Revista Brasileira de Ciência do Solo

Division - Soil Use and Management | Commission - Soil Pollution, Remediation and Reclamation of Degraded Areas

Influence of soil nutrients on net primary productivity in post-mining forests in the Colombian Pacific

Harley Quinto Mosquera[(1)*], **Hamleth Valois Cuesta**[(1)] and **David Pérez Abadía**[(1,2)]

[(1)] Universidad Tecnológica del Chocó Diego Luis Córdoba, Facultad de Ciencias Naturales, Programa de Biología, Departamento del Chocó, Ciudad de Quibdó, República de Colombia.
[(2)] Universidad de Valladolid, Instituto Universitario De Investigación en Gestión Forestal Sostenible, Programa de Conservación y Uso Sostenible de Sistemas Forestales, Palencia, España.

*** Corresponding author:**
E-mail: d-harley.quinto@utch.edu.co

Received: May 23, 2023

Approved: October 17, 2023

How to cite: Mosquera HQ, Cuesta HV, Abadía DP. Influence of soil nutrients on net primary productivity in post-mining forests in the Colombian Pacific. Rev Bras Cienc Solo. 2024;48:e0230053
https://doi.org/10.36783/18069657rbcs20230053

Editors: José Miguel Reichert and Jeferson Dieckow.

Copyright: This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided that the original author and source are credited.

ABSTRACT: Tropical forests have the highest rates of net primary productivity (NPP) in terrestrial ecosystems and, therefore, may contribute significantly to the mitigation of global climate change. Although NPP is influenced by soil fertility, and recently, in some regions, mining activity in forest ecosystems has intensified. Little is known about how soils determine the restoration of NPP in forests degraded by mining. We evaluated the influence of soil nutrients on wood NPP of post-mining forests in the biogeographic Chocó region (Colombia), with emphasis on the effects of nitrogen (N) and phosphorus (P) limitations in post-mining forests under successional stages of 12-15 or 30-35 years. For this, permanent plots were established in secondary post-mining forests in Jigualito (Colombian Pacific), the wood NPP (accumulated and current) was evaluated, and it was related to soil properties such as organic matter (OM), acidity, Al, total N, available P, magnesium (Mg), potassium (K), calcium (Ca), and texture. An accumulated wood NPP of 0.72 t ha^{-1} yr^{-1} was recorded in post-mining forests 12-15 years old. Meanwhile, in post-mining forests of 30-35 years, the accumulated wood NPP was 6.52 t ha^{-1} yr^{-1}. The current wood NPP was 4.25 t ha^{-1} yr^{-1} in post-mining forests with 30-35 years of recovery. Accumulated NPP positively correlated with soil OM, total N, Ca, Mg, and effective cation exchange capacity–ECEC in post-mining forests. In post-mining forests, a slow recovery of the wood NPP was denoted in the first years. Soil nutrients determined the wood NPP, and a multiple limitation of nutrients with the succession was observed, which corroborates the need to restore the degraded ecosystem in the region.

Keywords: biogeographic Chocó, global climate change, nutrient limitation, restoration, succession.

INTRODUCTION

Tropical forests are considered the most important terrestrial ecosystem in terms of net primary productivity (NPP) and have a key role as sinks and reservoirs of atmospheric carbon (Phillips et al., 1998; Clark et al., 2001b; Grace, 2004; Pan et al., 2011). Specifically, it has been estimated that these forests store about 40 % of the existing carbon in the terrestrial ecosystems of the planet (Dixon et al., 1994), they represent 36 % of the global NPP (Field et al., 1998; Beer et al., 2010) and capture about 1.19 petagrams of carbon annually (Pg C yr^{-1}) (Pan et al., 2011), thus contributing significantly to carbon fixation and balance, and global climate change mitigation (Grace, 2004; IPCC, 2014). Consequently, there is a growing interest in evaluating the NPP of these forests, and the environmental and anthropic factors that determine it (Phillips et al., 1998; Clark et al., 2001a; Malhi et al., 2004; IPCC, 2014).

Several studies have documented that the NPP of tropical forests is influenced by factors such as precipitation, climate, solar radiation, temperature, soil type and its fertility, as well as by other factors related to the dynamics (disturbances) of the ecosystem, structure and species composition (Schuur, 2003; Del Grosso et al., 2008, Jiménez et al., 2009; Cleveland et al., 2011; Malhi et al., 2011; Wu et al., 2011; van der Sande et al., 2018; Linger et al., 2020); for this reason, a wide range of aboveground NPP has been shown in tropical rainforests, between 1.2 and 15.2 Mg ha^{-1} yr^{-1} (Clark et al., 2001b).

Soil nutrient content has shown a positive effect on NPP of tropical forests (Alvarado and Raigosa, 2012; van der Sande et al., 2018). In this sense, it has been determined nutrients tend to be more correlated with NPP are N, P, K and Ca (Paoli and Curran, 2007; Cleveland et al., 2011); which are part of the nutrients considered physiologically essential for plant growth (Lambers et al., 2008a). For example, Vitousek (1984) conducted an analysis of N, P and Ca recycling and determined the availability of P, but not N, limited the litter production (a component of the NPP). Meanwhile, Paoli and Curran (2007) observed that the NPP of tropical forests increased with the availability of P, N, K, Ca, Mg, and ECEC. Similarly, Aragão et al. (2009) reported Amazon's NPP (total and fine roots) increases significantly with the P content of the soil. Likewise, some years ago, in a meta-analysis on NPP in tropical forests, Cleveland et al. (2011) reported P availability positively influences the NPP rates. On the other hand, Quinto et al. (2017) observed that the production of leaves and fine roots increased with soil fertility in forests of the biogeographic Chocó. In summary, these studies show the importance of soil nutrients on NPP and mitigating global climate change.

However, in recent decades, tropical forests have been severely deforested and degraded due to human activities such as logging, agriculture, cattle ranching, and mining, among others (Primack, 2008), which affect the ability of these ecosystems to mitigate global climate change (Grace, 2004; IPCC, 2014). Particularly, open-pit mining strongly impacts the NPP, once vegetation and soil covers are removed (Diaz and Elcoro, 2009; Valois, 2016; Maus et al., 2022; Giljum et al., 2022). Not only soil and vegetation are affected, but all the ecological processes of the ecosystem (Holl, 2002; ELAW, 2010). In this sense, with mining, there is a reduction in the capture of atmospheric CO_2 due to the loss of vegetation, the carbon balance is altered, and CO_2 emissions into the atmosphere increase, which accentuates global warming (ELAW, 2010). It is estimated that from 2001 to 2013, about 1680 km^2 of South American tropical forests were lost (Primack and Vidal, 2019), with threatening effects not only to the region's biodiversity, but also to soil organic carbon (SOC) and to the capacity of ecosystems to mitigate global climate change.

This situation is currently taking place in Colombia, in the Chocó (Colombian Pacific) department, where open-pit gold mining is damaging soil and rivers of the natural ecosystems (Valois, 2016). Nonetheless, about 840 thousand hectares of mature forest were recently granted licenses for mining exploitation in the territory (Ángel et al., 2019). Now, it is necessary to develop restoration projects and programs to recover the functionality and NPP of the ecosystem. Knowing the environmental factors that limit the NPP of post-mining ecosystems is necessary to achieve this purpose.

In this sense, Kalamandeen et al. (2020) reported an increase in NPP of post-mining forests in the Amazon, in areas where soil had higher N content, denoting the influence of soil nutrients on the restoration of degraded ecosystems. Likewise, it has been hypothesized that, in tropical soils, in initial successional stages, there is a limitation of the NPP by N, which over time is mitigated due to colonization of plants with capacity to fix atmospheric N_2 symbiotically (Walker, 1993). Therefore, in the ecosystem, to the extent that there is a greater colonization of N-fixing plants, and succession advances, this limitation of the NPP would be reduced (Cleveland et al., 1999; Walker and del Moral, 2008). Unlike N, the levels of soil P tend to be high in the first successional stages, and over time, its availability to plants tends to decrease due to losses by leaching and immobilization in Fe and Al oxides (Walker and Syers, 1976; Vitousek et al., 2010). With this, a limitation of the NPP is expected due to low availability of P in advanced successions and mature forests (Vitousek, 1984).

Based on the above discussion and taking into account that the region is one of the most biodiverse on the planet (Rangel, 2004), and has one of the highest levels of precipitation (Poveda et al., 2004); that possibly affects the edaphic limitation and availability of nutrients due to leaching (Austin and Vitousek, 1998; Posada and Schuur, 2011; Quinto and Moreno, 2016); this study aimed to evaluate the soil nutrients influence on the wood NPP of post-mining forests in the biogeographic Chocó, and, contribute with experimental elements to the restoration of the NPP of these degraded ecosystems.

MATERIALS AND METHODS

Study area

This study was carried out in forested areas previously degraded by open-pit gold mining, in the locality of Jigualito (5° 06’ 01” N - 76° 32’ 44” W), in the municipality of Condoto, department of Chocó, Colombia. Average annual precipitation is 8000 mm, the mean annual temperature is 26 °C, and altitude is 70 m with flat topography. This locality is part of the biogeographic subregion of North Central Chocó, which includes the upper basins of the Atrato and San Juan rivers, in Piedemonte and Colinas lowland landscape units with humid soils and a type of transitional sedimentary rock (Poveda et al., 2004). The localities lie within the Tertiary Sedimentary Hills geomorphological unit formed by low-altitude sedimentary rocks composed of sandy clayey, sandstone and limestone. The forests are mostly secondary, with different recovery ages since mining has been carried out in the area at different times.

Soils of the post-mining forests are Alisols (WRB) or Ultisols (Soil Taxonomy) and, due to mining, they have rocky material and sand. The A horizon was removed during mining, with irregular return of organic material after mining. In addition, they are acidic and have high OM, total N, available P, Al and clay contents; while the contents of Ca, K, Mg, ECEC and silt are low (Quinto et al., 2022). In these forests, the most dominant tree species are *Cecropia peltata, Vismia baccifera, Cosmibuena macrocarpa, Ochroma pyramidalis, Welfia regia, Pityrogramma calomelanos, Cespedesia spathulata, Inga chocoensis,* and *Pourouma bicolor* (Ramírez and Rangel, 2019).

This study assessed two post-mining forests with different succession times. These forests were secondary forests that grew in abandoned illegal mining areas. The first post-mining forest was 12-15 years old (F12-15) and the second forest was 30-35 years old (F30-35), being that the time of restoration after mining ended. In the post-mining forests F12-15, 103 plots of 5 × 5 m (25 m^2) were installed as NPP sampling units; while in the forests F30-35, 37 plots of 10 × 10 m (100 m^2) were installed. Plot size and replicates in each forest were different due to irregular site characteristics, which only allowed sampling in this way.

Physical and chemical soil properties

In each plot (103 and 37 in the post-mining forest of 12-15 and 30-35 years, respectivity), composite samples of soil were taken at a depth of 0.20 m, to which the parameters of acidity (pH), aluminum content (Al), organic matter (OM), total N, available P, calcium (Ca), potassium (K), magnesium (Mg), effective cation exchange capacity (ECEC), and texture (percentages of sand, silt, and clay), according to the following laboratory techniques: Bouyoucos for textural fractions, potentiometric in water solution (1:2) for pH, Walkley and Black for OM, Micro- Kjeldahl 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, described in Osorio (2014), and Quinto et al. (2022). Soil sampling was carried out in 2020 and 2021.

Diameters and height of trees

In the installed plots, the sampling criteria for the forest inventory was stratified sampling by succession time forests; here the circumference at breast height (1.30 m above ground level) was measured with a measuring tape in all trees with circumference >31.4 cm (Diameter at breast height- DBH >10 cm) in each quadrat; subsequently, the circumference values were transformed to DBH. The perimeter of the tree trunk where the DBH was measured was marked with yellow paint to ensure that subsequent measurements were made in the same strip as the first measurement. Measurement of tree heights was carried out with a Clinometer at fixed distances of 15 m from the tree. All measured trees were marked with aluminum plates. Additionally, growth habits were identified, and the characteristics of each individual were recorded. Trees were measured each August of 2020, 2021 and 2022 in F30-35; while in F12-15, inventories were carried out only in 2020 due to armed conflicts in the area. In total, 114 trees were excluded from the analysis because they died during the sampling period.

Botanical identification

Trees were identified at the highest possible taxonomic level (species, genus, botanical family) in the herbarium of the Technological University of Chocó “Herbario Chocó”. This identification was made using the specialized key of Gentry (1993), and the scientific names of species and families were corroborated on the “Tropicos” website. (https://www.tropicos.org/home). This taxonomic information was used to determine the wood density.

Wood density

We used values published in two international databases of wood density obtained for tropical forests (Brown, 1997; Baker et al., 2004). In case a species or genus found in the plots was not reported in these databases, the average of the genus or family of the species was used.

Aboveground biomass and wood net primary productivity (wood NPP)

The allometric model proposed by Álvarez et al. (2012) (Equations 1, 2 and 3), based on data from the same region, was used to determine the trees’ aboveground biomass (AB).

$$AB\ (\text{kg}) = \exp\{-2.889 + \ln[(DBH^2) \times H \times \rho]\} \quad \text{Eq. 1}$$

$$\text{Current } \textit{wood NPP} = (\text{final AB} - \text{initial AB}) / \text{time in years} \quad \text{Eq. 2}$$

$$\text{Accumulated } \textit{wood NPP} = \text{AB/the succession time in years} \quad \text{Eq. 3}$$

in which: AB is the aboveground biomass in kilograms; DBH is the diameter in cm; H is the height of the tree in m; ln is the natural logarithm; and ρ is the wood density. Aboveground biomass was determined at the ecosystem, species, and tree individual levels. The AB was estimated by applying harvest-based allometric regression equations to measurements of the diameters of all trees in a plot that are above the minimum size, and was expressed in tons per hectare (Mg ha^{-1}) (Clark et al., 2001a). *Current wood NPP* (2) was estimated from two successive stand-level AB estimates; that is to say, the annual increment of the AB was used, which was determined as the final AB of the trees, minus the initial AB, divided by time in years (Clark et al., 2001a). These determination of the *Current wood* NPP could only be carried out in F30-35. Meanwhile, the *Accumulated wood* NPP (3) was calculated as the AB divided by the succession time, in years (Silver et al., 2000). Wood NPP values were expressed in tons per hectare per year (Mg ha^{-1} yr^{-1}) (Clark et al., 2001a). The NPP includes not only the growth of primary producers (biomass accumulation and tissue turnover above and belowground in terrestrial ecosystems) but also the C transfer to herbivores and root symbionts (for example, mycorrhizal fungi), the excretion of organic C from algae, and the production of root exudates and plant volatile organic compounds (VOCs) (Clark et al., 2001a).

Statistical analysis

Assumptions of normality and homogeneity of variances were first evaluated with Bartlett, Hartley and Kurtosis statistical tests (between + 2.0 and -2.0). Data distribution was evaluated for each treatment using the Shapiro-Wills statistical test. Initially, mean values of wood NPP between post-mining forests (12-15 years vs 30-35 years) was compared with the Mann-Whitney (MW) test because the data did not meet the normality assumption and did not present a normal distribution (Hoshmand, 1998). The wood NPP and soil data were log-transformed whenever possible to achieve a normal distribution. Subsequently, to determine the relationship between wood NPP and soil physical and chemical properties, General Linear Models (GLM) with mixed effects, Spearman rank correlation analysis, and linear regression models (Hoshmand, 1998) were used. Spearman analyses were performed for each of the post-mining forests, and then the two post-mining forests were taken as a single ecosystem. Meanwhile, the General Linear Models (GLM) and the Linear Regression Models were carried out taking the post-mining forests as a single forest ecosystem, due to the geographic proximity and the floristic and structural similarity (Ramírez and Rangel, 2019). Analyses were performed in the R programming environment (R Development Core Team, 2013).

RESULTS

Post-mining forests between 12-15 years of succession presented a mean NPP of 0.72 ± 0.13 Mg ha^{-1} yr^{-1} (± standard error), while in post-mining forests between 30-35 years old, the wood NPP was 6.52 ± 0.64 Mg ha^{-1} yr^{-1} (table 1). Among these post-mining forests, there were statistically significant differences in the accumulated wood NPP (MW = -8.5; p = 0.0001) (Table 1). For its part, the current wood NPP was 4.25 ± 0.8 Mg ha^{-1} yr^{-1} in post-mining forests with 30-35 years of recovery (Table 1).

On the other hand, when evaluating the post-mining forests as a single ecosystem, it was denoted by the GLM that OM, Ca, and Mg contents were significantly related to the accumulated wood NPP, and those soil properties explained 40.6 % of its variation (R^2 = 40.6 %) (table 2). For its part, Spearman's correlation showed that the accumulated wood NPP was positively and significantly related to Al, OM, total N, available P, Ca, Mg, and ECEC; while, with pH and clay, the relationship was negative (Table 3). Likewise, it was noted that the accumulated wood NPP presented the highest correlations with OM (R^2 = 25 %), Ca (R^2 = 23 %), Mg (R^2 = 14.4 %), total N (R^2 =11.4 %), and ECEC (R^2 = 23 %) (Figure 1).

Table 1. Aboveground biomass and wood net primary productivity of two post-minigng forests in the Colombian Pacific

Post-mining forest type	N	Aboveground biomass	Cumulative wood NPP		Current wood NPP	
			Means ± SE	Range	Means ± SE	Range
		Mg ha^{-1} yr^{-1}		Mg ha^{-1} yr^{-1}		Mg ha^{-1} yr^{-1}
12-15 years	103	9.44 b ± 1.7 b	0.72 ± 0.13 *b*	0.01 – 9.82		
30-35 years	37	180.28 a ± 22.7 a	6.52 ± 0.64 *a*	0.12 – 19.23	4.25 ± 0.8	0.01 – 20.48
Mann-Whitney Test		-8.75***	-8.55***			

Means ± standard error; NPP is the net primary productivity in tons per hectare per year (t ha^{-1} yr^{-1}), the letters *a* and *b* indicate significant differences between the medians. Asterisks indicate statistically significant differences *: p<0.05; **: p<0.01; ***: p<0.001. SE is the standard error.

Finally, a very weak negative correlation with Mg was evidenced when evaluating the wood NPP of post-mining forests with 12-15 years of recovery (Table 3). Meanwhile, the accumulated wood NPP of 30-35 years post-mining forests showed a negative correlation with the total N (Table 3). For its part, the current wood NPP of post-mining forests of 30-35 years of recovery showed a negative and not significant correlation with sand, but, positive and also insignificant with silt and clay (Table 3).

DISCUSSION

Carbon sequestration in post-mining secondary forests

Wood NPP of post-mining secondary forests in the Colombian Pacific was between 0.01 and 9.82 Mg ha^{-1} yr^{-1}, with an average of 0.75 Mg ha^{-1} yr^{-1} in areas with ages between 12-15 years. Those figures are partially similar to those of 0.70-9.15 Mg ha^{-1} yr^{-1} reported for secondary post-mining forests in Cértegui (Chocó, Colombia), with an average of 3.51 Mg ha^{-1} yr^{-1} in areas between 1.5 and 6.0 years of restoration (Quinto et al., 2013). Likewise, such wood NPP was similar to the 0.4-5.4 Mg ha^{-1} yr^{-1} reported for 3-4 years forest succession in abandoned mining areas in the Amazon (Kalamandeen et al., 2020).

Table 2. Analysis of variance of wood net primary productivity based on the soil physicochemical properties

Source	Sum of squares	Df	Mean square	F-Ratio	p-value
Model	247.711	10	24.7711	7.00	0.0000
Residuals	360.983	102	3.53905		
Total (Corr.)	608.693	112			
Sum of squares Tipe III					
pH	9.2308	1	9.2308	2.61	0.1094
Aluminium	3.6679	1	3.6679	1.04	0.3111
Organic matter	22.6767	1	22.6767	6.41	0.0129
Total nitrogen	1.81426	1	1.81426	0.51	0.4756
Phosphorus	3.80631	1	3.80631	1.08	0.3022
Potassium	2.16343	1	2.16343	0.61	0.4361
Calcium	86.1554	1	86.1554	24.34	0.0000
Magnesium	16.7606	1	16.7606	4.74	0.0318
Sand	0.940579	1	0.940579	0.27	0.6073
Clay	4.20319	1	4.20319	1.19	0.2784
Residuals	360.983	102	3.53905		
Total (corrected)	608.693	112			

Statistical method was General Linear Model. R^2 = 40.6 %.

Therefore, it seems wood NPP of post-mining forests with less than 20 years of recovery, in the Colombian Pacific and in the Amazon (Quinto et al., 2013; Kalamandeen et al., 2020) are within the range of 0.01 to 32.7 Mg ha^{-1} yr^{-1} reported for Neotropical secondary forests (Poorter et al., 2016).

However, the 0.75 Mg ha^{-1} yr^{-1} of NPP in recent post-mining areas (12-15 years of restoration) is much lower than that of the majority of secondary tropical forests (of approximately 6.1 Mg ha^{-1} yr^{-1}) after the abandonment of activities such as cattle ranching, agriculture and logging (Silver et al., 2000; Poorter et al., 2016). For example, in the central Amazon, a wood NPP rate of 11.0 Mg ha^{-1} yr^{-1} was recorded for 14 years of recovery after the abandonment of grazing (Feldpausch et al., 2004). Likewise, in secondary forests with ten years of recovery, 5.5 Mg ha^{-1} yr^{-1} of wood NPP was obtained in another ecosystem of the same Amazonian macro-basin (Johnson et al., 2000). Those results show the influence of the type of the previous disturbance on the recovery capacity of the ecosystem (Silver et al., 2000; Guariguata and Ostertag, 2001; Chazdon et al., 2016). Specifically, it is corroborated that open-cast mining significantly affects the ecosystem, which generates a slow biomass recovery and functionality, as has been suggested in previous analyses of tropical successions (Guariguata and Ostertag, 2001).

Wood NPP of recent post-mining forests (<20 years) is low is probably due to the impact that mining has on the ecosystem. Soil organic horizon is removed, and the overall soil structure is altered, mainly leaving rocks and sand on the surface (Ramírez et al., 2019).

Table 3. Spearman correlations of carbon sequestration and physicochemical properties of post-mining forests in the Colombian Pacific

Soil	General-Cumulative wood NPP	Wood NPP (12-15 years)	Wood NPP (30-35 years)	
	Cumulative	Cumulative	Cumulative	Current
pH	<u>-0.25</u>	0.12	-0.05	0.05
p-value	<u>0.003</u>	0.209	0.758	0.767
Aluminium	<u>0.17</u>	-0.12	0.05	0.03
p-value	<u>0.049</u>	0.216	0.744	0.854
Organic matter	<u>0.53</u>	0.10	-0.25	-0.10
p-value	<u>0.000</u>	0.318	0.133	0.534
Total nitrogen	<u>0.44</u>	0.13	<u>-0.36</u>	-0.19
p-value	<u>0.000</u>	0.188	<u>0.029</u>	0.263
Phosphorus	<u>0.21</u>	-0.03	0.02	-0.02
p-value	<u>0.012</u>	0.760	0.895	0.925
Potassium	0.11	0.11	-0.19	0.04
p-value	0.194	0.275	0.259	0.789
Calcium	<u>0.44</u>	-0.11	-0.09	-0.20
p-value	<u>0.000</u>	0.273	0.605	0.221
Magnesium	<u>0.31</u>	<u>-0.17</u>	-0.09	-0.25
p-value	<u>0.000</u>	<u>0.080</u>	0.582	0.131
ECEC	<u>0.40</u>	-0.15	-0.06	-0.23
p-value	<u>0.000</u>	0.121	0.725	0.163
Sand	0.10	0.00	0.11	<u>-0.53</u>
p-value	0.270	0.971	0.703	<u>0.068</u>
Silt	-0.06	0.00	-0.02	<u>0.52</u>
p-value	0.509	0.963	0.939	<u>0.071</u>
Clay	<u>-0.21</u>	-0.04	-0.23	<u>0.50</u>
p-value	<u>0.027</u>	0.691	0.428	<u>0.083</u>

Vegetation and the soil/regolith that covers mineral deposits are removed (Diaz and Elcoro, 2009; Valois, 2016), affecting soil fertility (Quinto et al., 2022), plant biomass (Quinto et al., 2013) and many other ecological processes (Holl, 2002; ELAW, 2010), like nutrient recycling (Quinto et al., 2022) and carbon sequestration (NPP) (Kalamandeen et al., 2020). Such effects are stronger than those generated by other anthropic activities like selective felling of trees, subsistence agriculture, and grazing (Silver et al., 2000), which still preserve the organic horizon, texture, and soil nutrients (Guariguata and Ostertag, 2001).

On the other hand, the post-mining forests between 30-35 years of recovery had average wood NPP of 4.25 and 6.52 Mg ha^{-1} yr^{-1}, comparable to the report of 6.1 Mg ha^{-1} yr^{-1} for Neotropical secondary forests (Silver et al., 2000; Poorter et al., 2016), or higher than reports of 1.01 to 4.36 Mg ha^{-1} yr^{-1} for secondary rainforests between 23 and 40 years of recovery after logging in the biogeographic Chocó (Forero-Peña et al., 2022). Possibly, this increase in the wood NPP of the post-mining areas with the regeneration age is due to the increase in the edaphic content of OM and nutrients (total N, Ca, Mg, ECEC) that occurs with the succession (Quinto et al., 2022). Likewise, over the succession, there is an increase in activity, abundance, functionality (ammonification and nitrification), richness and post-mining microbial biomass (Sansupa et al., 2021). In addition, the edaphic colonization of mycorrhizae may increase (Zhang et al., 2017). In early succession

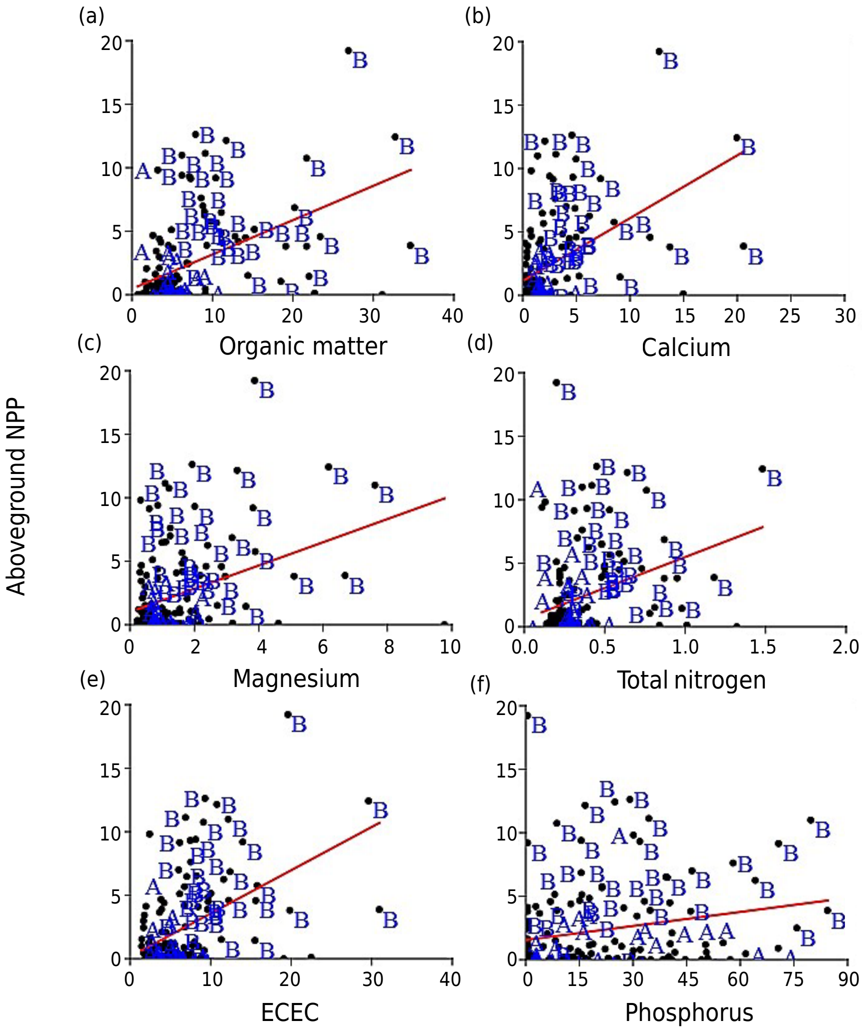

Figure 1. Linear regressions of above-ground tree net primary productivity (NPP) and soil nutrients in post-mining forests in the Colombian Pacific. (a) Wood NPP vs Organic matter (r^2 = 25 %; p<0.0001); (b) Wood NPP vs Calcium (r^2 = 23 %; p<0.0001); (c) Wood NPP vs Magnesium (r^2 = 14.4 %; p<0.00001); (d) Wood NPP vs total Nitrogen (r^2 = 11.4 %; p = 0.00004); (e) Wood NPP vs ECEC (r^2 = 23 %; p<0.00001); (f) Wood NPP vs. Available Phosphorus (r^2 = 4.7 %; p = 0.009).

ecosystems (<20 years), the presence of mycorrhizae is low. In contrast, in post-mining forests with a longer recovery time, such as in mines >30 years of abandonment, surely the presence of arbuscular mycorrhizae and edaphic proteins related to glomalin favor recalcitrant carbon components, which benefit the accumulation of soil organic carbon (SOC) and OM in tropical forests (Zhang et al., 2017). This surely explains the higher wood NPP in these advanced succession post-mining forests.

Another factor that explains the higher wood NPP of advanced succession post-mining forests (>30 years) in the Colombian Pacific is the colonization by tree species, either pioneer or climax, that store greater amounts of carbon in a shorter time (Guariguata and Ostertag, 2001). The composition of tree species recorded in these abandoned mines were *Cecropia peltata, Vismia baccifera, Cosmibuena macrocarpa, Ochroma pyramidalis, Welfia regia, Pityrogramma calomelanos, Cespedesia spathulata, Inga chocoensis*, and *Pourouma bicolor*) (Ramírez and Rangel, 2019). Those species have been commonly reported for previously degraded ecosystems, secondary forests and areas with different stages of ecological succession (Alves et al., 1997; Guariguata and Ostertag, 2001). These species are possibly the ones with the greatest tolerance to adverse conditions (isolation, high temperatures, stress, acidity, herbivory, infertility and Al toxicity) that occur in areas degraded by mining (Diaz and Elcoro, 2009; Valois, 2016; Quinto et al., 2022). For this reason, it can be deduced that this physiological capacity contributes significantly to the wood NPP of the previously degraded ecosystem.

What influences do soil nutrient contents have on wood NPP of post-mining forests of the biogeographical region of Chocó?

Soil conditions were essential for the restoration of the wood aboveground biomass (wood AB) and wood NPP in abandoned mines in tropical regions (León and Osorio, 2014). However, in our study, the current wood NPP (Clark et al., 2001b) did not show a significant relationship with soil nutrient content variations; similar to what was observed by Oberleitner et al. (2021) in measurements of an increase in wood AB in secondary forests of Costa Rica. Likewise, Poorter et al. (2016) recorded only a significant association between the accumulation of wood AB and ECEC in tropical secondary forests. For this reason, annual changes in wood NPP of the trees could have little relationship with the spatial variation in the contents of soil nutrients. This is surely due to the fact that most trees growing on acidic and nutrient-poor soils are adapted to low nutrient availability (Whitmore, 1998; Lambers et al., 2008b), and changes in their availability generate responses. In the long term, which is not easily evidenced from one year to the next, as has happened in some studies when the tree wood NPP is evaluated in annual inventories (Aragão et al., 2009; Cleveland et al., 2011; Quinto and Moreno, 2017; Oberleitner et al., 2021); as it happens in this study carried out in post-mining forests.

On the other hand, in the accumulated wood NPP, calculated as the wood AB divided by the succession age in years (Silver et al., 2000), a positive relationship was evidenced between the wood NPP and soil nutrients (OM, total N, Ca, Mg, and ECEC) in post-mining forests, which together show that small soil patches of higher fertility tend to facilitate carbon accumulation and the recovery of ecosystem functionality. Such wood NPP rate observed in more fertile soils of abandoned mines is similar to that reported by Kalamandeen et al. (2020), who reported a higher wood NPP in abandoned mines with higher total N content. Likewise, Poorter et al. (2016) determined that the percentage of AB accumulation is determined by soil fertility (CEC) in Neotropical secondary forests in different successional stages. Likewise, Tucker et al. (1998), in secondary forests with more than 15 years of succession, compared the recovery of the basal area (indirect measure of the forest biomass) in fertile and nutrient-rich soils, with the recovery on infertile soils, Oxisols; and found that in fertile soils the basal area was much greater over the succession time, and in such forest, the AB of a primary forest was reached more quickly (Tucker et al., 1998). Thus, the positive influence of edaphic fertility on wood NPP in tropical forests is evidenced (Moran et al., 2000; Guariguata and Ostertag, 2001; Lu et al., 2002) at local and regional scales, as occurs in areas previously degraded by open pit mining. Meanwhile, Feldpausch et al. (2004) recorded a higher accumulation of AB and wood NPP in secondary forests (12-14 years of recovery) of the Amazon in areas with higher edaphic content of total N. This evidences the strong influence of soil nutrients on the wood NPP of tropical secondary forests, including those generated by mining.

It is important to mention that, although some studies have not shown a significant relationship between soil nutrients and AB accumulation in tropical secondary forests (Poorter et al., 2016; Oberleitner et al., 2021), fertilization experiments developed to evaluate the nutritional limitation of wood NPP in secondary forests, have had different revealing results (Vitousek and Farrington, 1997; Harrington et al., 2001; Davidson et al., 2004). For example, Harrington et al. (2001) reported higher wood NPP with N and P application in secondary forests limited by N (young secondary forest) and P (old secondary forest), respectively. Likewise, Campo and Vázquez-Yanes (2004) observed a greater litter production (NPP component) with the application of N+P in young (10 years) and old (60 years) secondary dry forests, respectively. Similarly, Davidson et al. (2004) recorded a higher wood NPP with the application of N and N+P in six-year-old secondary forests in the Amazon. These experiments show the limitation of N in early successional stages (Davidson et al., 2004) and the restriction of P in late successional stages (Harrington et al., 2001). Likewise, these results show the influence of different soil nutrients on the wood NPP in successional processes, which denotes a multiple nutritional limitation (Kaspari et al., 2008; Sullivan et al., 2014), as could be asserted in the present study.

The fact of registering a higher wood NPP in post-mining forests with high OM and total N contents is similar to that reported in secondary forests of the Amazon, where a higher wood carbon capture was observed in forests with higher total N in the soil (Feldpausch et al., 2004; Kalamandeen et al., 2020). In particular, the fact that wood NPP increases with total N is crucial, because this nutrient is considered one of the limiting factors for plant growth (Lambers et al., 2008a) and NPP of primary tropical forests (Paoli and Curran, 2007; LeBauer and Treseder, 2008; Quinto and Moreno, 2017) and secondary (Feldpausch et al., 2004; Kalamandeen et al., 2020). Total N is fundamental to photosynthesis, formation of ATP and NADPH+ molecules, and in the constitution of chlorophyll (Lambers et al., 2008a); therefore, it is fundamental for the wood NPP of the post-mining forests of the Colombian Pacific. Likewise, the influence of other nutrients (Ca, Mg and ECEC) on the wood NPP, denotes a limitation due to multiple nutrients (Paoli and Curran, 2007; Kaspari et al., 2008), which shows the need to develop active restorations, applying various nutrients in abandoned mines.

A particular aspect observed in the present investigation was wood NPP did not present a significant relationship with the availability of edaphic P in post-mining forests; which is contrary to what has been reported in old secondary forests (Vitousek and Farrington, 1997; Harrington et al., 2001), and in mature tropical forests (Cleveland et al., 2011), such as those of the Amazon (Aragão et al., 2009), Indonesia (Paoli and Curran, 2007) and the biogeographic Chocó (Quinto et al., 2017). Possibly, the little relationship registered between the wood NPP and the P available in post-mining forests is due to reasons such as: 1) the little variation registered in the P available from the post-mining soil, since with mining and the subsequent succession edaphic always presented high values (P available = 26.02 *vs* 32.09 ppm) (Quinto et al., 2022), with which, there was no true deficiency gradient in the soil; 2) the adaptive strategies developed to acquire edaphic P, such as mycorrhizal associations and the growth of a "cluster" network of fine roots that extract the P present in insoluble inorganic phosphates in the soil (Lambers et al., 2008b); with which, the wood NPP rates tend to be similar and make it difficult to show relationships with the P available from the soil.

Could it be that there are limitations of the wood NPP due to the availability of soil nutrients (N and P) in post-mining forests, as suggested by the published hypotheses (Vitousek, 1984; Lambers et al., 2008b; Kalamandeen et al., 2020)?

The hypothesis of nutritional limitation of the wood NPP of the forest has been raised by soil P availability and total N with the succession (Walker and Syers, 1976); according to which, in tropical soils with initial successional ages, there is little availability of N, due to its reduced biological fixation and scarcity of leguminous plants (Walker, 1993; Davidson et al., 2004). However, to the extent that there is a greater colonization of N-fixing plants, the biomass of the ecosystem increases and the succession advances, its availability increases, and this limitation is reduced (Cleveland et al., 1999; Walker and del Moral, 2008). Whereas, the levels of P in the soil tend to be high in the first successional stages, and over time its availability tends to decrease and be limited in the ecosystem (Vitousek et al., 2010), due to losses by leaching and immobilization in Fe and Al oxides, especially in tropical clayey soils (Walker and Syers, 1976; Vitousek et al., 1993; Reed et al., 2011).

This hypothesis was partially corroborated in the present investigation, given it was observed wood NPP and the total N are positively correlated in post-mining forests; as has been proposed for secondary forests (Vitousek and Farrington, 1997; Harrington et al., 2001; Davidson et al., 2004; Feldpausch et al., 2004); while there was no significant correlation with the available P content. Which is similar to what has been recorded in other investigations (Feldpausch et al., 2004). However, in the post-mining forests, there was also a correlation between the wood NPP and the OM, Ca and Mg contents of the soil; which shows that, in initial stages of the succession, not only can there be a limitation by total N (Kalamandeen et al., 2020), but also, there is a limitation by multiple soil nutrients, in areas previously degraded by mining.

CONCLUSIONS

In post-mining forests, soil nutrients determined the wood NPP, and multiple limitations of nutrients with the succession were observed, corroborating the need to restore the degraded ecosystem. The rates of carbon sequestration reported in post-mining forests in the Colombian Pacific denote the degradation of the functioning of the ecosystem generated by mining and reveal its negative influence on the role of these ecosystems in the carbon balance and in mitigating global climate change. The first years of post-mining forest recovery, when less carbon sequestration and greater damage to the ecosystem is evident compared to other anthropic activities such as agriculture and livestock, show the need to develop restoration processes after mining.

Likewise, the fact that post-mining forests present high rates of wood NPP and carbon sequestration after a few decades of deforestation and mining is an opportunity for the development of reforestation programs of forests, which allow the mitigation of global climate change and the conservation of the Colombian Pacific region.

ACKNOWLEDGEMENTS

This research was financed through the project: Evaluation of the effect of soil fertilization on the net production of the ecosystem in areas degraded by mining, as a strategy to promote carbon capture and the sale of environmental services in the Chocó Biogeographic (CODE 1128 -852-72243), presented by the Technological University of Chocó DLC, National University of Colombia Medellín, University of Valladolid (Spain), John Von Neumann Pacific Environmental Research Institute, and SENA, and approved by the Ministry of Science, Technology and Innovation.

AUTHOR CONTRIBUTIONS

Conceptualization: Harley Quinto Mosquera (lead).

Data curation: David Pérez Abadía (lead).

Formal analysis: Hamleth Valois Cuesta (lead).

Investigation: David Pérez Abadía (equal), Hamleth Valois Cuesta (equal) and Harley Quinto Mosquera (equal).

Methodology: David Pérez Abadía (equal) and Harley Quinto Mosquera (equal).

Project administration: Harley Quinto Mosquera (lead).

Resources: Harley Quinto Mosquera (lead).

Writing – original draft: David Pérez Abadía (equal), Hamleth Valois Cuesta (equal) and Harley Quinto Mosquera (equal).

Writing – review & editing: Hamleth Valois Cuesta (equal) and Harley Quinto Mosquera (equal).

REFERENCES

Alvarado A, Raigosa J. Nutrición y fertilización forestal en regiones tropicales. Universidad de Costa Rica. San José. Costa Rica: Asociación Costarricense de la Ciencia del Suelo; 2012.

Álvarez E, Duque A, Saldarriaga J, Cabrera K, De las Salas G, del Valle I, Lema A, Moreno F, Orrego S, Rodríguez L. Tree aboveground biomass allometries for carbon stocks estimation in the natural forests of Colombia. Forest Ecol Manag. 2012;267:297-308. https://doi.org/10.1016/j.foreco.2011.12.013

Alves D, Soares JV, Amaral S, Mello E, Almeida S, Silva OF, Silveira A. Biomass of primary and secondary vegetation in Rondonia, Western Brazilian Amazon. Glob Change Biol. 1997;3:451-61. https://doi.org/10.1046/j.1365-2486.1997.00081.x

Ángel J, Ordoñez M, Olivero J, Echavarría C, Ayala H, Cabrera M. Consideraciones sobre la minería en el departamento del Chocó y recomendaciones para mejorar la gestión. Cali – Colombia: Geopatrimonio - Universidad de Cartagena - IIAP - WWF; 2019. Available from: http://biblioteca.udea.edu.co:8080/leo/handle/123456789/6278

Aragão LEO, Malhi Y, Metcalfe DB, Silva-Espejo JE, Jiménez E, Navarrete D, Almeida S, Costa ACL, Salinas N, Phillips OL, Anderson LO, Baker TR, Goncalvez PH, Huamán-Ovalle J, Mamani-Solórzano M, Meir P, Monteagudo A, Peñuela MC, Prieto A, Quesada CA, Rozas-Dávila A, Rudas A, Silva Junior JA, Vásquez R. Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils. Biogeosciences. 2009;6:2441-88. https://doi.org/10.5194/bg-6-2759-2009

Austin A, Vitousek P. Nutrient dynamics on a precipitation gradient in Hawai'i. Oecologia. 1998;113:519-29. https://doi.org/10.1007/s004420050405

Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Lloyd J, Monteagudo A, Neill DA, Patiño S, Pitman NA, Silva JNM, Martinez RV. Variation in wood density determines spatial patterns in Amazonian forest biomass. Glob Change Biol. 2004;10:545-62. https://doi.org/10.1111/j.1365-2486.2004.00751.x

Beer C, Reichstein M, Tomelleri E, Ciais P, Jung M, Carvalhais N, Papale D. Terrestrial gross carbon dioxide uptake: Global distribution and covariation with climate. Science. 2010;329:834-8. https://doi.org/10.1126/science.1184984

Brown S. Estimating biomass and biomass change of tropical forests: A primer. Rome: FAO; 1997. (Forestry paper, 134).

Campo J, Vázquez-Yanes C. Effects of nutrient limitation on aboveground carbon dynamics during tropical dry forest regeneration in Yucatán, Mexico. Ecosystems. 2004;7:311-9. https://doi.org/10.1007/s10021-003-0249-2

Chazdon RL, Broadbent EN, Rozendaal DMA, Bongers F, Zambrano AMA, Aide TM, et al. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Science Advances. 2016;2:e1501639. https://doi.org/10.1126/sciadv.1501639

Clark DA, Brown S, Kicklighter DW, Chambers JD, Thomlinson JR, Ni J, Holland E. Net primary production in forest: An evaluation and sinthesis of existing field data. Ecol Appl. 2001b;11:371-84. https://doi.org/10.1890/1051-0761(2001)011[0371:NPPITF]2.0.CO;2

Clark DA, Brown S, Kicklighter DW, Chambers JD, Thomlinson JR, Ni J. Measuring net primary production in forest: Concepts and field methods. Ecol Appl. 2001a;11:356-70. https://doi.org/10.1890/1051-0761(2001)011[0356:MNPPIF]2.0.CO;2

Cleveland CC, Townsend AR, Schimel DS, Fisher H, Howarth RW, Hedin LO, Perakis SS, Latty EF, Von Fischer JC, Elseroad A, Wasson, MF. Global patterns of terrestrial biological nitrogen (N_2) fixation in natural ecosystems. Global Biogeochem Cy. 1999;13:623-45. https://doi.org/10.1029/1999GB900014

Cleveland CC, Townsend AR, Taylor P, Alvarez-Clare S, Bustamante M, Chuyong G, Dobrowski SZ, Grierson P, Harms KE, Houlton BZ, et al. Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. Ecol Lett. 2011;14:939-47. https://doi.org/10.1111/j.1461-0248.2011.01658.x

Davidson EA, Carvalho CJR, Vieira ICG, Figueiredo RD, Moutinho P, Ishida FY, Santos MTP, Guerrero JB, Kalif K, Saba RT. Nitrogen and phosphorus limitation of biomass growth in a tropical secondary forest. Ecol Appl. 2004;14:150-63. https://doi.org/10.1890/09-0636.1

Del Grosso S, Parton W, Stohlgren T, Zheng DL, Bachelet D, Prince S, Hibbard K, Olson R. Global potential net primary production predicted from vegetation class, precipitation, and temperature. Ecology. 2008;89:2117-26. https://doi.org/10.1890/07-0850.1

Diaz WA, Elcoro S. Plantas colonizadoras en áreas perturbadas por la minería en el Estado Bolívar, Venezuela. Acta Bot Venez. 2009;32:453-66.

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J. Carbon pools and flux of global forest ecosystems. Science. 1994;263:185-90. https://doi.org/10.1126/science.263.5144.185

Environmental Law Alliance Worldwide - ELAW. Guidebook for evaluating mining project EIAs. Eugene, Oregon: ELAW; 2010. Available from: www.elaw.org.

Feldpausch TR, Rondon MA, Fernandes E, Riha SJ, Wandelli E. Carbon and nutrient accumulation in secondary forests regenerating on pastures in central Amazonia. Ecol Appl. 2004;14:S164-76. https://doi.org/10.1890/01-6015

Field CB, Behrenfeld MJ, Randerson JT, Falkowski P. Primary production of the biosphere: Integrating terrestrial and oceanic components. Science. 1998;281:237-40. https://doi.org/10.1126/science.281.5374.237

Forero-Peña LA, Leiva-Rojas EI, Ramírez-Pisco R. Is it possible that the structure of tropical rainforests has recovered 40 years after clear-cutting? For Stud. 2022;76:64-75.

Gentry A. A field guide to the families and genera of woody plants of northwes South América. Washington, D.C. Conservation International; 1993.

Giljum S, Maus V, Kuschnig N, Luckeneder S, Tost M, Sonter LJ, Bebbington AJ. A pantropical assessment of deforestation caused by industrial mining. PNAS. 2022;19:e2118273119. https://doi.org/10.1073/pnas.2118273119

Grace J. Understanding and managing the global carbon cycle. J Ecol. 2004;92:189-202. https://doi.org/10.1111/j.0022-0477.2004.00874.x

Guariguata MR, Ostertag GR. Neotropical secondary forest successions: Changes in structural and functional characteristics. Forest Ecol Manag. 2001;148:185-206. https://doi.org/10.1016/S0378-1127(00)00535-1

Harrington RA, Fownes JH, Vitousek PM. Production and resource use efficiencies in N and P-limited tropical forests: a comparison of responses to long-term fertilization. Ecosystems. 2001;4:646-57. https://doi.org/10.1007/s10021-001-0034-z

Holl KD. Tropical moist forest. In: Perrow MR, Davy AJ, editors. Handbook of ecological restoration. Vol 2: Restoration in practice. Cambridge: Cambridge University Press; 2002. p. 539-58.

Hoshmand AR. Statistical methods for environmental and agricultural sciences. 2nd ed. Boca Raton: CRC Press; 1998.

Intergovernmental Panel on Climate Change - IPCC. Climate change 2014: Synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the intergovernmental panel on climate change.Geneva, Switzerland: IPCC; 2014. Available from: https://www.ipcc.ch/report/ar5/syr/.

Jiménez EM, Moreno FH, Lloyd J, Peñuela MC. Fine root dynamics for forests on contrasting soils in the Colombian Amazon. Biogeosciences. 2009;6:2809-27. https://doi.org/10.5194/bg-6-2809-2009

Johnson CM, Zarin DJ, Johnson AH. Post-disturbance aboveground biomass accumulation in global secondary forests. Ecology. 2000;81:1395-401. https://doi.org/10.1890/0012-9658(2000)081[1395:PDABAI]2.0.CO;2

Kalamandeen M, Gloor E, Johnson I, Agard S, Katow M, Vanbrooke A, Ashley D, Batterman SA, Ziv G, Holder-Collins K, Phillips OL, Brondizio ES, Vieira I, Galbraith D. Limited biomass recovery from gold mining in Amazonian forests. J Appl Ecol. 2020;57:1730-40. https://doi.org/10.1111/1365-2664.13669

Kaspari M, Garcia MN, Harms KE, Santana M, Wright SJ, Yavitt JB. Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecol Letts. 2008;11:35-43. https://doi.org/10.1111/j.1461-0248.2007.01124.x

Lambers H, Chapin III FS, Pons TL. Plant physiological ecology. 2nd ed. New York: Springer Science; 2008a. https://doi.org/10.1007/978-0-387-78341-3

Lambers H, Raven JA, Shaver GR, Smith SE. Plant nutrient-acquisition strategies change with soil age. Trends Ecol Evol. 2008b;23:95-103. https://doi.org/10.1016/j.tree.2007.10.008

LeBauer DS, Treseder KK. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology. 2008;89:371-9. https://doi.org/10.1890/06-2057.1

León JD, Osorio NW. Role of litter turnover in soil quality in tropical degraded lands of Colombia. Sci World J. 2014;2014:693981. https://doi.org/10.1155/2014/693981

Linger E, Hogan A, Cao M, Zhang W, Yang X, Hu Y. Precipitation influences on the net primary productivity of a tropical seasonal rainforest in Southwest China: A 9-year case study. Forest Ecol Manag. 2020;467:118153. https://doi.org/10.1016/j.foreco.2020.118153

Lu D, Moran E, Mausel P. Linking Amazonian secondary succession forest growth to soil properties. Land Degrad Dev. 2002;13:331-43. https://doi.org/10.1002/ldr.516

Malhi Y, Baker TR, Phillips OL, Almeida S, Alvarez E, Arroyo L, Chave J, Czimczik C, Difiore A, Higuchi N, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Montoya LM, Monteagudo A, Neill DA, Vargas PN, Patiño S, Pitman NA, Quesada CA, Salomão R, Silva JNM, Lezama AT, Martínez RV, Terborgh J, Vinceti B, Lloyd J. The above-ground coarse wood productivity of 104 neotropical forest plots. Glob Change Biol. 2004;10:563-91. https://doi.org/10.1111/j.1529-8817.2003.00778.x

Malhi Y, Doughty C, Galbraith D. The allocation of ecosystem net primary productivity in tropical forests. Phil Trans R Soc B. 2011;366:3225-45. https://doi.org/10.1098/rstb.2011.0062

Maus V, Giljum S, Silva DM, Gutschlhofer J, Rosa RP, Luckeneder S, Gass SLB, Lieber M, McCallum I. An update on global mining land use. Sci Data. 2022;9:433. https://doi.org/10.1038/s41597-022-01547-4

Moran EF, Brondizio E, Tucker JM, Silva-Fosberg MC, McCracken S, Falesi I. Effects of soil fertility and land-use on forest succession in Amazônia. Forest Ecol Manag. 2000;139:93-108. https://doi.org/10.1016/S0378-1127(99)00337-0

Oberleitner F, Egger C, Oberdorfer S, Dullinger S, Wanek W, Hietz P. Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica. Forest Ecol Manag. 2021;479:118580. https://doi.org/10.1016/j.foreco.2020.118580

Osorio NW. Manejo de nutrientes en suelos del trópico. Colombia: Editorial L. Vieco S.A.S; 2014.

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Hayes DA. Large and persistent carbon sink in the world's forests. Science. 2011;333:988-93. https://doi.org/10.1126/science.1201609

Paoli G, Curran L. Soil nutrients limit fine litter production and tree growth in mature lowland forest of southwestern Borneo. Ecosystems. 2007;10:503-18. https://doi.org/10.1007/s10021-007-9042-y

Phillips OL, Malhi Y, Higuchi N, Laurance W, Núñez P, Vásquez M, Laurance S, Ferreira L, Stern M, Brown S, Grace J. Changes in the carbon balance of tropical forest: Evidence from long-term plots. Science. 1998;282:439-42. https://doi.org/10.1126/science.282.5388.439

Poorter L, Bongers F, Aide TM, Almeyda AM, Balvanera P, Becknell JM, et al. Biomass resilience of Neotropical secondary forests. Nature. 2016;530:211-4. https://doi.org/10.1038/nature16512

Posada JM, Schuur EAG. Relationships among precipitation regime, nutrient availability, and carbon turnover in tropical rain forests. Oecologia. 2011;165:783-95. https://doi.org/10.1007/s00442-010-1881-0

Poveda IC, Rojas CA, Rudas A, Rangel JO. El Chocó biogeográfico: Ambiente físico. In: Rangel JO. Colombia Diversidad Biótica IV. El Chocó biogeográfico/Costa Pacífica. Bogotá: Instituto de Ciencias Naturales, Universidad Nacional de Colombia; 2004. p. 1-21.

Primack RB. A primer of conservation biology. 4th ed. Sunderland: Sinauer Associates Inc; 2008.

Primack RB, Vidal O. Introducción a la biología de la conservación. México: Fondo de Cultura Económica; 2019.

Quinto H, Ayala-Vivas G, Gutiérrez H. Contenido de nutrientes, acidez y textura del suelo en áreas degradadas por la minería en el Chocó biogeográfico. Rev Acad Colomb Cienc Exacr Fis Nat. 2022;46:514-28. https://doi.org/10.18257/raccefyn.1615

Quinto H, Cuesta-Nagles J, Mosquera-Sánchez I, Palacios-Hinestroza L, Peñaloza H. Biomasa vegetal en zonas degradadas por minería en un bosque pluvial tropical del Chocó Biogeográfico. Rev Biodivers Neotrop. 2013;3:53-64. https://doi.org/10.18636/bioneotropical.v3i1.127

Quinto H, Mena-Domínguez Y, Valoyes-Hinestroza H. Relación entre la producción de hojarasca y las condiciones edáficas en bosques pluviales tropicales del Chocó Biogeográfico, Colombia. Actual Biol. 2017;39:29-40. https://doi.org/10.17533/udea.acbi.v39n106a03

Quinto H, Moreno F. Net primary productivity and edaphic fertility in two pluvial tropical forests in the Chocó biogeographical region of Colombia. PLoS ONE. 2017;12:e0168211. https://doi.org/10.1371/journal.pone.0168211

Quinto H, Moreno FH. Precipitation effects on soil characteristics in tropical rain forests of the Chocó biogeographical region. Rev Fac Nac Agron Medellín. 2016;69:7813-23. https://doi.org/10.15446/rfna.v69n1.54749

R Development Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2013. Available from: http://www.R-project.org/.

Ramírez G, Quinto H, Vargas-Porras L, Rangel JO. Temporary effect of mining on breathing and on the physicochemical conditions of soil. Mod Environ Sci Eng. 2019;5:837-48. https://doi.org/10.15341/mese(2333-2581)/09.05.2019/007

Ramírez G, Rangel-Ch JO. Sucesión vegetal en áreas de minería a cielo abierto en el bosque pluvial tropical del departamento del Chocó, Colombia. Rev Acad Colomb Cienc Exacr Fis Nat. 2019;43:673-88. https://doi.org/10.18257/raccefyn.896

Rangel JO. Colombia Diversidad Biótica IV. El Chocó biogeográfico/Costa Pacífica. Bogotá: Instituto de Ciencias Naturales, Universidad Nacional de Colombia; 2004.

Reed SC, Townsend AR, Taylor PG, Cleveland CC. Phosphorus cycling in tropical forests growing on highly weathered soils. In: Bünemann E, Oberson A, Frossard E, editors. Soil Biology - Phosphorus in action. Berlin, Heidelberg: Springer; 2011. https://doi.org/10.1007/978-3-642-15271-9_14

Sansupa C, Purahong W, Wubet T, Tiansawat P, Pathom-Aree W, Teaumroong N. Soil bacterial communities and their associated functions for forest restoration on a limestone mine in northern Thailand. PLoS ONE. 2021;16:e0248806. https://doi.org/10.1371/journal.pone.0248806

Schuur EA. Productivity and global climate revisited: The sensitivity of tropical forest growth to precipitation. Ecology. 2003;84:1165-70. https://doi.org/10.1890/0012-9658(2003)084[1165:PAGCRT]2.0.CO;2

Silver WL, Ostertag R, Lugo AE. The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. Restor Ecol. 2000;8:394-407. https://doi.org/10.1046/j.1526-100x.2000.80054.x

Sullivan BW, Alvarez-Clare S, Castle SC, Porder S, Reed SC, Schreeg L, Cleveland CC, Townsend AR. Assessing nutrient limitation in complex forested ecosystems: Alternatives to large-scale fertilization experiments. Ecology. 2014;95:668-81. https://doi.org/10.1890/13-0825.1

Tucker JM, Brondizio ES, Moran EF. Rates of forest regrowth in eastern Amazonia: A comparison of Altamira and Bragantina Regions, Parâ State, Brazil. Interciencia. 1998;23:64-73.

Valois-Cuesta H. Sucesión primaria y ecología de la revegetación de selvas degradadas por minería en el Chocó, Colombia: Bases para su restauración ecológica [thesis]. España: Universidad de Valladolid; 2016.

van der Sande MT, Arets EJMM, Peña-Claros M, Hoosbeek MR, Cáceres-Siani Y, van der Hout P, Poorter L. Soil fertility and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest. Funct Ecol. 2018;32:461-74. https://doi.org/10.1111/1365-2435.12968

Vitousek PM. Litterfall, nutrient cycling and nutrient limitation in tropical forests. Ecology. 1984;65:285-98. https://doi.org/10.2307/1939481

Vitousek P, Porder S, Houlton BZ, Chadwick OA. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecol Appl. 2010;20:5-15. https://doi.org/10.1890/08-0127.1

Vitousek PM, Farrington H. Nutrient limitation and soil development: Experimental test of a biogeochemical theory. Biogeochemistry. 1997;37:63-75. https://doi.org/10.1023/A:1005757218475

Vitousek PM, Walker LR, Whiteaker LD, Matson PA. Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. Biogeochemistry. 1993;23:197-215. https://doi.org/10.1007/BF00023752

Walker LR. Nitrogen fixers and species replacements in primary succession. In: Miles J, Walton DWH, editors. Primary succession on land. Oxford: Blackwell; 1993. p. 249-72.

Walker LR, del Moral R. Lessons from primary succession for restoration of severely damaged habitats. Appl Veg Sci. 2008;12:55-67. https://doi.org/10.1111/j.1654-109X.2009.01002.x

Walker TW, Syers JK. The fate of phosphorus during pedogenesis. Geoderma. 1976;15:1-19. https://doi.org/10.1016/0016-7061(76)90066-5

Whitmore TC. An introduction to Tropical Rain Forests. 2nd ed. Oxford: Oxford University Press; 1998.

Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. Glob Change Biol. 2011;17:927-42. https://doi.org/10.1111/j.1365-2486.2010.02302.x

Zhang J, Tang X, Zhong S, Yin G, Gao Y, He X. Recalcitrant carbon components in glomalin-related soil protein facilitate soil organic carbon preservation in tropical forests. Sci Rep. 2017;7:2391. https://doi.org/10.1038/s41598-017-02486-6