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Functional analysis of wood traits, soil, and aboveground biomass in Terra firme and Igapó forests

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ABSTRACT

Introduction: Wood traits are intrinsic properties of variables used in aboveground biomass (AGB) models, such as wood density and maximum height, whose behavior may vary with soil nutrient availability. In recent decades, knowledge of functional trait ecology has become a valuable tool in biomass and productivity studies.

Objective: To analyse the stocks and storage rates of AGB in tropical moist gallery forests of the Colombian Orinoquia (Tomo River, Vichada) based on wood traits and edaphic variables.

Methods: We evaluated variables associated with functional and edaphic response on tree vegetation from permanent monitoring plots, three in Terra Firme and two in the floodplain (igapó). For this, we included measurements of wood traits from dominant species, calculated functional diversity indexes, and identified clustering patterns and functional strategies.

Results: It was found that higher functional richness was associated with higher storage rates in both forest types. Quadratic entropy and functional dispersion showed similar trends to functional richness but were not statistically significant. Functional evenness and divergence showed contrasting patterns between forests. In both forests, acquisitive functional types had the highest AGB values. Fiber traits, such as fiber length, were associated with AGB, but parenchyma traits were not. We recognized that phosphorus is a nutrient driver of AGB.

Conclusions: Our results demonstrate similar functional trends in igapó and terra firme forests.

Key words: tree community ecology; wood anatomical traits; forest carbon dynamics.



RESUMEN

Análisis funcional de rasgos xilemáticos, suelos y biomasa aérea en bosques de tierra firme e igapó

Introducción: Los rasgos xilemáticos son propiedades intrínsecas de las variables usadas en los modelos de biomasa aérea (BA), así como densidad de la madera y altura máxima, cuyo comportamiento puede variar ante la disponibilidad de nutrientes en el suelo. En las últimas décadas, el conocimiento de la diversidad funcional se ha convertido en una herramienta valiosa en los estudios de biomasa y productividad.

Objetivo: Analizar la función de acumulación de biomasa aérea en bosques húmedos tropicales de galería de la Orinoquia colombiana, a partir de rasgos xilemáticos y variables edáficas.

Métodos: Se evaluaron variables asociadas a la respuesta funcional y edáfica de la vegetación arbórea de parcelas permanentes de monitoreo, tres de tierra firme y dos de plano inundable (igapó). Para esto, se incorporaron las mediciones de rasgos xilemáticos de especies dominantes, se calcularon índices de diversidad funcional, y se identificaron patrones de agrupación y estrategias funcionales.

Resultados: Se encontró que, a mayor riqueza funcional, mayor tasa de almacenamiento en ambos tipos de bosque. Del mismo modo, la diversidad (entropía cuadrática) y la dispersión, a pesar de no ser significativas, manifestaron la misma tendencia que la riqueza funcional. La equidad y la divergencia mostraron comportamientos contrastantes en los dos bosques. Los tipos funcionales adquisitivos concentraron la mayor proporción de biomasa en los dos bosques. Por otra parte, los rasgos de fibras se asociaron a las existencias y tasas de almacenamiento de BA, mientras que los parenquimáticos no. Se detectó que el fósforo es el nutriente explicativo de la BA.

Conclusión: Nuestros resultados demuestran que funcionalmente los bosques inundables y de tierra firme presentan comportamientos similares.

Palabras clave: ecología de comunidades arbóreas; rasgos xilemáticos; dinámica del carbono en bosques.

INTRODUCTION

Estimation models for aboveground biomass use stem variables, such as diameter at breast height (DBH), total height, and wood specific gravity or wood density (Chave et al., 2014). Despite this, leaf traits are the main ones in most functional ecology studies related to aboveground biomass due to their importance in carbon fixation in photosynthesis and for generating global spectra (Wright et al., 2004). Nevertheless, Conti & Díaz (2013) found that leaf traits do not significantly relate to carbon storage. Additionally, leaf traits' overlap and plasticity make functional grouping delimitation harder. On the other hand, wood traits are measurable morphological characteristics associated with eco-physiological processes and wood functions (Beeckman, 2016). Among these traits, wood density is a complex trait that gathers several anatomical properties, which are known as wood's hard traits, mainly associated with fibers and parenchyma (Fortunel et al., 2014). Likewise, the maximum height is associated with vessels morphology (Preston

et al., 2006), especially area and density per unit area. Wood density has different trends depending on the availability of soil nutrients, showing inversely proportional relationships with fertility (Goldstein et al., 2013). Also, flooding conditions can modify wood density (Mori et al., 2024). For example, in tropical moist Amazonian forests, trees in igapó's soils have significantly higher wood density than in terra firme, despite being found in areas nearby (Phillips et al., 2019). For this reason, recognizing the mechanisms of community assemblages based on hard traits and soil variables is essential to interpreting the response of plant communities to contrasting ecological conditions (Keddy, 1992), where functional diversity can explain shifts in aboveground biomass (Finegan et al., 2015). Likewise, plant functional types (PFT) are useful for understanding the effect of species clustering on productivity (Díaz & Cabido, 1997). The functional balance of species in a community is achieved as different groups integrate specific traits for coexistence, with PFTs then exhibiting conservative (persistence), acquisitive (fast growth), and

intermediate strategies (Lohbeck et al., 2015). These tools are an indispensable resource for evaluating restoration processes and forest resilience, and recently wood traits have been included in such analyses (Rosell et al., 2022).

There are several studies on the functional ecology of natural Colombian forests in tropical dry and Andean forests. Nevertheless, research in tropical moist forests has been focused on the Chocoan and the Amazon forests. The Orinoquia region is generally characterized by a need for more research and a complex dynamic of anthropic pressure (Parrado-Roselli et al., 2016). Therefore, the area requires continuity in analyses to produce management guidelines. In this context, our research analyses the function of aboveground biomass accumulation in the tree vegetation of tropical moist forests of terra firme and igapó in the Colombian Orinoquia using wood traits (diversity and functional types) and soil variables. Then, we aimed: 1) to interpret the relationship patterns between functional diversity and stocks and rates of increase in AGB, 2) to recognize wood traits and soil nutrients that explain biomass stocks, and 3) to evaluate plant functional types as predictors of AGB. We hypothesize that there will be a directly proportional and significant relationship between the functional diversity indices and the stocks and rates of increase of aboveground biomass, as indicated by the diversity hypothesis (Tilman et al., 1997). We also expect that the fiber and parenchyma traits, due to their support and storage functions, positively impact biomass (Chave et al., 2009). Also, soil nutrients will condition productivity, even in poor soils and flooding gradients (Mudrák et al., 2015). Finally, if tree species tend to generate acquisitive strategies in moist life zones (Chain-Guadarrama et al., 2017), we propose that acquisitive functional types are going to concentrate the largest proportion of the biomass.

MATERIAL AND METHODS

Study area: We processed the databases from the permanent monitoring plots

established and monitored by Correa-Gomez and Stevenson (2010), Casas et al. (2017) and González-Abella et al. (2021) in the Tomo Grande Reserve (Santa Rosalía, Vichada, Colombian Orinoquia) (Fig. 1), where oxisols are common (Estrada-Villegas et al., 2022). Five permanent plots of 1 hectare (trees with DBH ≥ 10 cm) were measured according to the RAINFOR methodology. The collected variables were: 1) taxonomic identity, 2) diameter at breast height (DBH), 3) total height (H), and 4) wood density (WD). There are two forest types: terra firme and igapó. Terra firme forests are characterized by kaolinitic clays with lower ionic activity. Igapó forests are floodplain areas with seasonal flooding by rivers influenced by the presence of leaf litter. The area is a tropical moist forest according to Holdridge's life zone classification (1967). Three plots on terra firme and two on igapó were located. There are two measurements over the time for the plots: the first one was in 2009, for terra firme, and in 2010, for igapó, and the second ones were in 2014, for both forests.

Data collection and analysis: We adjusted the plots databases, prioritizing the main stem (Chi et al., 2015) when there were numerous ramets, and excluding the dead trees (Wyckoff & Clark, 2002). Likewise, we replaced the data of the second measurement (DBH and Height), where the value was lower than the first measurement, with the lower value between the measurements (> 0) to nullify the difference (Kohyama et al., 2003). We used the same process with a delta in the DBH higher than 75 mm per year (Condit et al., 1993) and with heights that did not follow the rising trend concerning diameter (Fang & Bailey, 1998) to avoid the negative or very great rates and to reduce the effect of wrong measurements. The previous adjustments are recommended in other studies, although they could be interpreted as a bias in data management. For example, the abrupt reductions or expansions in the diameter are due to loss (Martínez-Pastur et al., 2007) or absorption in the water content (Volland-Voigt et al., 2011). Nevertheless, dendrochronological



Fig. 1. Location of permanent monitoring plots. Acronyms: TF, terra firme; FP, igapó. Numbers are the sequential reference of the plot.

studies in tropical trees have found rates close to 0 but not negative (Inga & del Valle, 2017). Additionally, diametric reductions are related to dry seasons that cause dead of the tree (Scholz et al., 2014) and truncating the growth rates to 75 mm is prudent, considering that the highest mean increment per year in the Amazon Forest reaches 6 cm (Esquivel-Muelbert et al., 2020). Then, we calculated aboveground biomass using the I.3-Tm model of Alvarez et al. (2012) in trees (Equation 1) and the general model of Goodman et al. (2013) in palms (Equation 2). Finally, we identified the species that gathered 70 % of the aboveground biomass in each plot (Slik et al., 2013), recognizing the importance of dominance in ecosystem functioning (Lohbeck et al., 2016). Although recent

research indicates that dominant species gather 50 % of individuals (Milton & Ostling, 2025), the prioritized variable in our study was the AGB. The percentage of species contributing to this proportion of the aboveground biomass was similar across both forests: 15.1 ± 2.1 % in terra firme and 17.1 ± 5.8 % in igapó.

$$AGB = e^{(-2.261 + 0.937(\ln(D^2 \cdot H \cdot \rho)))} \quad \text{Equation 1}$$

$$AGB = e^{(-3.3488 + 2.7483(\ln(D)))} \quad \text{Equation 2}$$

AGB aboveground biomass (kg); D diameter at breast height (cm); H total height (m); ρ wood density (g cm^{-3}).

We collected wood cores from the selected species, 23 in terra firme (65 individuals) and nine in igapó (30 trees) (Díaz-C. et al., 2025),

following Chave's method (2006) and recorded the wood specific gravity (Williamson & Wiemann, 2010). Wood traits were measured according to the parameters of Alfonso et al. (1989) and Scholz et al. (2013). We delineated PFTs through the Ward method and Euclidean metric; they were also related to the type of functional strategy representative for each species group (acquisitive, intermediate, and conservative and palms). The PFTs were associated with the values of AGB stocks and storage rates. We employed an analysis of variance and the Tukey test to evaluate the effect of plant functional types in aboveground biomass stocks and storage rates; normality and variance homogeneity were checked before ANOVA with Shapiro's and Levene's tests ($\alpha > 0.05$) respectively. Also, we calculated the following functional diversity indices to interpret their patterns concerning AGB: 1) community weight mean (CWM) (mono-trait index); 2) functional richness (FRic), 3) functional evenness (FEve), 4) functional divergence (FDiv), 5) functional dispersion (FDis) and 6) Rao's quadratic entropy (multi-trait indices). Linear regression analyses between multi-trait indices and aboveground biomass were included to identify proportional trends.

The soil database used in this study were obtained by the Universidad de Los Andes (González-Abella et al., 2021) and correspond to 25 samples per plot (125 for the five sampling units), collected at a depth of 20 cm in the center of quadrats of 20 x 20 m. Physico-chemical analyses were performed on each sample (% textures, pH, base content, organic carbon, nitrogen, phosphorus, aluminum, and cation exchange capacity) in the soil and water laboratory of the Faculty of Agronomy of the Universidad Nacional de Colombia. We carried out a canonical correspondence analysis to prioritize soil variables and accepted a model that included variables with a variance inflation factor of less than four (Mudrák et al., 2015). We evaluated significant differences between forests for soil variables using a t-test.

For wood traits, we prioritized fiber and ray traits and vessel diameters. The decision

was based on the variables that were explanatory traits of the clustering factors of the PFTs for both forest types (Díaz-C. et al., 2025). We included structural equation models by forest type and plotted in path models relating soil variables and traits with AGB stocks. Also, we made generalized linear models -GLM- (gaussian response) among traits, soils, stocks, and storage rates for terra firme and igapó. The values of the traits for both models were transformed into natural logarithms. The Kolmogorov-Smirnov test was performed to evaluate the normality of the residuals in the GLMs ($\alpha > 0.05$) and not significant deviances were found (Hartig, 2024). We used R to process data (Venables et al., 2024). Specifically, we employed the libraries FD, vegan, agricolae, stats, lavaan, car, semPlot, and DHARMa.

RESULTS

In terra firme and igapó, the higher the functional richness, the higher the aboveground biomass stocks ($R^2 > 0.8$) and storage rates ($\alpha < 0.05$). Similarly, Rao's quadratic entropy and functional dispersion ($R^2 > 0.4$) showed an increase trend proportional to the storage rate and stocks. In contrast, divergence and functional evenness indices were directly proportional to the stocks and biomass increase in the igapó but inversely proportional in terra firme ($\alpha < 0.1$) (Fig. 2). The canonical correspondence analysis between soil variables and aboveground biomass had the highest explained proportion in the first components (Table 1); 59.3 % of the variance was explained by CCA1 and 37.6 % by CA1. The prioritized variables had a canonical coefficient of an absolute value between 0.1 and 0.5 in the components number 1, where pH showed the lowest coefficients and was excluded. Calcium, nitrogen, potassium, and phosphorus were prioritized in both forests. On terra firme, only soil nutrients were significant on AGB ($\alpha < 0.1$) (Fig. 3). On the other hand, the fiber length ($\alpha < 0.05$), phosphorus ($\alpha < 0.01$), and potassium ($\alpha < 0.1$) in both forests explained the stocks and storage rates (Table 2). The parenchyma traits

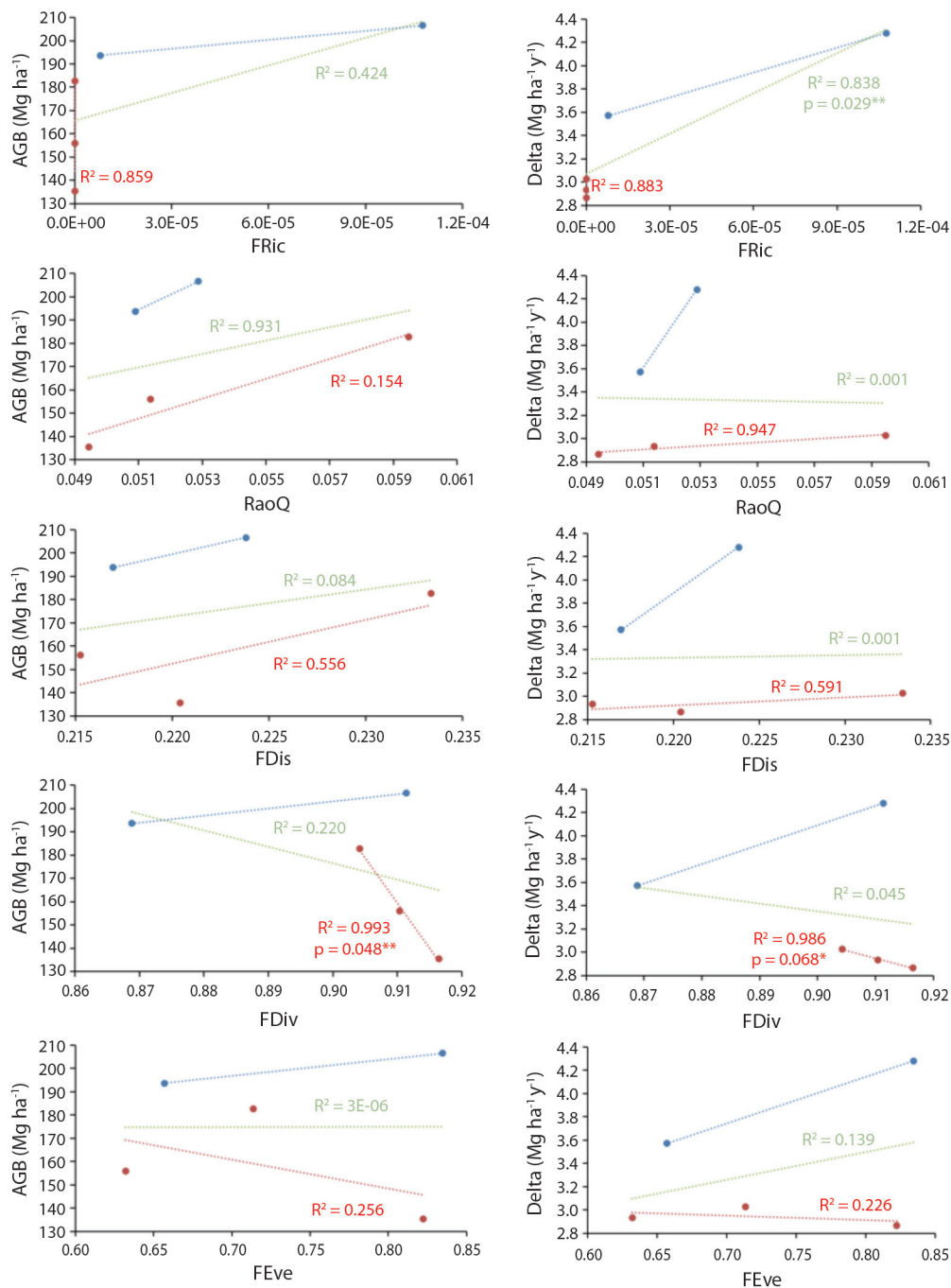


Fig. 2. Functional diversity indices vs. stocks (AGB) and storage rates (Delta) of aboveground biomass in tropical moist forests of the Colombian Orinoquia. FRic: functional richness; RaoQ: Rao's quadratic entropy; Fdis: functional dispersion; Feve: functional evenness; Fdiv: functional divergence; Mg: megagrams; ha: hectare; y: year. Points and lines represent values and trends for the sampling units: red=terra firme; blue = igapó; green = set of five plots. Significant trends: * $\alpha < 0.1$; ** $\alpha < 0.05$.

Table 1
Canonical correspondence analysis of soil variables in igapó and terra firme.

Soil Variables	Limited Components		Unlimited Components	
	CCA1	CCA2	CA1	CA2
pH	-0.051	0.038	0.010	0.011
Organic Carbon (OC)	0.099	0.001	-0.243	-0.044
Nitrogen (N)	0.051	0.041	-0.327	0.066
Calcium (Ca)	0.129	-0.216	0.091	0.324
Potassium (K)	-0.129	0.084	-0.390	0.012
Magnesium (Mg)	0.094	-0.314	-0.141	-0.067
Sodium (Na)	0.101	0.187	0.224	-0.228
Aluminum (Al)	-0.071	0.059	-0.176	0.077
Phosphorus (P)	-0.516	0.335	-0.213	0.059
Cation Exchange Capacity (CEC)	-0.035	-0.069	-0.240	-0.025
Clay Proportion (Cla)	-0.050	-0.012	-0.244	-0.016
Silt Proportion (Sil)	-0.399	-0.035	-0.088	0.016
Sand Proportion (San)	0.474	0.016	0.411	-0.004
Explained Proportion	0.593	0.027	0.376	0.004
Variance Inflation Factor	3.567			

CCA: Limited Components; CA: Unlimited Components. Numbers correspond to the dimensions generated in the analysis.

Table 2
Generalized linear models for igapó and terra firme forests.

	AGB~traits				Delta~traits			
	Estimate	Std. Error	t-value	p-value	Estimate	Std. Error	t-value	p-value
(Intercept)	38.567	12.635	3.052	0.004***	0.843	0.313	2.692	0.011**
FL	-0.044	0.019	-2.327	0.026**	-0.001	0.000	-2.175	0.036**
RR	2.113	4.537	0.466	0.644	0.014	0.112	0.121	0.904
RW	-0.045	0.098	-0.458	0.650	0.001	0.002	0.414	0.682
VD	0.041	0.062	0.663	0.512	0.001	0.002	0.689	0.495
Dispersion parameter = 126.168					Dispersion parameter = 0.077			
Null Deviation = 5 262.9					Null Deviation = 3.1			
AIC = 313.7					AIC = 17.8			
	AGB~soil				Delta~soil			
	Estimate	Std. Error	t-value	p-value	Estimate	Std. Error	t-value	p-value
(Intercept)	7.082	3.407	2.079	0.045**	0.145	0.085	1.717	0.095*
P	1.253	0.371	3.381	0.002***	0.033	0.009	3.582	0.001***
K	80.167	31.837	2.518	0.016**	1.530	0.791	1.934	0.061*
N	-51.243	28.326	-1.809	0.079*	-1.020	0.704	-1.450	0.156
Ca	-2.438	1.945	-1.254	0.218	-0.059	0.048	-1.222	0.230
Dispersion parameter = 91.003					Dispersion parameter = 0.056			
Null Deviation = 5 262.9					Null Deviation = 3.1			
AIC = 300.6					AIC = 5.0			

Significant values: * $\alpha < 0.1$; ** $\alpha < 0.05$; *** $\alpha < 0.01$. AGB: aboveground biomass stocks; Delta: storage rate; P: phosphorus; K: potassium; Ca: calcium; N: nitrogen; RW: ray width; FL: fiber length; RR: runkel ratio; VD: vessel diameter; AIC: Akaike information criterion.

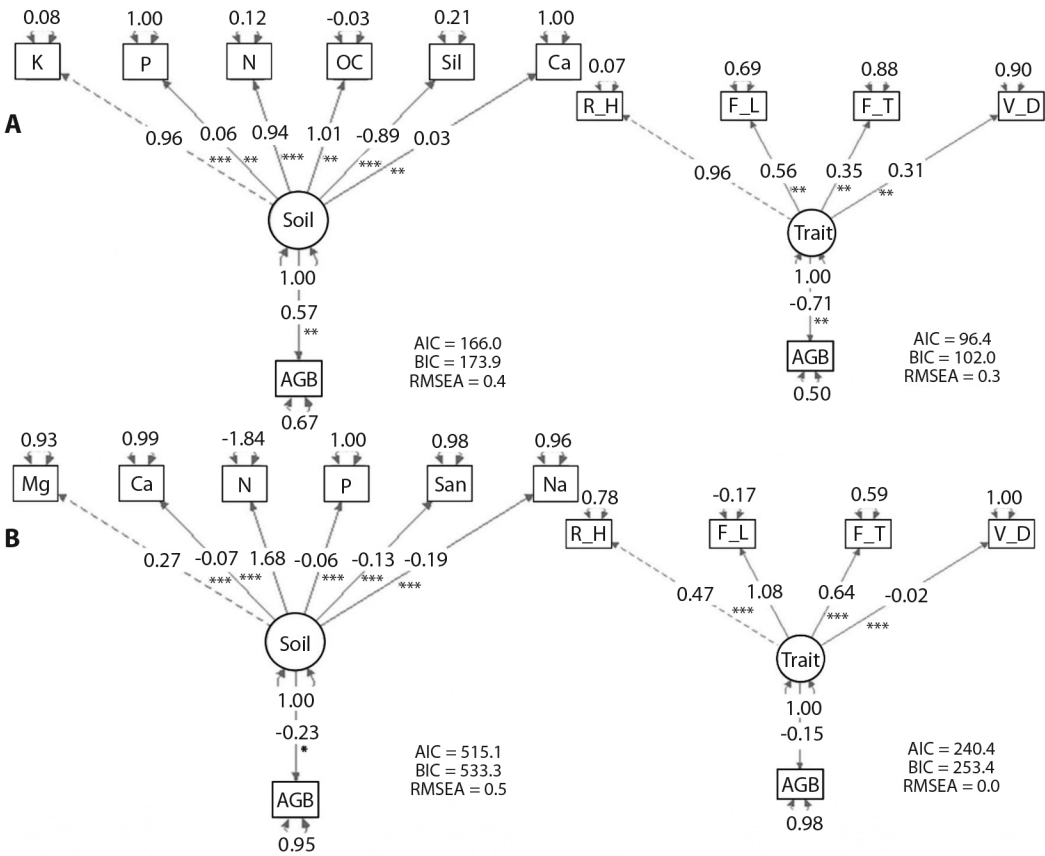


Fig. 3. Pathway models obtained from structural equations using wood traits and soil variables to explain AGB stocks. **A.** Igapó, **B.** Terra firme. Diagrams' numbers correspond to beta correlation coefficients. Significant values: *, $\alpha < 0.1$; **, $\alpha < 0.05$; ***, $\alpha < 0.01$. AGB: aboveground biomass stocks; P: phosphorus; K: potassium; Ca: calcium; N: nitrogen; Na: sodium; Mg: magnesium; OC: organic carbon; San: sand proportion; Sil: silt proportion; R_H: ray height; F_L: fiber length; F_T: fiber wall thickness; V_D: vessel diameter; AIC: Akaike information criterion; BIC: Bayesian information criterion; RMSEA :root mean square error of approximation.

of terra firme forests had the highest values in the coefficients of variation (Table 3). There were significant differences in several soil variables for both forests, except for calcium, magnesium, sodium, and organic carbon (Table 4). The nitrogen-to-phosphorus ratio and the sand proportion were higher in terra firme than in igapó ($\alpha < 0.01$). Finally, the intermediate acquisitive plant functional type had a higher average aboveground biomass stock and storage rates than the conservative ones (Fig. 4). There are significant differences only in igapó ($\alpha < 0.05$). On terra firme, palm PFT's (*Attalea*

maripa (Aubl.) Mart., *Oenocarpus* spp.) storage rate did not shift, and it has a similar trend to the acquisitive PFT stocks despite not being statistically significant.

DISCUSSION

Aboveground biomass and functional diversity: We found that the higher the stocks and aboveground biomass storage rates, the higher the functional diversity indices (richness, quadratic entropy, and dispersion). These results are similar to studies of neotropical

Table 3

Community weighted mean (CWM) of wood traits of tree vegetation in igapó (FP) and terra firme (TF) forests.

Trait	FP $\bar{X}$	FP SD	FP CV (%)	TF $\bar{X}$	TF SD	TF CV (%)
Fiber Length (μm)	615.83	25.84	4.2	1 198.70	207.12	17.3
Fiber Wall Thickness (μm)	2.74	0.67	24.5	4.80	1.26	26.3
Runkel Ratio	0.80	0.15	19.4	1.00	0.32	32.3
Fiber Area ($\mu\text{m}^2 \text{mm}^{-2}$)	825 109.8	33 344.89	4.0	644 064.4	213 367.17	33.1
Ray Height (μm)	225.91	17.81	7.9	355.86	97.69	27.5
Ray Width (μm)	19.06	8.67	45.5	31.07	5.72	18.4
Ray Density (# mm^{-1})	20.40	5.91	29.0	12.01	2.32	19.3
Vessels Density (# mm^{-2})	21.95	7.26	33.1	20.34	7.43	36.5
Vessel Diameter (μm)	77.38	7.82	10.1	98.22	11.18	11.4
Axial Parenchyma Area ($\mu\text{m}^2 \text{mm}^{-2}$)	92 432.64	16 883.74	18.3	321 006.07	237 934.56	74.1
Wood Density (g cm^{-3})	0.62	0.01	1.0	0.52	0.08	15.7

 $\bar{X}$: mean; SD: standard deviation; CV: coefficient of variation.

Table 4

t-test for soil variables in tropical moist forest of terra firme (TF) and igapó (FP) from Colombian Orinoquia.

Variable	FP		TF	p-value
N (mg kg^{-1})	2 639.29 $\pm$ 1 712.21	>	1 722.22 $\pm$ 251.17	0.084*
P (mg kg^{-1})	7.89 $\pm$ 0.40	>	1.95 $\pm$ 0.80	0.003***
N:P Ratio	430.22 $\pm$ 248.38	<	1 132.49 $\pm$ 215.88	0.000***
K ($\text{cmol}_c \text{kg}^{-1}$)	0.22 $\pm$ 0.13	>	0.11 $\pm$ 0.02	0.012**
Al ($\text{cmol}_c \text{kg}^{-1}$)	4.05 $\pm$ 1.16	>	2.90 $\pm$ 0.21	0.006***
CEC ($\text{cmol}_c \text{kg}^{-1}$)	15.20 $\pm$ 5.83	>	10.72 $\pm$ 1.89	0.012**
Clay (%)	34.10 $\pm$ 13.13	>	22.96 $\pm$ 2.49	0.004***
Silt (%)	50.98 $\pm$ 9.35	>	23.31 $\pm$ 9.84	0.000***
Sand (%)	14.93 $\pm$ 3.78	<	53.74 $\pm$ 12.33	0.000***

Significant differences: * $\alpha < 0.1$; ** $\alpha < 0.05$; *** $\alpha < 0.01$. $\text{cmol}_c \text{kg}^{-1}$: centimoles of charge per soil kilogram; mg kg^{-1} : milligrams per kilogram.

forests that have used specific leaf area and leaf nitrogen to calculate monotrait indices (Finegan et al., 2015). Although, our models using multitrait indices showed significant relationships with forest productivity and lower statistical uncertainty when compared to coefficients obtained by leaf traits (Mensah et al., 2016). This could be because wood traits are associated with the stem, and their multitrait diversity indices have a higher effect on volumetric stocks in tropical forests (Bongers et al., 2021). However, this hypothesis was partially confirmed, as we found that the higher the stocks and storage of AGB, the lower the functional evenness and divergence in terra

firme forests, where floristic richness is higher (Aldana et al., 2017). This trend indicates a low temporal stability in productivity (Guo et al., 2021) and suggests that terra firme forests are still in a secondary successional state where they may show variations between productivity and functional diversity, as Lohbeck et al. (2012) found in tropical moist forests of Central America. Likewise, we observed that terra firme forests interact with the savannah, and their composition is characterized by acquisitive PFTs and palms (*Jacaranda copaia* (Aubl.) D. Don, *Pourouma minor* Benoist, *A. maripa*, and *Oenocarpus* spp.), which are common species of secondary forests.

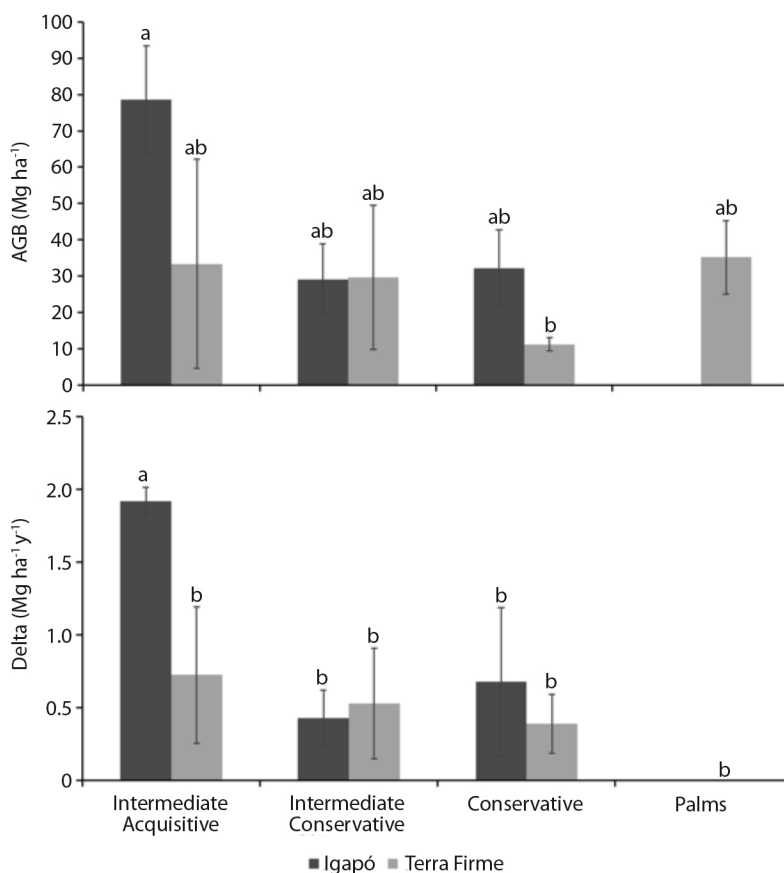


Fig. 4. Diagram of stocks (AGB) and aboveground biomass storage rate (Delta) in plant functional types. The error bars correspond to the standard deviation. Different letters indicate significant differences ($\alpha < 0.05$).

Aboveground biomass, soil variables, and wood traits: Phosphorus was related to aboveground biomass and productivity. Soil phosphorus acts as a biomass driver, according to the pattern identified by Condit et al. (2013) in tropical moist forests, where they emphasized that the limitation of this macronutrient reduces the stocks and storage rates of AGB. This is attributed to the role of phosphorus in essential molecules involved in photosynthetic processes (ADP, ATP, GTP, NADPH) and in the phosphodiester bridges that link nucleotides during cell division (White & Hammond, 2008). Additionally, acquisitive PFTs were related to soil nutrients and higher values of AGB, with significant differences observed in igapó. Recent studies

indicate that trees in soils with high phosphorus and potassium contents (Angélico et al., 2021) possess solitary vessels and with larger diameters, which are traits focused on hydraulic efficiency. Similarly, research on *Eucalyptus* demonstrates that the higher the phosphorus availability, the higher the aboveground biomass and the lower the wood density (Thomas et al., 2006). This aligns with our findings in acquisitive PFTs, which show lower wood density and a functional strategy aimed at hydraulic efficiency (Hietz et al., 2017). Nevertheless, it contradicts the assertion that igapó forests have higher AGB stock than terra firme forests because igapó species are characterized by high wood density (González-Abella et al., 2021). In

addition, magnesium showed no influence in our models for igapó, despite being a variable highlighted by Castaño et al. (2024) in lowland forest soils.

On the other hand, we found no significant differences in functional types and AGB within the terra firme forests. Some studies suggest that lower rates of carbon sequestration are linked to a high nitrogen-to-phosphorus (N : P) ratio in the soil (Buzzard et al., 2019). This observation aligns with our findings, which showed a higher N : P ratio in terra firme than in igapó. While our results for the ratio are higher than other records for terra firme forests in the Brazilian Amazon (Lange et al., 2024), they are consistent with soil values reported for secondary forests in Colombia (Velasquez et al., 2005) that may exhibit a similar ratio. Furthermore, the high values and variance of parenchyma traits on terra firme, where palms are an independent functional type (Díaz-C. et al., 2025), are associated with a height-focused strategy, attributed to a predominant parenchyma investment (Lourenço, Bittencourt et al., 2022). This may explain why ray height emerged as a significant trait in the model developed for terra firme. Conversely, vessel and fiber traits were significant in igapó, reflecting their roles in the hydraulic and support functions required by species adapted to flooding (Lourenço, Enquist et al., 2022).

Aboveground biomass and plant functional types: The intermediate acquisitive functional types concentrated the highest proportion of AGB in igapó. Terra firme had the same trend, but there were no significant differences. We confirmed our hypothesis that species with higher growth rates contribute to stocks and storage rates. This pattern has been identified in floodplain forests with soil nutrient limitations, where lower wood density and higher values of traits associated with hydraulic conductivity are prevalent (Lovelock et al., 2006). Likewise, research in tropical wet forests shows that the functional types composed of fast-growing species had the highest proportion

of basal area (Chazdon et al., 2010), which can be considered a common trend in rainforests. Conversely, our results differ from trends observed in tropical dry forests (Prado-Junior et al., 2016), where conservative PFTs, clustered based on leaf traits, were better predictors of biomass productivity. However, the intermediate acquisitive functional strategy makes species vulnerable to cavitation and compromises long-term survival during drought (González-M. et al., 2020), what should be considered in next studies. Finally, the relationship between fiber traits and stocks and storage rates, particularly fiber length, highlights the essential role of the species with an intermediate acquisitive strategy in the ecosystem function of the analysed forests. Nevertheless, while wood density is one of the main proposed indicators of functional recovery (Poorter et al., 2021), this characteristic variable of conservative PFTs does not necessarily imply higher stocks and productivity in terra firme and igapó forests. For this reason, we recommend that future research consider other wood traits, such as fiber traits.

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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