaluar la influencia de la PPA sobre la disponibilidad de N, P y K del suelo, se observaron tendencias contrastantes. De un lado, se encontró una tendencia curvilínea positiva entre la disponibilidad de N y el aumento en PPA. Por otro lado, el contenido de P disponible disminuyó significativamente con el incremento en PPA, mientras que el contenido de K edáfico no presentó una relación significativa con PPA. En conclusión, la PPA excesiva ocasionó incrementos en N total y baja disponibilidad de P, lo cual se altera la dinámica de nutrientes y el balance de carbono de los bosques húmedos tropicales.

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Average annual precipitation (AAP) is one of the principal environmental factors that regulate processes of terrestrial ecosystems (Chapin III *et al*., 2002). The effect of variations in frequency, intensity, and seasonality of the AAP has been documented on fundamental processes such as photosynthesis (Salisbury and Ross, 1994), net primary productivity (NPP) (Schuur, 2003), development and meteorization of soils (Jenny, 1941; Buol *et al*., 1981) and availability and recycling of nutrients (Schuur and Matson, 2001; Santiago *et al*., 2005; Alvarez-Clare and Mack, 2011), among others. Increasing AAP increases depth of carbonates, inorganic nitrogen and clay, as well as soil acidity and losses of nutrients through lixiviation (Jenny, 1941; Austin and Vitousek, 1998). In addition, greater AAP changes the C/N ratio and the concentration of foliar nutrients, and reduces organic matter (OM) decomposition rates, mineralization of soil N and organic P, as well as nitrification (Schuur and Matson, 2001; Schuur, 2003; Santiago *et al*., 2005; Alvarez-Clare and Mack, 2011; Posada and Schuur, 2011).

Soil nutrient availability affects soil fertility, photosynthesis, plant growth, and productivity of terrestrial ecosystems (Salisbury and Ross, 1994; Chapin III *et al*., 2002). It has been documented that contents of N, P, and K limit the biological processes of tropical ecosystems (Tripler *et al*., 2006; Elser *et al*., 2007; LeBauer and Treseder, 2008; Vitousek *et al*., 2010) and that AAP levels affect the availability of nutrients (Austin and Vitousek, 1998; Posada and Schuur, 2011). Evaluating the relationship between these two variables is vital for improving the understanding of the ecology of tropical rainforests, and particularly for understanding the effect of changing AAPs that may result from shifts in global climate.

Results of studies on relationship between AAP and concentrations of N, P, and K in the soil of tropical forests are diverse. For example, Austin and Vitousek (1998) reported significant reductions of soil total N, available P, and exchangeable K with increasing AAP. Contrarily, Jenny (1941), Santiago *et al.* (2005) and Posada and Schuur (2011), reported increases in total soil N with increased AAP, whereas Alvarez-Clare and Mack (2011) did not find evidence of reduced edaphic P or N with an increase in AAP. A methodological limitation may have caused this variation because the majority of the studies were carried out in sites with AAPs under 5,000 mm yr^{-1}. Only Posada and Schuur (2011) presented data from forests with AAP of up to 9,510 mm yr^{-1}.

The central Pacific region of Colombia, which presents some of the highest AAPs in the world (> 7000 mm yr^{-1}) (Poveda *et al*., 2004), offers a tremendous opportunity to evaluate hypotheses related to the influence of AAPs on N, P, and K concentrations in soils. As a result, this study is aimed to explore the relationship between edaphic concentrations of N, P, and K with the AAP of tropical rainforests and, in particular, the differences in the contents of these nutrients in soils of tropical rainforests of the Colombian Pacific region, which is subjected to high AAP levels. In order to accomplish these goals, the edaphic fertility of three tropical rainforests in the Colombian Pacific region was evaluated, and a bibliographic review was carried out that included data on the edaphic content of N, P, and K of Ultisol soils from low-altitude tropical rainforests.

MATERIALS AND METHODS

Location

The study area is located in the tropical rainforests of the localities of Pacurita (municipality of Quibdó), Salero (municipality of Unión Panamericana) and Opogodó (municipality of Condoto), in the department of Chocó, Colombia. These locations form part of the ecogeographic subregion of the Central North of Chocó biogeographical area, which contains the high-altitude watersheds of the Atrato and San Juan rivers, with piedmont and low hills, and moist, terraced soils developed from transitional sedimentary rock. These sites are on tertiary sedimentary hills between 100 and 200 m in altitude and were formed by sedimentary rocks composed of sandy argillite, sandstone and limestone (Poveda *et al*., 2004). The characteristics of the study sites are described in Table 1.

Plot Establishment

Seven permanent 1-ha plots were established between 2005 and 2013 using the BIOTROP methodology (García *et al*., 2003; Melo and Vargas, 2003). The two plots in Salero consisted of 20 x 500 m rectangles and the other five plots established in Opogodó and Pacurita consisted of 100 x 100 m squares. These plots were divided into 25, 20 x 20 m sampling units (400 m^2) in which soil samples were taken for the present study.

Table 1. Environmental characteristics of the three study sites in the tropical rainforests of Chocó, Colombia.

Sites	Salero	Opogodó	Pacurita
Municipality	Unión Panamericana	Condoto	Quibdó
Geographic location*	5º18´950´´ N 76º36´742´´ W	5°04´079" N 76°64´74" W	5°41' 55.8" N 76°35'59.4" W
Temperature (°C)	26 – 30	26 – 30	26
Precipitation (mm yr^{-1})	7500	8000	10000
Altitude (m)	100 – 150	70	106 – 130
Relative humidity (%)	90	90	87
Soil type	Ultisol	Ultisol	Ultisol
Topography	Slightly inclined to steep	Flat to slightly inclined	Slightly inclined to steep
Drainage	Imperfect to excessive	Imperfect to excessive	Imperfect to excessive
Geomorphologic unit	Structural to erosional knoll	Colluvial alluvial piedmont	Structural to erosional knoll
Parent material	Sedimentary tertiary rock	Sedimentary tertiary rock	Sedimentary tertiary rock
Life zone	Tropical wet forest	Tropical rain forest	Tropical rain forest l
Dominant tree species*	*Mabea chocoensis* *Pouteria* sp *Oenocarpus bataua* *Eschweilera pittieri* *Croton jorgei*	*Wettinia quinaria*, *Mabea occidentalis* *Calophyllum auratum* *Eschweilera sclerophylla* *Oenocarpus bataua*	*Calophyllum auratum* *Eschweilera sclerophylla* *Jessenia bataua* *Protium apiculatum* *Brosimum utile*
Dominant botany families*	Sapotaceae Lecythidaceae Arecaceae Euphorbiaceae Chrysobalanaceae	Arecaceae, Fabaceae Lecythidaceae Hypericaceae, Sapotaceae Euphorbiaceae	Arecaceae, Sapotaceae Lecythidaceae Clusiaceae, Moráceae Chrysobalanaceae

*Information recorded directly on sample sites.
Information from West (1957), Malagon *et al.* (1995), Holdridge (1996), Garcia *et al.* (2003), Poveda *et al.* (2004), Ruiz–Murcia (2010), and Gardi *et al.* (2014).

Soil Analysis

In order to evaluate soil fertility, compound soil samples were taken from each sampling unit that was a mixture of 5 samples taken at a depth of 20 cm from the four corners and the center of the sampling plots. In each of the seven plots, 25 compound samples were taken for a total of 175 samples. Clay, sand and silt percentage, pH, OM content, and N, P, K, Ca, Mg concentrations were analyzed using the following techniques: Bouyoucos for textural fractions, potentiometric in water solution (1:2) for pH, Walkley and Black for OM, Micro- Kjeldahl technique for total N, ascorbic acid in an UV-VIS spectrophotometer after extraction with the Bray II method for available P, atomic absorption for Ca, Mg, and K extracted with ammonium acetate (Osorio, 2014).

In order to relate the edaphic concentration of nutrients to the AAP, a bibliographic review was conducted including data from similar depth to the one used in this study (0-20cm) for Ultisols from tropical rainforests. The studies included in the analysis came from Alvarez-Clare and Mark (2011), Aragão *et al.* (2009), John *et al.* (2007), Palmiotto *et al.* (2004), Powers *et al.* (2005), Ruokolainen *et al.* (2007), and Santiago *et al.* (2005). This analysis covered an AAP range of 1,800 to 10,000 mm yr^{-1}, and altitudes between 50 and 900 m.

Statistical analysis

In order to compare the soil characteristics (texture, OM, pH, Al, N, P, Ca, K, Mg, ECEC) of the three study sites (Salero, Opogodó and Pacurita), the non-parametric test of Mann-Whitney was used for total N and the Kruskal Wallis test was used for the other soil characteristics because they did not comply with the assumptions of normality and homogeneity of variance for the data, as evaluated with the tests of Bartlett and Hartley. Spearman correlation analysis between sand percentage and other soil characteristics was used. Lineal and polynomial regression analyses were used to relate soil N, P, and K concentrations to AAP (Hoshmand, 1998). The analyses were carried out with the Statgraphics Centurion XV (StatisticalGraphics Corp., 2002) and The R Project for Statistical Computing (www.r-project.org/) software.

RESULTS AND DISCUSSION

Characteristics of the rainforest soils of the Chocó biogeographical region

The soils of the tropical rainforests Salero, Opogodó and Pacurita were extremely acidic, with high Al saturation in Salero (38.5%) and Pacurita (57.2%) and low in Opogodó (12.7%). Likewise, high concentrations of soil OM and total N were seen in the majority of the sampling units in Opogodó (OM = 11.9%; N = 0.61%). However, the soil P, Mg, and Ca were very low, while the values of K were intermediate and the ECEC was low in the three zones. The low pH of soils from the forests of this study agreed with studies in low-altitude tropical rainforests (Buol *et al.*, 1981; Vitousek, 1984; Vitousek and Sanford, 1986; Malagón *et al.*, 1995; Powers *et al.*, 2005; Posada and Schuur, 2011). The acidic condition is mainly generated by the lixiviation of basic cations (Ca, Mg, K and Na) and the accumulation of acid cations (Al and H) because of environmental factors such as high AAP; among other causal factors of acidification in these soils are high OM contents that release carbonic acid and the symbiotic fixation of N_2 that releases H^+ ions (Jenny, 1941; Sadzawka and Campillo, 1993).

With the exception of exchangeable Ca, all of the fertility parameters presented significant differences among sites (Table 2). The soils from Pacurita, which were subjected to the highest AAP (10,000 mm yr^{-1}), presented higher acidity, clay contents, Al saturation, and ECEC, and lower concentrations of OM, total N, K, and Mg. The soils from Opogodó, which were subjected to the lowest precipitation among the studied sites (8,000 mm yr^{-1}), presented higher contents of sand, OM, and total N. Finally, the soils of Salero, registered high silt content.

Table 2. Soil characteristics in three tropical rainforests of the Colombian Pacific region.

Fertility parameters	Salero	Opogodó	Pacurita	Statistical test
pH	4.8 ± 0.16 b	5.0 ± 0.28 a	4.0 ± 0.16 c	114.9 ***
Aluminum (Al $cmol_c$ kg^{-1})	0.48 ± 0.09 b	0.12 ± 0.05 c	0.94 ± 0.21 a	149.9 ***
Al saturation (%)	38.5 ± 8.40 b	12.7 ± 5.25 c	57.2 ± 9.61 a	143.1 ***
Organic matter (%)	6.7 ± 2.30 b	11.9 ± 3.85 a	4.1 ± 1.27 c	113.1 ***
Nitrogen (%)	ND	0.61 ± 0.22 a	0.20 ± 0.06 b	1815.0 ***
Phosphorous (mg kg^{-1})	1.64 ± 0.62 a	1.32 ± 0.60 b	1.36 ± 0.64 ab	11.4 **
Potassium ($cmol_c$ kg^{-1})	0.22 ± 0.06 a	0.23 ± 0.08 a	0.17 ± 0.09 b	19.5 ***
Magnesium ($cmol_c$ kg^{-1})	0.27 ± 0.12 a	0.28 ± 0.21 a	0.18 ± 0.05 b	28.7 ***
Calcium ($cmol_c$ kg^{-1})	0.32 ± 0.15 a	0.38 ± 0.22 a	0.35 ± 0.10 a	5.5 NS
ECEC ($cmol_c$ kg^{-1})	1.3 ± 0.28 b	1.0 ± 0.38 c	1.6 ± 0.26 a	73.0 ***
Clay (%)	16.9 ± 4.12 b	1.0 ± 2.31 c	18.5 ± 3.69 a	121.5 ***
Silt (%)	45.5 ± 6.34 a	13.2 ± 4.97 c	28.1 ± 6.21 b	124.6 ***
Sand (%)	37.5 ± 6.34 c	85.7 ± 6.57 a	53.4 ± 6.73 b	130.1 ***
Carbon (C %)	3.9	6.9	2.4	113.1 ***
Precipitation (mm yr^{-1})	7,500	8,000	10,000	ND
Topography (%)	24.5	<7.5	25.5	ND
Number of samples	50	75	50	ND

Data are means ± S.D. Letters a, b, and c denote significant differences at $P \leq 0.05$. ***, **, and * indicate values ≤0.001, 0.01, and 0.05, respectively. NS: not significant. ND: non-determined values. ECEC Effective cation exchange capacity.

The OM concentrations were high in the studied ecosystems of Chocó, with significant variations between sites, which can be attributed to differences in the AAP, but mainly due to litterfall (Unpublished data from a companion study) and topographical conditions (Table 2). For example, in Salero and Pacurita, the terrain presented higher sloping (topography ≈ 24.5%) and small hills that favor drainage and the mechanical dragging of OM over the soil by surface runoff; while in Opogodó, the topography was flatter (topography=7.5%), which reduces the loss of OM from the soil.

The high accumulation of OM in the soils of Salero, Pacurita, and Opogodó can be explained by the abundant AAP and its consequent lixiviation of soil, which have the potential of decreasing the decomposition rate of OM (Schuur 2001) and the foliar concentrations of N, P, Ca, and Mg, as well as increasing C/N ratio (Austin and Vitousek, 1998; Schuur and Matson, 2001; Santiago *et al.*, 2005; Posada and Schuur, 2011). The decomposing activity of microorganisms can be reduced by the low availability of nutrients (Kaspari *et al.*, 2008) and lack of oxygen in the soil (Schuur and Matson, 2001; Schuur, 2003). As a result, turnover time of organic C in the soil may increase (Posada and Schuur, 2011), and consequently greater amounts of OM accumulate.

In the soils of Pacurita and Opogodó, total N concentration was high, which was probably due to high biological fixation rates resulting from the abundance of legumes in these forests (Cleveland *et al.*, 1999). On the other hand, the concentrations of P, Mg, and Ca were very low, possibly due to the strong influence of the lixiviation caused by the intense rainfall (Jenny, 1941; Austin and Vitousek, 1998; Santiago *et al.*, 2005). These results suggest that nutrient inputs to the soil through the meteorization of the sedimentary rocks, the OM production, and the deposition by rain and foliage washing are not enough to compensate for the losses caused by lixiviation. Consequently, these forests seem to be limited by P, Mg, and Ca availability, which has significant effects on NPP, soil microbial activity, and nutrient recycling (Austin and Vitousek, 1998; Kaspari *et al.*, 2008).

Soil texture showed significant correlations with several soil parameters (Table 3). For example, putting together the data of the three plots, sand percentage was positively correlated with pH, OM, total N, and Mg; correlations were negative with Al, P, and ECEC. Inversely, the percentage of clay was negatively correlated with pH, OM, total N, and Mg, while with Al and ECEC the association was positive. However, the magnitude and direction of individual correlations varied among sites. According to these results, in general, the higher clay content in the soils, the more acidic and poorer in nutrients, which could occur because the exchange positions of soil matrix are occupied by Al, which displaces nutrients of such positions (Sadzawka and Campillo, 1993). Consequently, it is expected that forests in clayey soils show lower growth and productivity because of limitations imposed by lower nutrient levels (Kaspari *et al.*, 2008).

Table 3. Spearman rank correlations of texture and fertility parameters in three tropical rainforests of the Pacific region, Colombia.

	Salero			Opogodó			Pacurita			General		
	Sand	**Silt**	**Clay**	**Sand**	**Silt**	**Clay**	**Sand**	**Silt**	**Clay**	**Sand**	**Silt**	**Clay**
pH	**0.49****	-0.10ns	**-0.61****	**0.4****	**-0.41****	-0.20ns	0.18ns	-0.06ns	**-0.32***	**0.50*****	**-0.44*****	**-0.72*****
Aluminum	-0.29ns	0.03ns	0.31ns	-0.06ns	0.05ns	0.07ns	-0.10ns	0.14ns	-0.01ns	**-0.67*****	**0.61*****	**0.83*****
Organic matter	**0.48****	**-0.37***	-0.18ns	**0.42****	**-0.37****	**-0.54*****	-0.09ns	0.04ns	0.25ns	**0.67*****	**-0.63*****	**-0.77*****
Nitrogen	ND	ND	ND	**0.36****	**-0.31****	**-0.45*****	-0.07ns	0.02ns	0.27ns	**0.79*****	**-0.74*****	**-0.80*****
Phosphorous	**-0.47****	0.23ns	**0.44****	0.10ns	-0.12ns	0.10ns	**0.41****	**-0.36***	**-0.30***	**-0.16***	0.16ns	0.12ns
Calcium	-0.02ns	0.04ns	-0.07ns	0.01ns	-0.02ns	-0.01ns	-0.11ns	0.07ns	-0.04ns	0.14ns	-0.14ns	-0.08ns
Magnesium	**0.36***	-0.25ns	-0.19ns	0.03ns	-0.01ns	-0.21ns	0.14ns	-0.22ns	0.07ns	**0.21****	**-0.18***	**-0.33*****
Potassium	0.09ns	-0.04ns	-0.17ns	-0.02ns	0.01ns	-0.02ns	**-0.30***	**0.38****	-0.17ns	0.10ns	-0.05ns	-0.28ns
ECEC	-0.01ns	-0.04ns	0.03ns	-0.01ns	0.01ns	-0.04ns	-0.20ns	0.15ns	0.07ns	**-0.44*****	**0.41*****	**0.56*****

Bold letters and asterisks indicate significant correlations (*) $P < 0.05$; (**) $P < 0.01$; (***) $P < 0.0001$; ns $P > 0.05$

Influence of precipitation on the concentration of nutrients (N, P, and K) in the soil of tropical rainforests
A significant relationship was found between AAP and total soil N of ultisols of low-altitude tropical rainforests ($P < 0.001$). The total N increased with increasing AAP, from 2,000 mm yr^{-1} to 8,000 mm yr^{-1}, but over this precipitation level, total N tended to decrease (Figure 1, Table 4). Under 8,000 mm yr^{-1}, the total N increased linearly with rainfall, which agrees with results reported by Jenny (1941), Santiago *et al.* (2005), and Posada and Schuur (2011), who also documented increases in the soil N content with increased AAP. However, other authors reported different results: Austin and Vitousek (1998) and Schuur and Matson (2001) found that the total N decreased with increased rainfall, while Alvarez-Clare and Mack (2011) found a weak relationship between total N and rainfall in soils of Costa Rica. These differences in the association between AAP and total N are probably due to the influence of other environmental factors, occurring at the local level in each site that overcome the effect of AAP on the total available N in the soil. Among those factors are the variation of texture (see Table 3), litter quality, rates of OM decomposition (Austin and Vitousek, 1998; Santiago *et al*., 2005), and availability of nutrients, which affect the biological fixation of N (Vitousek *et al*., 2010).

The linear increase of total N with rainfall for precipitation under 8,000 mm yr^{-1} is probably because the lower decomposition rate of litter as well as nitrification and mineralization of N with increased AAP (Austin and Vitousek, 1998; Schuur and Matson, 2001; Santiago, 2003, Santiago *et al*., 2005; Alvarez-Clare and Mack, 2011). As a result, N tends to accumulate on the soil. The reduction of the mineralization of N is perhaps due to the changes in the litter quality due to foliar washing of nutrients (Santiago *et al*., 2005), to the anaerobic conditions, which can occur as a result of excessive rainfall (Wright *et al*., 2001; Schuur and Matson, 2001), and to low availability of nutrients such as P and Ca due to lixiviation. This would affect the activity of aerobic soil microorganisms under conditions of high rainfall, as seen in the forests of Chocó. When AAP surpassed 8000 mm yr^{-1}, soil total N decreased. Unfortunately, there are no data in the literature for sites that have such a high precipitation, so it is not possible to compare our results. This result was unexpected, so we considered that local factors determine this behavior. In effect, as shown above, the terrain of the evaluated plots in this location present a topography with hills and ravines (Table 2), which favors the soil drainage, the lixiviation, and flow of nutrients and, as a consequence, increased the probability of mineralization and loss of edaphic N.

There was also a significant relationship between AAP and soil available P ($P < 0.001$) (Figure 1, Table 4). Soil available P decreased with increased AAP in tropical areas of the world. Similar tendencies were reported by Austin and Vitousek (1998) and Santiago *et al.* (2005) in tropical soils. Contrary to this, Alvarez-Clare Mack (2011) did not find significant correlations between the extractable P in the soil and the AAP in tropical moist forest in Costa Rica. According to these authors, these differences were due to fact the total P was measured, which is less susceptible to changes in AAP, while the present study evaluated the available P.

Prior studies have documented that soil available P is determined by several environmental factors, including the meteorization rate of rocks, type of clay mineral, retention of oxides of Fe and Al, pH, texture, OM content, microorganism activity and lixiviation (Schlesinger, 1997; Osorio, 2014). The decrease of available P in the soil with the increased AAP showed in Figure 1 was probably associated with various processes unleashed by high precipitation: firstly, the strong influence of lixiviation, which produces P losses that exceed the inputs from meteorization of rocks (Austin and Vitousek, 1998). Additionally, the high AAP give rise to the accumulation of acid cations (Al and H) and the formation of oxides and sesquioxides of Fe and Al in the soil (Sadzawka and Campillo, 1993), which tend to immobilize P by adsorption on the surface of these minerals (Schlesinger, 1997) and also by the formation of phosphates of Al and Fe ($AlPO_4 \cdot 2H_2O$, $FePO_4 \cdot 2H_2O$) when reacting with free ions of Fe^{3+} and Al^{+} in the soil solution.

Finally, the edaphic content of exchangeable K did not present a significant correlation with AAP ($P > 0.7$) (Figure 1). Santiago *et al.* (2005) and Schuur and Matson (2001) did not observe correlations between the exchangeable K content and the AAP either. On the other hand, Austin and Vitousek (1998) found significant reductions in the edaphic concentration of exchangeable K with an increase in rainfall in the tropical soils of Hawaii. This decrease in soil K was probably caused by lixiviation that increased with rainfall (Austin and Vitousek, 1998), which can generate K losses of 120 – 250 kg ha^{-1} yr^{-1} in tropical soils (Osorio, 2014). The stability of the edaphic concentration of K with the increased AAP found in the present study was probably due to the total losses being compensated for by the inputs into the soil from the forest ecosystem. In effect, this ion is very soluble, resulting in high losses due to lixiviation in humid tropics, as well as high inputs to the soil due to washing from the forest canopy by rainfall, with values of 13 - 220 kg ha^{-1} yr^{-1} (Vitousek and Sanford, 1986). Additionally, K^+ is easily released to the soil from decomposing organic residues (Osorio, 2014). However, the lack of an effect of increased AAP on soil K deserves further mechanistic studies to test them.

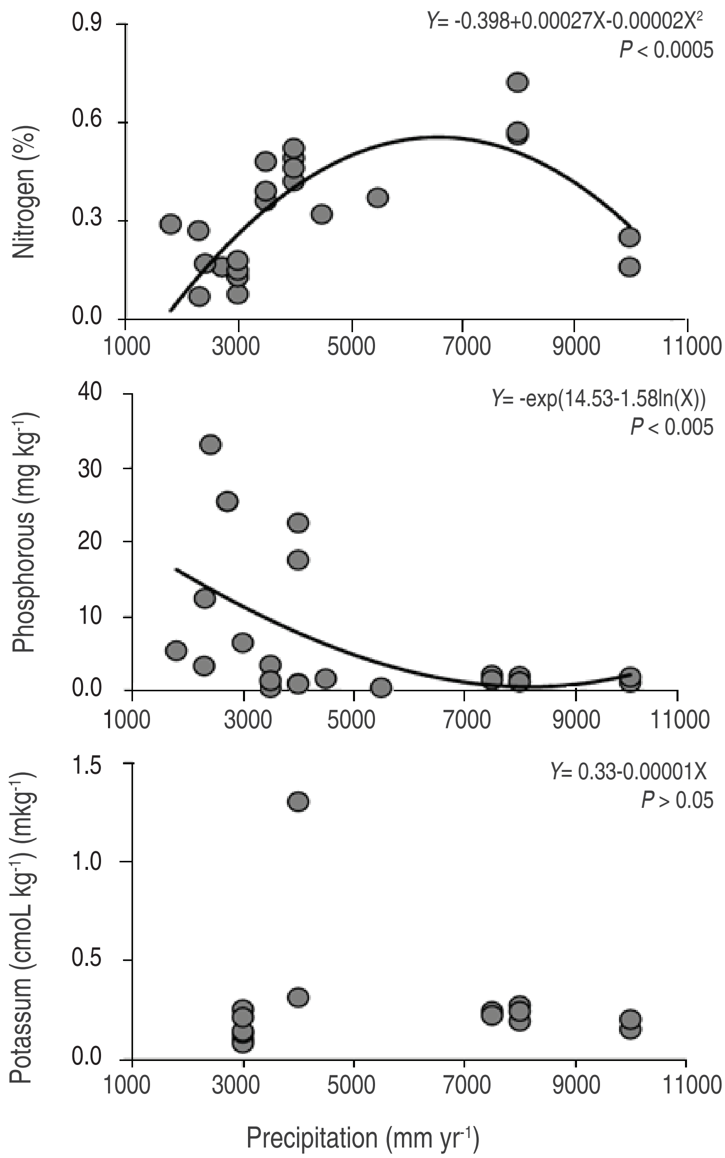

Figure 1. Relationship between soil concentrations of total N, available P, and exchangeable K and the annual precipitation in ultisols of tropical rainforests.

Data points corresponding to precipitation lower than 7,000 mm were taken from published literature (see methods). Data points corresponding to precipitation greater than 7,000 mm are from this study.

Table 4. Fertility parameters, soil type, nutrients, texture, elevation and precipitation in tropical rainforests.

Site	Soil type	pH	Al*	C (%)	N (%)	P (ppm)	Ca*	K*	Mg*	Na*	ECEC*	Sand (%)	Silt (%)	Clay (%)	Rainfall mm yr^{-1}	Altitude (m)
[1] Kaniku, Hawaii	-	6.34	-	-	1.94	2848	-	-	-	-	-	-	-	-	500	700
[1] Kaupulehu, Hawaii	-	6.8	-	-	2.64	2771	-	-	-	-	-	-	-	-	900	680
[1] Manuka, Hawaii	-	6.6	-	-	1.93	2104	-	-	-	-	-	-	-	-	1500	710
[2] Panama	Ultisols	6.5	-	2.52	0.29	5.3	-	-	-	-	-	-	-	-	1800	-
[3] Tapajos, Amazonia, Brasil	Oxisols	-	-	-	0.14	15.5	-	-	-	-	-	-	-	89	1968	-
[1] Kaloko, Hawaii	-	5.9	-	-	2.09	2754	-	-	-	-	-	-	-	-	2000	705
[4] Cocha Cashu, Perú	Oxisols	4.5	-	0.83	0.09	221	1.39	1.90	2.12	0.06	-	-	-	-	2165	333
[4] Cocha Cashu, Perú	Oxisols	3.8	-	0.30	0.03	167	0.53	5.31	5.09	0.40	-	-	-	-	2165	333
[4] Cocha Cashu, Perú	Entisols	6.7	-	4.45	0.43	777	40.35	8.36	32.97	0.35	-	-	-	-	2165	333
[3] Manaus, Amazonia, Brasil	Oxisols	-	-	-	0.16	7.3	-	-	-	-	-	-	-	66	2272	-
[5] Manaos, Amazonia, Brasil	Spodosols	4.7	0.18	1.34	0.08	1.0	0.03	0.04	0.06	0.01	0.31	96	2	2	2286	50
[5] Manaos, Amazonia, Brasil	Oxisols	3.9	1.82	2.59	0.15	1.9	0.11	0.10	0.10	0.06	2.19	21	13	66	2286	90
[6] Manaos, Amazonia, Brasil	Oxisols	4.2	2.30	1.61	0.17	121.3	-	-	-	-	2.49	23	-	-	2286	75
[7] Madre de Dios, Amazonia, Perú	-	4.1	1.69	-	-	-	4.52	0.23	0.92	0.02	7.38	52	-	-	2300	250
[2] Pipeline Road, Panama	Ultisols	5.3	-	2.86	0.27	3.2	-	-	-	-	-	-	-	-	2300	-
[3] Caxiuana, Amazonia, Brasil	Ultisols	-	-	-	0.07	12.3	-	-	-	-	-	-	-	16	2314	-
[3] Caxiuana, Amazonia, Brasil	Oxisols	-	-	-	0.13	12.3	-	-	-	-	-	-	-	48	2314	-
[3] Caxiuana, Amazonia, Brasil	-	-	-	-	0.17	80.0	-	-	-	-	-	-	-	41	2314	-
[5] Caxiuana, Amazonia, Brasil	Oxisols	3.8	1.88	1.68	0.13	2.3	0.13	0.05	0.15	0.08	2.28	33	14	54	2359	62
[3] Tambopata, Amazonia, Perú	Inceptisols	-	-	-	0.16	32.3	-	-	-	-	-	-	-	7	2417	-
[3] Tambopata, Amazonia, Perú	Ultisols	-	-	-	0.17	33.1	-	-	-	-	-	-	-	10	2417	-
[4] Barro Colorado, Panamá	Oxisols	5.6	-	4.25	0.42	931.0	10.29	0.59	3.50	0.22	-	-	-	-	2600	171
[4] Barro Colorado, Panamá	Oxisols	5.3	-	3.93	0.40	1025	6.25	0.58	5.86	0.15	-	-	-	-	2600	171
[4] Barro Colorado, Panamá	Alfisols	5.5	-	3.65	0.36	361.0	23.59	0.59	22.16	0.30	-	-	-	-	2600	171
[8] Barro Colorado, Panamá	Oxisols	5.7	11.27	-	0.19	2.9	8.64	0.43	2.46	-	22.80	-	-	-	2600	171
[4] Brazil	Spodosols	4.3	-	1.94	0.11	-	-	-	-	-	-	-	-	-	2650	100
[4] Brazil	Oxisols	4.1	-	3.92	0.26	-	-	-	-	-	-	-	-	-	2650	100
[4] Brazil	Oxisols	4.4	-	3.68	0.24	-	-	-	-	-	-	-	-	-	2650	100
[3] Amazonia, Colombia	Ultisols	-	-	-	0.16	25.4	-	-	-	-	-	-	-	42	2723	-
[3] Amazonia, Colombia	Ultisols	-	-	-	0.16	25.4	-	-	-	-	-	-	-	43	2723	-
[3] Amazonia, Colombia	Spodosols	-	-	-	0.11	14.4	-	-	-	-	-	-	-	1	2723	-
[5] Tapajos, Amazonia, Brasil	Oxisols	3.8	2.33	2.54	0.17	7.6	0.30	0.07	0.23	0.04	2.97	3	8	89	2741	200
[9] Borneo, Malasia. (soils humults)	Ultisols	-	-	1.95	0.13	-	0.04	0.10	0.17	-	-	-	-	-	3000	465
[9] Borneo, Malasia. (soils humults)	Ultisols	-	-	1.93	0.13	-	0.05	0.08	0.18	-	-	-	-	-	3000	465
[9] Borneo, Malasia. (soils udults)	Ultisols	-	-	1.42	0.15	-	0.14	0.13	0.33	-	-	-	-	-	3000	465
[9] Borneo, Malasia. (soils udults)	Ultisols	-	-	1.67	0.18	-	0.40	0.14	0.72	-	-	-	-	-	3000	465
[8] Yasuní, Amazonia, Ecuador	Ultisols	4.6	19.97	-	0.08	6.3	2.04	0.25	0.92	-	-	-	-	-	3000	450

Site	Soil type	pH	Al*	C (%)	N (%)	P (ppm)	Ca*	K*	Mg*	Na*	ECEC*	Sand (%)	Silt (%)	Clay (%)	Rainfall mm yr^{-1}	Altitude (m)
[7] Loreto, Amazonia, Peru	-	3.8	5.67	-	-	-	1.22	0.12	0.27	0.02	-	70	-	-	3000	150
[7] Yasuní, Amazonia, Ecuador	Ultisols	3.6	9.91	-	-	-	3.52	0.21	1.25	0.04	-	82	-	-	3000	250
[2] Fort Sherman, Panama	Histosoles	4.2	-	7.07	0.53	2.9	-	-	-	-	-	-	-	-	3100	-
[10] Amacayacu, Amazonia, Colombia	-	4.3	0.70	1.82	-	4.6	0.90	0.28	0.53	-	2.33	30	45	25	3200	7
[11] Cuyabeno, Amazonia, Ecuador	-	3.3	9.58	-	-	6.4	0.25	0.18	0.30	0.06	-	8	61	31	3500	270
[12] Earth, Costa Rica	Inceptisols-Ultisols	4.8	-	5.17	0.48	1.2	-	-	-	-	-	-	-	-	3500	100
[7] Loreto, Amazonia, Peru	-	3.8	5.67	-	-	-	1.22	0.12	0.27	0.02	-	70	-	-	3000	150
[12] Mogos, Costa Rica	Ultisols	4.9	-	4.92	0.36	0.3	-	-	-	-	-	-	-	-	3500	100
[2] Santa Rita, Panama	Ultisols	5.1	-	3.96	0.39	3.3	-	-	-	-	-	-	-	-	3500	460
[4] La Selva, Costa Rica	Ultisols	4.0	-	5.77	0.49	873.0	0.96	1.30	7.76	0.43	-	-	-	-	4000	50
[4] La Selva, Costa Rica	Ultisols	4.1	-	4.70	0.42	1129	1.19	0.31	2.04	0.11	-	-	-	-	4000	50
[4] La Selva, Costa Rica	Inceptisols	3.9	-	4.77	0.45	1552	1.66	1.31	5.34	0.28	-	-	-	-	4000	50
[12] La Palma, Costa Rica	Entisols-Mollisols	5.3	-	4.13	0.38	0.4	-	-	-	-	-	-	-	-	4000	100
[12] La Selva, Costa Rica	Inceptisols-Ultisols	4.2	-	5.42	0.46	0.9	-	-	-	-	-	-	-	-	4000	100
[12] Mastatal, Costa Rica	Inceptisols-Ultisols	5.1	-	5.57	0.52	0.8	-	-	-	-	-	-	-	-	4000	900
[13] Indonesia (alluvial soil)	-	4.2	-	6.90	0.33	27.0	0.33	0.22	0.05	-	-	65	23	12	4125	300
[13] Indonesia (sedimentary soil)	-	4.5	-	3.80	0.24	9.9	0.22	0.15	0.05	-	-	61	30	9	4125	300
[13] Indonesia (granite)	-	4.5	-	4.10	0.23	5.3	0.20	0.14	0.02	-	-	68	19	13	4125	300
[14] Indonesia.	-	-	0.02	4.94	0.26	13.8	0.20	0.21	0.28	0.32	5.96	65	23	12	4125	300
[12] Dos Brazos, Costa Rica.	Ultisols	6.3	-	3.42	0.32	1.5	-	-	-	-	-	-	-	-	4500	200
[12] San Ramón, Costa Rica.	Inceptisols	5.2	-	11.88	0.87	0.2	-	-	-	-	-	-	-	-	4500	1000
[12] Tapantí, Costa Rica.	Inceptisols	4.7	-	7.96	0.63	0.9	-	-	-	-	-	-	-	-	5000	1200
[15] Peninsula Osa, Costa Rica.	Oxisols	5.4	-	11.39	0.56	557.0	-	-	-	-	-	-	-	-	5179	120
[15] Peninsula Osa, Costa Rica.	Molisoles	6.0	-	11.72	0.59	1051	-	-	-	-	-	-	-	-	5179	100
[16] Secd. Forest, Andes, Colombia	-	4.4	2.71	4.03	-	3.4	0.39	0.14	0.21	-	3.44	58	14	28	5500	570
[1] Waiakea, Hawaii	-	5.0	-	-	1.18	1762	-	-	-	-	-	-	-	-	5500	710
[12] Golfito, Costa Rica	Ultisols	5.1	-	4.65	0.37	0.3	-	-	-	-	-	-	-	-	5500	200
[17] E plot, Salero-Chocó, Colombia	Ultisols	4.7	0.50	3.27	-	2.0	0.30	0.24	0.24	-	1.28	34	48	18	7500	125
[17] U plot, Salero-Chocó, Colombia	Ultisols	4.8	0.48	4.50	-	1.3	0.35	0.22	0.29	-	1.33	41	43	16	7500	125
[17] Plot 1, Opogodó-Chocó, Colombia	Ultisols	4.7	0.13	8.29	0.72	1.8	0.25	0.19	0.33	-	0.91	87	13	1	8000	70
[17] Plot 2, Opogodó-Chocó, Colombia	Ultisols	5.2	0.13	5.84	0.56	1.1	0.39	0.27	0.27	-	1.05	86	13	1	8000	70
[17] Plot 3, Opogodó-Chocó, Colombia	Ultisols	5.0	0.12	6.66	0.57	1.1	0.53	0.24	0.25	-	1.13	85	14	2	8000	70
[17] Plot 1, Pacurita-Chocó, Colombia	Ultisols	3.9	0.94	2.86	0.25	1.0	0.35	0.15	0.19	-	1.62	52	28	20	10000	115
[17] Plot 2, Pacurita-Chocó, Colombia	Ultisols	4.2	0.95	1.86	0.16	1.7	0.36	0.20	0.16	-	1.67	55	28	17	10000	115

[1]Austin and Vitousek 1998; [2]Santiago et al., 2005; [3]Aragão *et al.*, 2009; [4]Powers *et al.*, 2005; [5]Malhi *et al.*, 2009; [6]Laurance *et al.*, 2010; [7]Ruokolainen *et al.*, 2007; [8]John *et al.*, 2007; [9]Palmiotto et al., 2004; [10]Barreto *et al.*, 2010; [11]Poulsen *et al.*, 2006; [12]Alvarez-Clare and Mark 2011; [13]Paoli *et al.*, 2006; [14]Paoli and Curran 2007; [15]Cleveland *et al.*, 2002; [16]Peña and Duque 2013; [17]This study.
* cmolc kg^{-1}

CONCLUSIONS

The positive correlation between AAP and soil total N, as well as the inversely proportional relationship between AAP and available P concentration in soils of low tropical forests, suggest that the availability of P, contrary to that of N, is potentially limited by the AAP in these ecosystems. Likewise, if significant changes occur in the AAP of tropical rainforests resulting from the global climate change, the recycling of nutrients will be considerably affected in these ecosystems, which would have significant consequences for their dynamics.

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