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Aboveground biomass in a post-mining forest succession in the Colombian Pacific

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ABSTRACT

Introduction: Mining is one of the main drivers of deforestation of tropical forests. This activity affects the storage of aboveground biomass of these ecosystems; therefore, their ability to contribute to the mitigation of global climate change.

Objective: To assess the influence of soil properties on the aboveground biomass storage of post-mining forests in the Colombian Pacific.

Methods: Plots were established in areas post-mining and with different successional ages (12-15 years, 30-35 years, and mature forest). The aboveground biomass and physicochemical parameters of the soil were measured.

Results: An aboveground biomass of 15.58 t ha^{-1}, 35.17 t ha^{-1}, and 178.32 t ha^{-1} was recorded at 12-15 years, 30-35 years, and mature forests, respectively. The species with the highest biomass content in post-mining forests were *Cespedesia spathulata* and *Clidemia septuplinervia*. The aboveground biomass was positively correlated with organic matter (OM), calcium (Ca), magnesium (Mg), CICE, total nitrogen (N), and silt. In contrast, the relationship was negative with sand, aluminum (Al), and potassium (K) content. It was evidenced that the relationship between aboveground biomass and soils differed in each successional age. When evaluating the changes of aboveground biomass and soils in the succession, it was observed that the aboveground biomass and total N increased with the recovery time. At the same time, the P and K decreased with succession. On the other hand, the contents of OM, Mg, Al, Ca, and CICE showed curvilinear tendencies since they increased in the first stages and then decreased in the advanced successional stages.

Conclusions: Aboveground biomass increases with forest recovery time in the study area. This increase is influenced by the presence of two dominant species shared among the investigated ecosystems and by the soil's N, P, and K content.

Key words: aluminum toxicity; carbon; Chocó biogeographical; nutrient limitation; restoration; plant succession.

RESUMEN

Biomasa aérea en una sucesión de bosques post-minería del Pacífico colombiano

Introducción: La minería es una de las principales causas de deforestación de los bosques tropicales. Esta actividad afecta el almacenamiento de biomasa aérea de estos ecosistemas; y, por tanto, su capacidad para contribuir a la mitigación del cambio climático global.

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Objetivo: Evaluar la influencia de las propiedades del suelo en el almacenamiento de la biomasa aérea de bosques post-minería del Pacífico colombiano.
Métodos: Se establecieron parcelas en áreas post-minería con diferentes edades de sucesión (12-15 años, 30-35 años y bosque maduro). Se midió la biomasa aérea y parámetros fisicoquímicos del suelo.
Resultados: Se registró una biomasa aérea de 15.58 t ha^{-1}, 35.17 t ha^{-1} y 178.32 t ha^{-1} en 12-15 años, 30-35 años y bosque maduro, respectivamente. Las especies con mayor contenido de biomasa en los bosques post-minería fueron *Cespedesia spathulata* y *Clidemia septuplinervia*. La biomasa aérea se correlacionó positivamente con la materia orgánica (MO), calcio (Ca), magnesio (Mg), CICE, nitrógeno total (N) y limo. Por el contrario, la relación fue negativa con el contenido de arena, aluminio (Al) y potasio (K). Se evidenció que la relación entre la biomasa aérea y los suelos difería en cada edad sucesional. Al evaluar los cambios de la biomasa aérea y los suelos en la sucesión, se observó que la biomasa aérea y el N total aumentaron con el tiempo de recuperación. Al mismo tiempo, el P y el K disminuyeron con la sucesión. Por otro lado, los contenidos de OM, Mg, Al, Ca, y CICE mostraron tendencias curvilíneas ya que aumentaron en los primeros estadios y luego disminuyeron en los estadios sucesionales avanzados.
Conclusiones: la biomasa aérea aumenta con el tiempo de recuperación del bosque en el área de estudio. Este incremento está influenciado por la presencia de dos especies dominantes compartidas entre los ecosistemas investigados y por el contenido de N, P y K del suelo.

Palabras clave: toxicidad de aluminio; carbono; Chocó biogeográfico; limitación de nutrientes; restauración; sucesión vegetal.

INTRODUCTION

Tropical forests are crucial in mitigating global climate change (Pachauri et al., 2014), as they store approximately 59 % of the total carbon in terrestrial ecosystems. Additionally, due to their high net primary productivity, these forests capture an estimated 30 % of the atmospheric carbon dioxide annually, significantly contributing to carbon sequestration worldwide (Yguel et al., 2019). These ecosystems are estimated to store 470 billion tons of CO_2 in aboveground and belowground biomass (Pan et al., 2011; Pugh et al., 2011). Despite their importance, tropical forests have faced significant deforestation and degradation in recent decades, resulting in net losses of 3.9 million hectares in Africa and 2.6 million hectares in South America over the last decade (FAO & PNUMA, 2020). Anthropogenic activities, particularly mining, have been the primary drivers of these alarming deforestation rates (Primack et al., 2019; FAO & PNUMA, 2020).

In particular, open-pit mining of metals, such as gold, has become one of the main drivers of deforestation and degradation of tropical forests (Kalamandeen et al., 2020; Primack et al., 2019). It is estimated that between 2001 and 2013, about 1 680 km^2 of tropical forests in South America were lost (Primack et al., 2019), of which 41 % corresponds to mining carried out in Guyana, 28 % in the Southwest of the Amazon, 11 % in the Tapajos Xingú forests in Brazil, and 9 % in the Magdalena basin in Colombia (Alvarez-Berríos & Aide, 2015). Between 2010 and 2017, it is estimated that between 57 000 and 60 000 ha of natural forests were lost to gold mining in Guyana and Peru, respectively (Kalamandeen et al., 2020), which not only affects the biodiversity of the region threatened but also affects the carbon content stored and the capacity of ecosystems to mitigate global climate change (Quinto et al., 2013).

Open pit mining affects the functioning of the ecosystem because it causes deforestation of forests, edaphic erosion, changes in the physicochemical conditions of the soil, chemical contamination by substances such as mercury, excavation of the subsoil, sedimentation of rivers and streams, loss of OM, changes in nutrient content, alteration of biogeochemical cycles, decrease in forest biomass and carbon, changes in species composition, and biodiversity loss (Kalamandeen et al., 2020; Quinto et al., 2013; Ramírez et al., 2019). However, due to the enormous carbon emissions into the atmosphere generated by this economic activity, it is considered to reduce the climate change mitigation potential of tropical forests substantially (Kalamandeen et al., 2020; Poorter et al., 2016). Therefore, to recover the functionality and role of the post-mining ecosystems in the carbon balance and the mitigation of global warming, it is necessary to evaluate the aboveground biomass storage and the environmental factors that favor it.

The biomass recovery in areas degraded by anthropogenic activities (mining, logging, livestock, and agriculture) is conditioned by factors such as climate, water availability (precipitation), recovery time, type and disturbance intensity, surrounding forest cover, soil conditions and fertility, among others (Guariguata & Ostertag, 2001; Kalamandeen et al., 2020; Oberleitne et al., 2021; Poorter et al., 2016). Due to this, secondary forests with 20 years of regeneration (without significant soil modification) present aboveground biomass ranges between 20 and 225 tons per hectare ($t\ ha^{-1}$), with 122 $t\ ha^{-1}$ on average (Poorter et al., 2016). Likewise, these areas can reach up to 90 % of the aboveground biomass of a primary forest in an average time of 66 years (Poorter et al., 2016). In areas affected by mining, the recovery of aboveground biomass is limited by soil nutrients, especially N (Kalamandeen et al., 2020). Therefore, it is evident that these factors are essential in forest recovery.

Although few studies directly link aboveground biomass with soil nutrients in post-mining areas, some research results in ecosystems under ecological succession (other than post-mining) indicate that as aerial biomass and succession increase, soil nitrogen (N) tends to increase. In contrast, phosphorus (P) tends to decrease (Feldpausch et al., 2004). This observation aligns with the hypothesis of nutritional limitation of available P and total N with succession (Walker & Syers, 1976). According to this hypothesis, tropical soils in early successional stages have limited availability of N (Davidson et al., 2004). However, as ecosystem biomass and succession progress, the availability of N increases (Davidson et al., 2004; Reed et al., 2011). On the other hand, P levels tend to be high in the initial successional stages, but over time, its availability diminishes and becomes limiting in the ecosystem (Reed et al., 2011; Vitousek et al., 1993; Vitousek et al., 2010; Walker & Syers, 1976). Nevertheless, these patterns and hypotheses have yet to be tested in post-mining areas.

The Colombian Pacific is one of the rainiest regions in the world, with places that have rainfall levels higher than 10 000 mm per year (Poveda et al., 2004). In this region, open pit gold mining generates the deforestation and degradation of more than 360 ha of forest annually (Ramírez & Ledezma, 2007). Due to this, these ecosystems offer us an opportunity to evaluate the hypotheses above about nutritional limitations. Therefore, our objective was to evaluate the influence of soil properties on the aboveground biomass storage of post-mining forests in the Colombian Pacific. The following questions guided this objective: How does aboveground biomass vary as a function of succession time in areas post-mining? Which tree species and botanical families have the highest aboveground biomass in areas post-mining? To what extent do edaphic conditions, especially soil nutrients, determine the aboveground biomass of areas post-mining in these high-rainfall tropical ecosystems? This inquiry is especially pertinent considering that, as noted by Austin & Vitousek (1998), high precipitation levels can lead to decreased nutrient content due to runoff and leaching.

MATERIALS AND METHODS

Study Area: The present study was carried out in forested areas previously degraded by open-pit gold mining in the town of Jigualito (5º06'01" N & 76º32'44" W), municipality of Condoto, in the Colombian Pacific, which has an average rainfall of 8 000 mm per year, an altitude of 70 m and flat topography. This locality is part of the Chocó biogeographical Chocó subregion, which includes the upper basins of the Atrato and San Juan rivers, in Piedemonte and Colinas low landscape units with humid terraced soils and with a type of transitional sedimentary rock (Poveda et al., 2004). The forests are primarily secondary, with different recovery ages, because mining has been carried out in the area at different times.

The soils are ultisols, but due to mining, they were characterized by a lot of rocky material and sand. In addition, they are acidic and have high contents of OM, total N, available P, Al, and clay. At the same time, the concentrations of Ca, K, Mg, CICE, and silt are deficient in areas of recent mining activity, but their content is higher in areas with more recovery time (Ramírez et al., 2019). On the other hand, the soils of the forested areas surrounding the mines present extreme acidity, with high contents of Al, MO, and total N and low amounts of P, Mg, and Ca. Likewise, the K contents are intermediate, and the CICE is low (Quinto & Moreno, 2016; Quinto et al., 2022).

Experimental Design: A design stratified by age of succession was used, with three strata for sampling. Stratum 1, Initial Age (IA) included areas post-mining, with a succession time of 12-15 years. This stratum presented a small shrubby and woody vegetation with a smaller average diameter and tree species richness. In contrast, in stratum 2, recovery Age (RA) corresponded to areas with a 30-35 year recovery time. In this tree, vegetation with greater diameter and specific richness was found. The stratum 3 corresponded to primary forests present in the region and was taken as the reference scenario.

Establishment of plots: In stratum 1 (EI), mine areas with a recovery time between 12-15 years were selected. In these mines, 21 permanent plots of 50 x 50 m (2 500 m^2) were installed; these plots were the sampling units. Similarly, in stratum 2 (ER), which corresponded to another forested area with more than 30-35 years of regeneration, 11 permanent plots of 50 x 50 m (2 500 m^2) were installed; these plots were the sampling units. In stratum 3, seven plots of one hectare (100 x 100 m) located in forests of the localities of Opogodó, Pacurita, and Salero, in the Colombian Pacific, were used, which were divided into 25 quadrants of 20 x 20 m (400 m^2).

Measurement of tree diameters: The circumference at breast height in cm (1.30 m above ground level) was measured with a tape measure for all trees with DBH ≥ 10 cm in each quadrant; later, the circumference values were transformed to DBH. The perimeter of the tree trunk where DBH was measured was marked with yellow spray to guarantee that subsequent measurements were made in the same strip as the first. All measured trees were marked with aluminum plates. Additionally, growth habits were identified, and the characteristics of each individual were recorded.

Botanical identification: Trees were identified to the highest possible taxonomic level (NN, species, genus, botanical family) in the herbarium of the Universidad Tecnológica del Chocó's "Herbario Chocó." Gentry (1993) specialized key was used to make this identification.

Estimation of wood density: To estimate this variable, the values published in two international databases of wood density were taken and generated in tropical forests (Brown, 1997). In cases where a species or genus found in the plots was not reported in these databases, the average genus or family of the species was used.

Estimation of aboveground biomass: To determine the aboveground biomass of the trees, the model of Álvarez et al. (2012) includes DBH and wood density as variables. The model was:

$$AB\ (kg) = EXP(1.59 - 1.22*\ln(DBH) + 1.23*(\ln(DBH^2) - 0.12*(\ln(DBH^3) + 0.69*(\ln(pi)))$$

Where AB is aboveground biomass, DBH is the diameter, Ln is the Neperian logarithm, and *pi* is the wood density. The aboveground biomass was determined at the ecosystem level, successional age, plant species, and botanical family. The biomass growth rate was estimated based on the forest age and the net aboveground biomass values.

Measurement of edaphic characteristics: In each sampling unit, five composite soil samples were taken at a depth of 20 cm in the corners and the center of each 10 x 10 m and 20 x 20 m quadrant. In total, 300 composite soil samples were taken, 125 in the EI and ER successional strata of areas post-mining and 175 in primary natural forests. The collected samples were sent to the Biogeochemistry Laboratory of the National University of Colombia, Medellin. In said laboratory, the samples were analyzed for texture (sand, silt, and clay), pH, OM content, Al, effective cation exchange capacity (ECEC), and nutrient content (N, P, K, Ca and Mg); using the techniques that are referenced below: the texture with the Bouyoucos technique, the pH with the Potentiometer of soils: water 1:2, the OM with the Walkley and Black technique and with volumetry, the available P with Acid L ascorbic acid, UV-VIS spectrophotometer, total N with the Micro-Kjeldahl analytical technique, Al with 1M KCl/Volumetry, NTC 5 263, nutrients (Ca, Mg, K) with the 1N ammonium acetate method, neutral, atomic absorption (Osorio, 2014).

Statistical analysis: To evaluate the variation of the aboveground biomass as a function of the recovery time, the non-parametric Kruskal-Wallis test was used since the assumptions of normality and homogeneity of variances of the data and their residuals were not met, evaluated with the Bartlett, Hartley, and Kurtosis statistics (between +2.0 and −2.0). Then, to determine the linear correlations and associations between edaphic variables of each successional stage and aboveground biomass, multiple regressions were used with the method of selection of significant variables "backward," for which the aboveground biomass and soil data were transformed with the natural logarithm, due to their lack of statistical normality. In addition, Spearman rank correlations and Pearson, as well as multiplicative, reciprocal, logarithmic, and linear regressions, were used to determine correlations and associations between the physical-chemical variables of the soil and aboveground biomass. Finally, regression models were used to evaluate the changes in the variables through successional time. These analyses were carried out for the strata of 12-15 and 30-35 years of recovery together and later separately. The analyses were performed in the R programming environment (R Core Team, 2013).

RESULTS

In areas post-mining, aboveground biomass increased significantly with recovery time (Kruskal-Wallis = 176.9; P = 0.00004). Specifically, in strata with 12-15 years of succession, it was 35.17 t ha^{-1}; in those with 30-35 years old it was 56.30 t ha^{-1}, and in the reference primary forests it was 178.32 t ha^{-1} (Fig. 1). Based on the aboveground biomass values and succession time, an aboveground biomass accumulation rate of 2.34 t $ha^{-1}year^{-1}$ for areas of 12-15 years of succession, and 1.87 t $ha^{-1}year^{-1}$ for areas with 30-35 years of recovery.

It was observed that aboveground biomass at the level of species, the stage from 12-15 years, presented a higher proportion in *Cespedesia spathulata*, *Cyathea* sp., *Hampea romeroi*, *Vismia* sp., and *Tovomita weddeliana* (Fig. 2A), while the stage from 30-35 years presented a higher proportion in *Tovomita weddeliana*, *Cespedesia spathulata*, *Clidemia septuplinervia*, *Inga lopadadenia*, and *Cecropia peltate* (Fig. 2B). On the other hand, at the level of botanical families, those with the highest aboveground biomass were Ochnaceae, Cyatheaceae, Malvaceae, Hypericaceae, Asteraceae, and Clusiaceae in stages of 12-15 years (Fig. 2C), while the families Clusiaceae, Ochnaceae, Fabaceae, Melastomataceae, and Urticaceae, were the most representative in the 30–35-year-old stage (Fig. 2D).

The aboveground biomass was positively correlated with OM, Ca, Mg, CEC, and total N (Table 1). In the areas with 12-15 years, aboveground biomass was positively related to CICE, but the association was negative with sand and

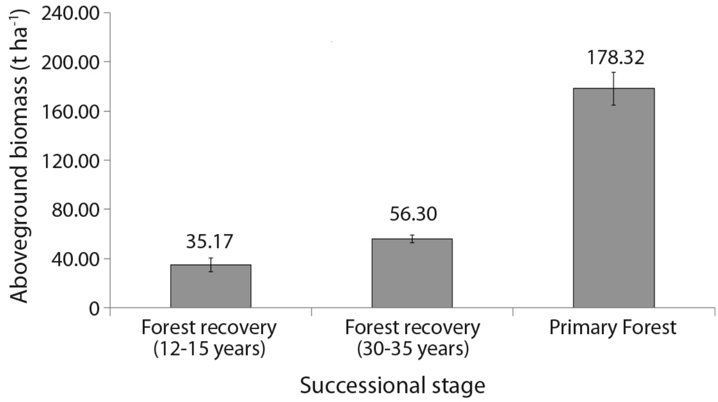

Fig. 1. Aboveground biomass in areas post-mining with different successional ages in Jigualito, Colombian Pacific.

Table 1
Correlations of aboveground biomass and soil parameters in areas post-mining, with 12-15 years and 30-35 years of recovery in Jigualito, Colombian Pacific.

Soil parameters	Aboveground biomass	
	Correlation of *Spearman*	Correlation of *Pearson*
Organic matter	0.34 (*0.016*)	
Calcium	0.44 (*0.0018*)	0.29 (*0.036*)
Magnesium	0.32 (*0.025*)	
ECEC	0.40 (*0.005*)	0.32 (*0.024*)
Nitrogen	0.29 (*0.039*)	

The values in brackets correspond to the p-value. Significant correlations are included in the table.

silt (Table 2). On the other hand, in the areas with 30-35 years, aboveground biomass was positively related to P and silt, but the relationship was negative with Ca (Table 3).

When evaluating the changes in aboveground biomass and physicochemical parameters of soil through the successional ages, it was observed that aboveground biomass and total N increased with the recovery time. At the same time, P and K decreased with succession (Fig. 3). On the other hand, OM, Mg, Al, Ca, and CICE showed curvilinear trends since they increased in early stages and then decreased in advanced stages (Fig. 3).

Table 2
Multiple regression of aboveground biomass based on edaphic variables in abandoned mines from 12-15 years in Jigualito, Colombian Pacific.

Source	Sum of Squares	Df	Mean Square	Test F	*P-value*
Model	6.9414	3	2.3138	4.62	0.0145
Residue	9.02074	18	0.501152		
Total (Corr.)	15.9621	21			
Parameter	Estimate	Standard Error	T Statistic	*P-value*	
Constant	10.1892	3.49669	2.91397	0.0093	
Ln(ECEC)	0.768866	0.30179	2.54768	0.0202	
Ln(Sand)	-1.31407	0.606447	-2.16683	0.0439	
Ln(Silt)	-1.00182	0.365238	-2.74292	0.0134	

Where R^2 = 43.48 %, R^2(adjusted) = 34.06 %. *Backward* variable selection method.

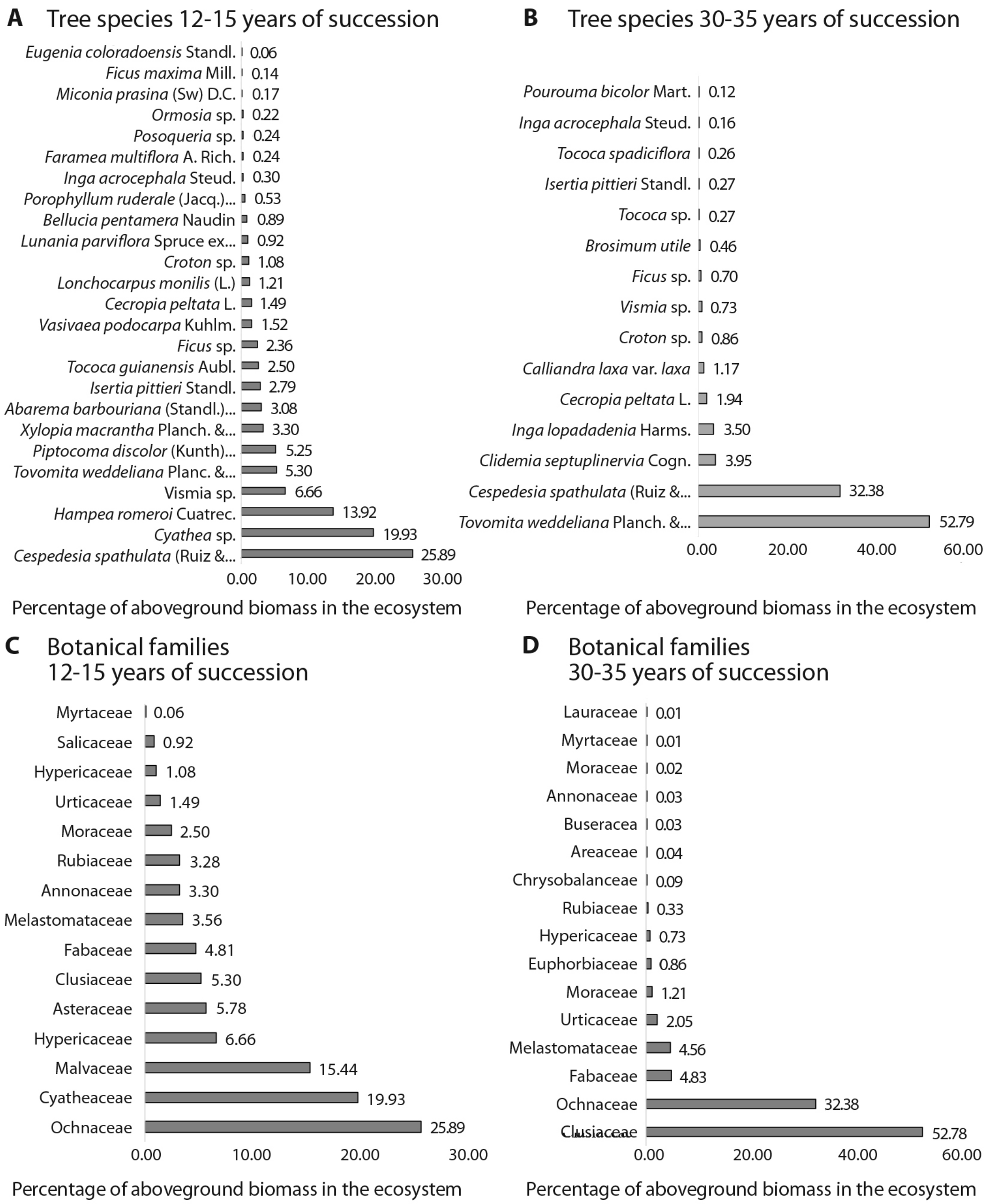

Fig. 2. Percentage of aboveground biomass of the dominant tree species and botanical families in areas post-mining in Jigualito, Colombian Pacific.

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Table 3
Multiple regression of aboveground biomass based on edaphic variables in abandoned mines aged 30-35 years in Jigualito, Colombian Pacific.

Source	Sum of Squares	Df	Mean Square	Test F	*P-value*
Model	1 679.22	3	559.739	4.60	0.0375
Residue	973.913	8	121.739		
Total (Corr.)	2 653.13	11			
Parameter	**Estimate**	**Standard Error**	**T Statistic**	***P-value***	
Constant	26.9221	11.0445	2.43759	0.0407	
Phosphorus	0.903366	0.32787	2.75526	0.0249	
Calcium	-9.31647	3.30217	-2.82132	0.0224	
Silt	1.56158	0.425212	3.67248	0.0063	

Where R^2 = 63.29 %, R^2(adjusted) = 49.5 %. *Backward* variable selection method.

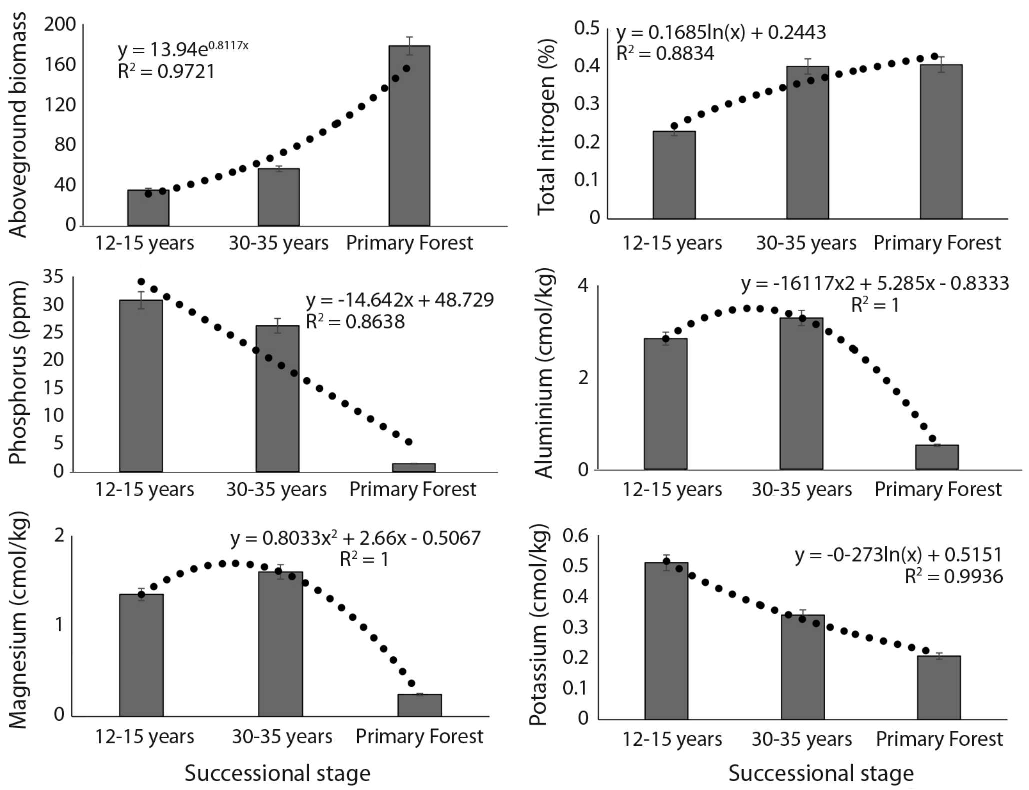

Fig. 3. Changes in aboveground biomass and chemical parameters of the soil in areas post-mining at different successional stages in Jigualito, Colombian Pacific.

DISCUSSION

After thirty years of succession, areas post-mining can recover up to 31.57 % of the aboveground biomass of a primary forest in the region. Contrary to this, Kalamandeen et al. (2020) reported an average aboveground biomass between 1.06 and 6.63 t ha^{-1} in areas post-mining for 3 and 4 years in the Guyanese Amazon. Consequently, in these ecosystems, after four years, only 1.62 % of the aboveground biomass of the mature reference forest was recovered (Kalamandeen et al., 2020). These results show that, both in the Amazon and in the Colombian Pacific, after mining, the forests take many years to recover the aboveground biomass characteristic of the primary forest of each region. Consequently, open-pit mining would affect not only the amounts of carbon in the ecosystem but also their ability to recover in times when they would do so with another type of intervention or disturbance, such as crop abandonment and forest use.

In the forests of the Colombian Pacific, Torres-Torres et al. (2017) measured aboveground biomass ranging from 62.6 to 136.1 t ha^{-1} in secondary forests aged 12 to 40 years, which had previously been impacted by logging and abandoned agriculture. This illustrates that, even within the same biogeographic region, there are variations in the recovery of aboveground biomass in tropical forests affected by different human-induced disturbances. Additionally, Alves et al. (1997) reported that secondary forests of varying ages and subjected to different types of human intervention in the Amazon region could achieve 40-60 % of the aboveground biomass of a primary forest after just 18 years of regeneration. Moreover, Oberleitner et al. (2021) documented that within a mere 20 years of regeneration, secondary forests in Costa Rica can recover up to 52 % of the area's aboveground biomass of primary forests. In an analysis carried out a few years ago, at the level of Neotropical forests, Poorter et al. (2016) reported that after 20 years' secondary forests can reach up to 122 t ha^{-1} of aboveground biomass in areas previously affected by livestock and agriculture. Additionally, this study concluded that, after about 66 years of recovery, they can reach up to 90 % of the aboveground biomass of a primary forest (Poorter et al., 2016), which is a situation contrary to what is recorded in areas post-mining, as mentioned before. Possibly, this difference is due to the influence of different factors that affect the succession in abandoned mines, among which we can mention the degree of damage caused to the soil and subsoil, which restricts the recovery of the ecosystem (Torres-Torres et al., 2023).

The impact of mining on the soil influences the type of ecological succession (primary or secondary) and the time required for aboveground biomass (AB) recovery in the ecosystem (Chazdon, 2003). Specifically, the differences in AB recovery between mining-affected areas and those impacted by other disturbances are determined by the type of succession that follows the disturbance (Chazdon et al., 2016; Guariguata & Ostertag, 2001). In the case of mining, primary succession is typically observed (Kalamandeen et al., 2020), as this activity involves the removal of the organic soil horizon, resulting in altered structure and texture, often leaving rocks and sand on the soil surface (Ramírez et al., 2019). This is akin to the processes observed in newly formed substrates, landslide areas, soils resulting from volcanic eruptions, and igneous rocks where primary successions occur (Walker, 1993). In contrast, secondary successions take place on soils with organic matter, high nutrient content, and seed banks, such as those following activities like livestock, agriculture, and logging (Guariguata & Ostertag, 2001), leading to a much faster recovery of species richness and biomass. The slow recovery of AB after mining underscores the necessity for ecosystem restoration.

Another factor that may be determining the recovery of the ecosystem in abandoned mines is the composition of tree species and their respective capacity to grow and store biomass. The species recorded in abandoned mines are commonly reported for degraded ecosystems and secondary forests with different stages of succession (Alves et al., 1997;

Guariguata & Ostertag, 2001). The composition, diversity, and biomass of these species are influenced by the fertility or toxicity of the soil in which they grow (Martins et al., 2015; Oberleitner et al., 2021; Poorter et al., 2016; Torres-Torres et al., 2023). Notably, in abandoned mines, a high concentration of Al was recorded, which is undoubtedly generating toxicity for plants (Carreño & Chaparro-Giraldo, 2013; Jansen et al., 2002; Quinto et al., 2022); and consequently, it follows that the species with the highest aboveground biomass are possibly the ones with the highest tolerance to Al toxicity (Carreño & Chaparro-Giraldo, 2013). Such is the case of trees from botanical families such as Melastomataceae, Rubiaceae, Euforbiaceae, and Lauraceae, among others, that in previous studies have been determined as tolerant and bioaccumulative of Al (Jansen et al., 2002¸ Watanabe & Osaki, 2002). This probably occurs in the post-mining forests under study, where species belonging to these botanical families are well represented (see floristic composition in Torres-Torres et al., 2023). Therefore, it would be worthwhile to verify this assumption in future research.

High levels of aluminum in the soil may restrict the aboveground biomass storage of some species in areas affected by mining. This is because the high availability of this mineral in many species with low tolerance to its excessive content leads to a decrease in root elongation, reduced stem growth, altered metabolic and physiological processes, and decreased ecosystem productivity (Shetty et al., 2021). Additionally, edaphic Al reduces nutrient absorption, causes nutritional stress, chlorosis, and necrosis, decreases leaf size, and affects photosynthesis (Chandra & Keshavkant, 2021). Consequently, Al toxicity may be responsible for the limited recovery of aboveground biomass observed in post-mining forests over a 30-year succession period.

The edaphic conditions are fundamental for recovering aboveground biomass in abandoned mines (León & Osorio, 2014). In this sense, this study evidenced a positive relationship between aboveground biomass and soil nutrients, showing that small soil patches with higher fertility facilitate carbon accumulation in the ecosystem. This higher aboveground biomass recorded in more fertile abandoned mines is similar to that reported by Kalamandeen et al. (2020), who reported a higher aboveground biomass in abandoned mines with higher N content. Likewise, Poorter et al. (2016) determined that soil fertility in Neotropical secondary forests determines the percentage of aboveground biomass accumulation. Similarly, Tucker et al. (1998), in forests with more than 15 years of succession, compared the recovery of basal area (an indirect measure of biomass) in nutrient-rich soils with that of infertile oxisols and found that in fertile soils, the basal area was much more significant with the passage of successional time, and reached the aboveground biomass of a primary forest more quickly. Thus, the positive influence of soil fertility on the recovery of aboveground biomass in tropical forests (Guariguata & Ostertag, 2001; Moran et al., 2000; Lu et al., 2002) at local and regional scales, as occurs in areas post-mining, is evidenced. Likewise, these results show the influence of different nutrients on the restoration of aboveground biomass, which denotes a limitation due to multiple nutrients (Kaspari et al., 2007; Sullivan et al., 2014), as previously evidenced by Paoli et al. (2005) and has been shown experimentally by Davidson et al., (2004) on secondary successions, and Vitousek & Farrington (1997), and Harrington et al. (2001) in primary successions. These multiple limitations show the need to develop restorations, applying various nutrients in the mines. In addition to soil nutrients, sandy soil texture negatively influenced aboveground biomass. This result is similar to that reported by Johnson et al. (2000), who showed that aboveground biomass accumulation on nutrient-poor sandy soils is lower than on non-sandy soils in secondary forests, which evidences the joint influence of soil fertility, texture, and moisture retention on succession (Chazdon, 2003; Johnson et al., 2000). Possibly, in abandoned mines, the greater macroporosity of the sand facilitates the leaching of nutrients, which favors a lower accumulation of aboveground biomass, as denoted in this study.

The hypothesis of aboveground biomass limitation by nutrients (K, P, and N) in plant succession in abandoned mines. Nutritional limitation of P and N has been hypothesized with succession (Walker & 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 (Davidson et al., 2004). However, to the extent that there is a more significant colonization of N-fixing plants, the biomass of the ecosystem increases and succession advances, its availability increases (Reed et al., 2011). While the levels of phosphorus in the soil tend to be high in the first successional stages, over time, its availability tends to decrease and be limited in the ecosystem (Vitousek et al., 2010) due to losses due to leaching and immobilization in carbon oxides. Fe and Al, especially in tropical clay soils (Reed et al., 2011; Vitousek et al., 1993; Walker & Syers, 1976). This hypothesis was corroborated in the present investigation since, when evaluating changes in aboveground biomass and nutrients (available P and total N) of the soil at different successional ages after mining, it was observed that aboveground biomass and total N increase with recovery time. Also, this result is supported by the recent findings of Quinto et al. (2024a), who observed significant increases in leaf nitrogen content after adding nitrogen to the soil. This demonstrates the limitation of forest productivity components by nitrogen, as trees generally show better responses when their scarcest resource is supplied (Quinto et al., 2024b).

However, the K content presented a similar trend to that of P, with which the hypothesis of nutritional limitation of edaphic P and K on the biomass and productivity of low-altitude tropical rain forests was corroborated. The contents of OM, Mg, Al, Ca, and CICE showed curvilinear trends since they increased in the first stages. Then, they tend to decrease their edaphic concentration in the advanced successional stages. This is undoubtedly because plants with progress in succession tend to store nutrients (K, Mg, and Ca) in their aboveground biomass (Feldpausch et al., 2004) as a strategy to reduce their losses by edaphic leaching and thus a way to make nutrient recycling more efficient (Chazdon, 2003; Guariguata & Ostertag, 2001).

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

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