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EDITED BY
Ezequiel Zamora-Ledezma,
Technical University of Manabi, Ecuador

REVIEWED BY
Alonso Barrios,
Tolima University, Colombia
Nathália Silva,
Probiodiversa Brasil, Brazil

*CORRESPONDENCE
Jéssica Merecí-Guamán
✉ jessica.mereci@biologie.uni-goettingen.de
Jürgen Homeier
✉ homeier@uni-marburg.de

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Tree growth in a neotropical dry forest and its dependence on functional traits and soil properties: key roles for tree size and wood density

Jéssica Merecí-Guamán[1]*, Karina Gonzalez-Valdiviezo[2], Frauke Möller[1], Keyla Cartuche[3], Cesar Feijoo[3], Darwin Pucha-Cofrep[4], Selene Báez[2], Christoph Leuschner[1,5] and Jürgen Homeier[5,6]*

[1]Plant Ecology and Ecosystems Research, University of Göttingen, Göttingen, Germany, [2]Departamento de Biología, Escuela Politécnica Nacional del Ecuador, Quito, Ecuador, [3]Maestría en Biodiversidad y Cambio Climático, Universidad Nacional de Loja, Loja, Ecuador, [4]Laboratorio de Dendrocronología, Carrera de Ingeniería Forestal, Universidad Nacional de Loja, Loja, Ecuador, [5]Faculty of Resource Management, HAWK University of Applied Sciences and Arts, Göttingen, Germany, [6]Philipps-Universität Marburg, Marburg, Germany

Tropical dry forests are among the most threatened ecosystems worldwide, yet the mechanisms controlling tree growth at local scales remain poorly understood. The aim of this study was to combine available information on environmental conditions and tree functional traits to better understand their relevance for tree growth in seasonal tropical dry forests. We used data from forest dynamics of six permanent one-ha plots at two elevations (lower elevation deciduous forest: ~600 m a.s.l.; upper elevation semi-deciduous forest: ~1,200 m a.s.l.) in southern Ecuador to calculate relative growth rate (RGR) based on stem diameter for all living stems over a two-year census interval. We combined functional traits of leaves (i.e., foliar nitrogen and phosphorus concentrations, leaf thickness, leaf toughness, specific leaf area) and stems (i.e., bark thickness, wood specific gravity, vessel density, vessel diameter, hydraulic conductivity) with soil chemistry data (phosphorus availability, carbon: nitrogen ratio and others) to build predictive models of tree growth. At both elevations, RGR declined strongly with increasing tree size, indicating a consistent size-dependent constraint on RGR. Functional traits emerged as significant predictors of RGR, with growth increasing in association with acquisitive traits and decreasing with conservative traits. In particular, high wood specific gravity (WSG) was negatively associated with RGR, consistent with species adopting conservative strategies characterized by greater investment in structural integrity and hydraulic safety at the expense of rapid growth. Soil properties showed only weak and inconsistent associations with RGR. Model comparisons confirmed that tree size and functional traits, notably WSG, explained substantially more variation in RGR than soil variables, while models including additional predictors did not improve model performance. Our findings highlight the dominant role of species functional strategies and tree size in explaining variation in tree growth in tropical dry forests.

KEYWORDS
Ecuador, relative growth rate (RGR), seasonal tropical dry forest, tree functional traits, Tumbesian dry forest

1 Introduction

Tropical dry forests (TDFs) harbor exceptionally high levels of biodiversity and endemism (DRYFLOR et al., 2016; Linares-Palomino et al., 2010; Stan and Sanchez-Azofeifa, 2019); however, they are among the most threatened tropical ecosystems worldwide (Pando et al., 2021; Ribeiro et al., 2022). Globally, they cover an estimated ~1.05 million km^2 (Miles et al., 2006; Siyum, 2020), and dry forests in America represent 54% of the global area (Portillo-Quintero and Sánchez-Azofeifa, 2010). The largest and best-preserved forests are found in Mexico, Brazil, and Bolivia. In contrast, Guatemala, Ecuador, Costa Rica, and Peru harbor much smaller dry forest extents and face alarming levels of degradation (Portillo-Quintero and Sánchez-Azofeifa, 2010; Camilo Fagua and Jantz, 2024). Ecuador has lost 30% of its dry forest area from 1990 to 2018 due to conversion to agricultural uses, resulting in reduced connectivity and disruption in ecosystem functioning (Rivas et al., 2024). Additionally, these forests have received considerably less attention in scientific research and conservation efforts than tropical humid forests, possibly due to the lack of intact areas suitable for conservation and accessible for research (Pennington et al., 2018; Stan and Sanchez-Azofeifa, 2019; Siyum, 2020; Schröder et al., 2021). This situation highlights the need to fill a critical gap in our understanding of the ecological processes that shape TDF structure and function, and to guide effective conservation and restoration efforts.

TDFs occur across gradients of climate, elevation, and soil types (Murphy and Lugo, 1986; DRYFLOR et al., 2016; Siyum, 2020). They are exposed to high temperatures (Sánchez-Azofeifa et al., 2005), 4–9 months of dry season, and annual precipitation may range from 600 to 1,800 mm (Murphy and Lugo, 1986). Soil fertility could influence tree performance and species coexistence (Caleño-Ruiz et al., 2023), but in TDFs soil conditions are usually outweighed in importance to tree growth by water limitation (Murphy and Lugo, 1986; Brienen et al., 2010; Gei and Powers, 2013). The strong environmental gradients generate shifts in functional strategies in TDFs, thereby providing a natural laboratory for understanding how functional traits mediate growth responses to environmental variability and how vegetation may change in response to climate change (Murphy and Lugo, 1986; Falcão et al., 2015; Rosell, 2016).

Environmental and topographic gradients shape the species composition of TDFs, with deciduous species dominating the driest environments mainly at lower elevations (Pennington et al., 2000; Buzzard et al., 2016; Werner and Homeier, 2024), whereas semi-deciduous and evergreen species increase in abundance at higher elevations with higher precipitation inputs (Huechacona-Ruiz et al., 2020; Khadanga et al., 2023; Camilo Fagua and Jantz, 2024). TDFs exhibit high functional diversity, reflecting wide ranges in trait variation, high variances, and large trait hypervolumes (Quintana et al., 2017; González-M et al., 2021; Fagundes et al., 2022), making the interactions between traits and climatic variability particularly relevant for understanding species responses at the local scale. Traits are expressed along a conservative–acquisitive spectrum: fast-growing, acquisitive species exhibit traits such as high specific leaf area, leaf nitrogen content, and large vessel diameter, while slow-growing, conservative species exhibit dense wood, and thick and tough leaves (Díaz et al., 2016; Fagundes et al., 2022).

This study investigates environmental factors influencing tree diameter growth, measured as relative growth rate (RGR), in two different forest formations in Ecuadorian Tumbesian dry forest. RGR was calculated from repeated inventories of six permanent forest plots of 1 ha. In parallel, important leaf and stem traits (Table 1) of the tree species growing on these plots were recorded and the chemical properties of the upper mineral soil were characterized. We focus on the combined influence of the species' functional traits and soil properties on RGR. Specifically, we address two questions: (1) which functional traits and soil properties most strongly influence tree RGR, and (2) what is the relative importance of functional traits and soil in explaining interspecific variation in RGR. We hypothesize that RGR is higher in species with resource-acquisitive traits (e.g., high specific leaf area, leaf nitrogen concentration and hydraulic conductivity) and growing on more fertile soils as compared to species with conservative traits. Finally, we predict that models combining traits and soil properties provide a mechanistic understanding of growth dynamics in TDFs.

2 Materials and methods

2.1 Study site

The research was conducted in the Reserva Natural Laipuna, a protected area situated on the southwestern slope of the Ecuadorian Andes (Figure 1). The reserve covers 2,562 ha of Tumbesian dry forest and encompasses one of the few well-preserved elevational gradients (590 to 1,480 m a.s.l.) of this forest type (Wurz et al., 2023). Tumbesian dry forests span a narrow strip of approximately 50,000 km^2 located between the Pacific Ocean and the Andes, extending from the southwestern tip of Ecuador to northwestern Peru (Best and Kessler, 1995). These forests are found at elevations ranging from sea level up to approximately 1,500 m a.s.l. and they exhibit high levels of plant endemism (Aguirre Mendoza et al., 2006; Best and Kessler, 1995).

In the study area, the rainy season extends from January to May, followed by a pronounced dry season from June to December (Pucha-Cofrep et al., 2015; Butz et al., 2018). At 600 m a.s.l., annual mean temperature is 23.7 °C and annual rainfall is approximately 540 mm, with high year-to-year variability (Pucha-Cofrep et al., 2015; Spannl et al., 2016). At higher elevations there is additional moisture input mainly from fog driven by westerly winds (Butz et

TABLE 1 Leaf and stem functional traits measured in all tree species.

Trait	Acronym	Unit
Specific leaf area	SLA	$cm^2\ g^{-1}$
Leaf toughness	tough	$kN\ m^{-1}$
Leaf thickness	thick	mm
Leaf nitrogen concentration	N	$mg\ g^{-1}$
Leaf phosphorus concentration	P	$mg\ g^{-1}$
Wood specific gravity	WSG	$g\ cm^{-3}$
Bark thickness	bark	mm
Vessel diameter	Vdia	µm
Vessel density	Vdens	mm^{-2}
Sapwood-specific hydraulic conductivity	K_s	$kg\ m^{-1}\ MPa^{-1}\ s^{-1}$

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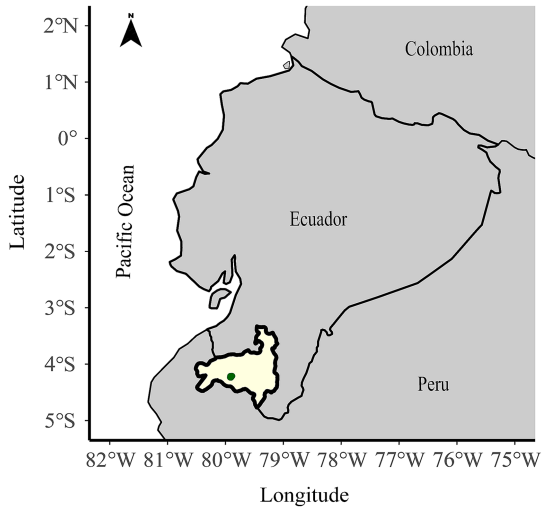

FIGURE 1
Location of Loja province (yellow) and the study area (green dot) in Ecuador.

al., 2018), and at 1,450 m a.s.l. the mean annual temperature is 16.1 °C, and rainfall is approximately 1,260 mm (Peters and Richter, 2011). As a result of the increasing humidity and hence more favorable growth conditions, there is an elevational increase of both the proportion of evergreen plant species and overall plant diversity (Aguirre Mendoza et al., 2006; Werner and Homeier, 2024). According to the Ecuadorian vegetation map (Ministerio del Ambiente del Ecuador, 2013), there are two forest formations present in the study area between 400 and 1,600 m a.s.l., a deciduous premontane forest at lower elevations and a semi-deciduous premontane forest at higher elevations. However, there are no distinct boundaries; rather, there is a continuous transition between these two formations within the Tumbesian dry forests (Aguirre Mendoza et al., 2006; Werner and Homeier, 2024). Canopy height averages 11–16 m regardless of elevation, with tallest tree individuals reaching up to 20 m. Aboveground tree biomass shows no significant trend with elevation (Werner and Homeier, 2024; Gonzalez-Valdiviezo et al., 2025).

Dominant soils of the study area are loamy cambisols characterized by high pH values, moderate to high cation exchange capacity and high base saturation. Low C/N ratios suggest a high nitrogen availability and overall favorable soil nutrient availability for the vegetation (Velescu et al., 2024).

2.2 Tree inventory and tree diameter growth

We established six one-ha plots in 2021, three at an elevation of about 600 m a.s.l. in the deciduous premontane forest formation and three at a higher elevation of about 1,200 m a.s.l. in the semi-deciduous premontane forest formation. All trees with a diameter at breast height (DBH) of ≥ 10 cm were tagged, inventoried, identified, and their DBHs were measured between November 2021 and January 2022 and again after two years in February/March 2024. Herbarium specimens have been collected and deposited at the Museo Ecuatoriano de Ciencias Naturales del Instituto Nacional de Biodiversidad, Quito, Ecuador (QCNE). In total, we recorded 3,148 stems from 53 different tree species.

Tree DBHs were used to calculate diameter increment and relative growth rate (RGR) for each stem:

$$\mathrm{RGR} = \frac{\log \mathrm{DBH}_i - \log \mathrm{DBH}_0}{t_i - t_0}$$

With DBH_i representing the diameter (in cm) at the second measurement and DBH_0 that at the first census. The time interval $t_i - t_0$ is given in years, and RGR is expressed in yr^{-1}. We used RGR because it represents the proportional change in diameter per unit of time, allowing to compare trees that differ in initial size.

2.3 Soil properties

We took 25 samples of the upper 10 cm of mineral soil per study plot in May 2022, each sample representing one of the 25 subplots (Homeier and Möller, 2026). The air-dried samples were analyzed at the Department of Plant Ecology, Göttingen University, Germany, applying a standard protocol for the chemical analysis of forest soils (for analytical details see Unger et al., 2010). Soil pH (H_2O) was measured in soil suspended in deionized water. The total concentrations of C and N were determined with a C/N elemental analyzer through gas chromatography (Vario EL III, elementar, Hanau, Germany) in the ground and dried soil. P availability was estimated as resin-exchangeable P, i.e., the exchange of phosphate ions by anion exchange resin, which may give a minimum estimate of plant-available P (P_{av}). The plant availability of Ca, K and Mg and also of potentially toxic Al was quantified by salt exchange (0.2 N $BaCl_2$ solution). The concentrations of exchangeable potassium (K), magnesium (Mg), calcium (Ca) and sodium (Na) were analyzed using ICP-OES (Thermo Scientific iCAP 7000, Thermo Fisher Scientific, Germany). Effective Cation Exchange Capacity (ECEC) was calculated as the sum of the exchangeable cations (K^+, Mg^{2+}, Ca^{2+}, and Na^+) expressed per gram of soil.

2.4 Leaf and stem functional traits

For functional trait analyses, one to nine individuals per tree species were randomly selected within the study plots, depending on species abundance. Sampling of all 53 tree species took place in the months March and April of the years 2022 and 2023. We followed the leaf sampling protocol of Homeier et al. (2021) and collected 2–3 branches per tree with all attached leaves from the top of the crown, which was as much sun exposed as possible, and took them in sealed polyethylene bags (filled with water-soaked tissues) to the Laipuna research station, where further processing took place. Twenty fully developed intact leaves were pooled to determine leaf thickness (acronym 'thick') and leaf toughness ('tough'), specific leaf area (SLA), and leaf nitrogen and phosphorus concentrations (N, P) for each tree.

Furthermore, bark thickness was measured in each stem at a stem height of 1.0 m with a bark gauge (Haglöf, Langsele, Sweden). We quantified wood specific gravity (WSG) for each studied tree by collecting a wood core (~5 cm length, 5.15 mm diameter) with an increment corer (Haglöf, Langsele, Sweden) at the same stem height. WSG was then calculated by dividing core dry mass by core fresh volume. A second wood core of the same dimension was stored in ethanol

(50%) and used for anatomical analyses at the Department of Plant Ecology, Göttingen University, Germany and at Dendrolab, Universidad Nacional de Loja, Ecuador.

From these samples, thin transverse cross-sections (20–100 μm) were prepared using a sliding microtome (G.S.L.1, WSL, Birmensdorf, Switzerland). The cross-sections were stained with safranin and astra-blue and mounted with Euparal (Carl Roth, Karlsruhe, Germany) on microscope slides. After drying for 2 weeks at 50 °C, samples were digitalized using a stereomicroscope (Zeiss SteREOV20, Carl Zeiss MicroImaging GmbH, Göttingen, Germany), and then edited with Adobe Photoshop CS6 (version 13.0.1, Adobe Systems Incorporated, USA) and the software ImageJ[1] (version 1.47) to estimate average vessel diameter and vessel density. For all samples, the outer sapwood was selected for the analyses, and the number of vessels analyzed varied between 60 and 6,000 depending on the characteristics of the tree species. Sapwood specific hydraulic conductivity K_s was calculated using the Hagen-Poiseuille equation (Tyree and Zimmermann, 2002; Poorter et al., 2010; Kotowska et al., 2015).

$$K_s = \left(\pi \times \rho \times \sum_{i=1}^{n} d_i^4 \right) / \left(128\eta \times A_{Xylem} \right)$$

where ρ is the density of water, η the viscosity of water, d_i the vessel diameter of each single vessel i, and n the number of vessels per unit cross-sectional xylem area (A_{Xylem}).

2.5 Data analyses

Each tree was assigned to the corresponding soil values of the subplot in which it occurred; therefore, all individuals within the same subplot shared identical soil conditions. Consequently, soil variable effects should be interpreted at the subplot scale rather than at the level of individual trees, given the spatial resolution of the soil measurements.

For both forest formations, we calculated the trait means across all occurring tree species and the community weighted means (CWMs) through weighting the species by their relative abundance.

To evaluate whether multivariate axes of functional traits and soil properties influenced RGR, we conducted separate PCAs for each dataset using the *prcomp()* function in R. Functional traits included leaf thickness, specific leaf area, leaf toughness, leaf nitrogen and phosphorus concentrations, wood density, vessel diameter and density, and hydraulic conductivity. Soil variables included N, P_{av}, K, Ca, Mg, pH, and base saturation. We considered the first two principal components as factors to be implemented in the subsequent growth models. From the species-specific coordinates in the trait PCA we additionally calculated the community weighted traits means (CWMs) of each forest formation weighting the tree species by their relative abundance.

We used two different approaches (correlation and linear mixed-effects models) to identify potential predictors of RGR. First, Pearson correlations were used to explore individual-tree patterns between RGR, functional traits and soil properties at both forest elevations. This approach provided a first assessment of the direction and strength of relationships (r^2). For this analysis, we used individual-level RGR data linked to the corresponding trait values available for the sampled individual trees. Sample size varied among traits due to differences in data availability across the species included in the study. Species-level trait means, standard deviations, and sampling effort per tree species are provided in Supplementary Table S1. Correlations were conducted using the original, unstandardized values and separately for each forest elevation with the *cor.test()* function in R. Pearson correlation coefficients (r), coefficient of determination (r^2) and associated p-values were obtained, and only significant relationships ($p < 0.05$) were retained for visualization. Second, linear mixed-effects models (LMMs) were used to account for the hierarchical structure of the data and to test the effects of traits on individual tree growth. This analysis was based on growth data of 2,883 stems and species trait means from 49 tree species. Four species were excluded because they occurred only in the first or the second plot inventory and no growth data could be calculated. For species occurring in both forest formations, trait means for the respective elevations were used to account for potential trait variation with elevation.

Although RGR was measured at the individual tree level, functional traits were represented by species mean values, reflecting the average ecological strategy of each species and providing a framework to assess how species-level traits influence individual growth performance. This approach does not account for intraspecific trait variation, which may additionally contribute to differences in growth among conspecific individuals.

Prior to LMM analysis, RGR was square-root-transformed after a minimum shift to account for negative values. For LMMs, all explanatory variables were standardized (z-scores: centered to zero mean and scaled to unit variance). The selection of variables for the growth models began with key functional traits identified in the literature as important drivers of tree growth in dry forests, such as SLA, WSG, and leaf thickness. We then examined pairwise correlations among functional traits and soil properties using a correlation matrix to assess multicollinearity, retaining variables with weak correlations ($|r| < 0.69$) suitable for multivariate modeling. In addition, we retained the major axes of variation from the PCA of trait and soil data. Variables with strong loadings on these axes were considered key descriptors of ecological strategies and were included in the LMMs. We ran six LMMs using the *lme4* package in R. Multiple candidate models were compared, including combinations of functional traits and soil properties (individual variables and PCA axes), elevation, and tree size (DBH) as fixed effects. Random effects accounted for species-elevation combinations and plot identity. Multicollinearity was evaluated using variance inflation factors (VIF), and only variables with VIF < 3 were retained in the final set of predictors. Model selection was based on Akaike Information Criterion (AIC), prioritizing models with the lowest AIC values, higher explained variance (marginal and conditional R^2), and greater parsimony. Standardized regression coefficients with 95% confidence intervals were reported for the final models. Model residuals were inspected to verify that model assumptions were met.

To assess the robustness of the main LMM analyses, we repeated the same analyses at individual tree level using only those 195 tree individuals with complete data on RGR and the ten functional traits. These complementary analyses allowed us to evaluate whether species-level patterns were consistent across levels of analysis. The results are provided in Supplementary material. All analyses were conducted in R version 4.4.3 (R Core Team, 2024).

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3 Results

3.1 Forest structure and tree diameter growth

We recorded 3,148 stems of 53 species at the two elevations in our six-ha study area. The lower-elevation forest comprised 24 species with 1,136 stems, whereas the upper-elevation forest comprised 41 species and 2,012 stems. A total of 12 species were shared between the two forest formations. Tree-size distributions differed between elevations, with a larger proportion of smaller stem diameters (< 20 cm) at the upper site (Supplementary Figure S1). Average diameter growth was slightly higher in the lower-elevation forest (0.28 cm yr^{-1}) than in the upper-elevation forest (0.22 cm yr^{-1}), as reflected in the RGRs (600 m: 0.006 yr^{-1}; 1,200 m: 0.005 yr^{-1}) (Supplementary Figure S2). However, when comparing RGRs of the 12 tree species that were present at both elevations, eight of them were growing faster at upper elevations. The species with the highest mean RGRs were the semi-deciduous *Bursera graveolens* and the deciduous *Cochlospermum vitifolium*, both of which reached maximum rates of 0.015 yr^{-1}. In contrast, the species with lowest RGRs were *Morisonia flexuosa* (evergreen), with 0.00092 yr^{-1} and *Maytenus durifolia* (semi-deciduous), with 0.00126 yr^{-1}.

We found a strong association between RGR and DBH, with larger individuals generally growing slower (Figure 2A). Leaf habit (Supplementary Table S2) significantly affected diameter growth; deciduous species were growing faster than evergreen species at both elevation levels (Figure 2B).

A PCA based on ten functional traits was conducted for 49 tree species with available trait data. Of these, 23 species occurred at the lower forest elevation, 38 species at the upper forest elevation, and 12 species were present at both elevations. The studied species were distributed along the principal functional axes according to their trait values (Figure 3). The first axis captured a gradient from conservative tree strategies (lower values) with thick, tough leaves, high wood density, and high vessel density to more acquisitive strategies (higher values) with higher SLA and foliar nutrient contents, larger vessel diameters, and higher K_s. There were no distinct patterns for the two compared elevation levels; tree species from both elevation levels were present in all sections of the trait space (Figure 3A). Consistent with this pattern, none of the evaluated functional traits differed significantly between lower- and upper-elevation forests (Wilcoxon tests, all $p > 0.05$; Table 2). However, when taking into account the species' abundance (CWMs), the lower-elevation forest had on average more acquisitive properties than the upper-elevation forest (Table 2).

When tree species were distinguished according to their leaf habits (Figure 3B), clear differences in resource-use strategies emerged. Most deciduous species were found in the acquisitive section of the trait space (higher values on PC1), while most evergreen species clustered in the conservative section of the functional space. However, there were many different realized trait combinations among the tree species in the Laipuna reserve, with the semi-deciduous species in particular showing a distribution across the entire trait space.

3.2 Associations of RGR and functional traits

In both forest formations, RGR was associated with leaf and wood spectra, increasing with acquisitive traits and decreasing with conservative traits (Figure 4). At lower elevation, RGR showed a positive correlation with SLA ($r^2 = 0.12$, $p < 0.005$) and negative correlations with WSG ($r^2 = 0.09$, $p < 0.005$), leaf thickness ($r^2 = 0.07$, $p < 0.001$), and leaf toughness ($r^2 = 0.07$, $p < 0.005$). At the upper elevation, RGR responded positively to acquisitive strategies. Particularly, it was positively correlated with specific leaf area ($r^2 = 0.04$, $p < 0.005$) and foliar nitrogen concentration ($r^2 = 0.06$, $p < 0.005$), and negatively associated with leaf toughness ($r^2 = 0.05$, $p < 0.005$).

3.3 RGR and soil properties

The first two components of the PCA based on subplot-level soil variables explained 67% of the total variance (Supplementary Figure S3, Supplementary Table S3). The first PCA axis represented a fertility and base-cation gradient, with negative loadings for pH, Ca, K, Mg, ECEC, and for C/N ratio. More negative PC1 scores, therefore, corresponded to subplots with higher

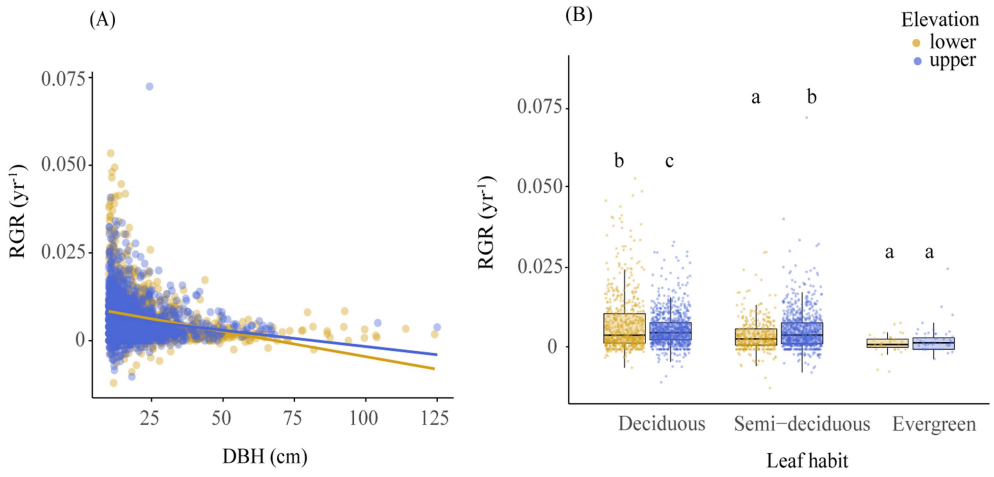

FIGURE 2
Relationships between RGR and **(A)** DBH and **(B)** leaf habit in the two forest formations. Lowercase letters indicate significant differences among leaf phenology groups according to one-way ANOVA followed by Tukey's post hoc test ($p < 0.05$). Groups sharing the same letter are not significantly different.

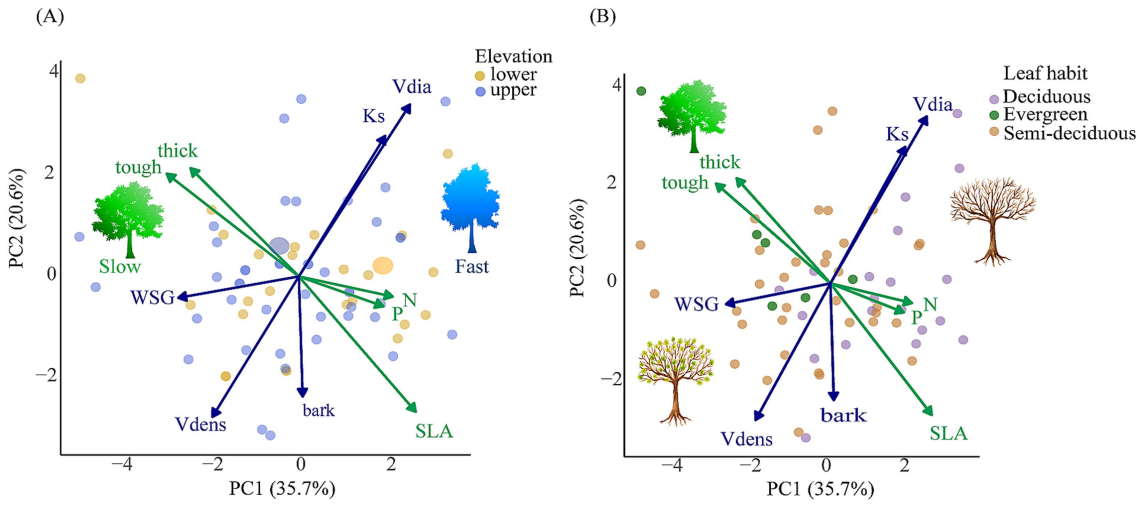

FIGURE 3
Principal component analysis (PCA) of 10 functional traits recorded in 49 tree species in the Laipuna dry forest (12 tree species occur at both elevations). The first two PCA axes explain 56.3% of the total variation. **(A)** Species separated by elevation. The smaller circles stand for the species, the two larger circles represent the community-weighted trait means of the two forest formations. **(B)** Species separated by leaf habit (deciduous, semi-deciduous, and evergreen).

TABLE 2 Summary statistics (mean ± SE and median) and community weighted means (CWM) of species functional traits in the lower and upper elevation forest.

Forest	Stand properties	SLA	thick	tough	N	P	bark	WSG	Vdens	Vdia	K_s
Lower elevation (23 species)	Mean ± SE	139.74 ± 11.82	0.21 ± 0.02	0.54 ± 0.10	30.02 ± 1.57	2.58 ± 0.20	5.29 ± 0.39	0.62 ± 0.05	20.12 ± 5.27	116.99 ± 10.22	30.37 ± 8.09
	Median	129.74	0.2	0.38	30.24	2.55	5	0.69	7.98	118.5	18.13
Upper elevation (38 species)	Mean ± SE	146.26 ± 8.75	0.22 ± 0.01	0.60 ± 0.05	27.08 ± 1.14	2.66 ± 0.17	5.47 ± 0.39	0.62 ± 0.03	33.19 ± 6.92	113.11 ± 10.88	31.25 ± 6.40
	Median	141.18	0.21	0.54	27.06	2.61	5.15	0.69	15.34	100	14.25
Lower elevation	CWM	164.29	0.17	0.30	31.19	2.89	4.75	0.42	6.73	150.97	48.40
Upper elevation	CWM	148.88	0.21	0.48	26.47	2.54	5.16	0.70	46.66	94.22	22.97

No statistically significant differences were detected between species functional trait means between lower and upper elevation forests for any of the evaluated traits (Wilcoxon tests, all $p > 0.05$). For variable abbreviations see Table 1.

base-cation concentrations and more alkaline soils, which were characteristic of the lower-elevation forest. The upper-elevation subplots showed slightly lower cation concentrations and pH values closer to neutral. PC2 (25%) captured a gradient of soils with higher P_{av} and K availability (negative loadings) to soils with higher ECEC (positive loadings). When considering soil properties as potential drivers of tree growth (Figure 5), only weak positive correlations were observed. RGR showed a weak positive correlation with the first ordination axis at both lower elevation ($r = 0.06$, $p < 0.05$) and upper elevation ($r = 0.08$, $p < 0.05$). RGR also showed a slight positive association with P_{av} ($r = 0.09$, $p < 0.05$), whereas other soil properties, including pH and C/N, were not linearly related to growth.

3.4 Modeling tree growth

We compared six candidate linear mixed-effects models to identify the main predictors of RGR in the studied dry forest. The models included DBH, functional traits and subplot-level soil properties (Table 3, Figure 6). Functional traits and soil variables included in the models were those with low pairwise correlations and high loadings on the first axes of the respective PCAs (Supplementary Figure S4). The full model (Table 3, model 1) incorporated the complete set of predictors (AIC = −14,646, $R^2 = 0.32$). The more parsimonious models (Table 3, models 2–6) had lower AIC values, while maintaining a similarly good model fit. Across models (Table 3, Figure 6), DBH consistently showed a strong negative effect on RGR (βstd = −0.33), similar to that of wood density (βstd = −0.30 to −0.39). Trait PCA axis 1 (representing resource acquisition traits) had a positive effect on RGR (βstd = 0.31–0.33). The soil variables pH and C/N had weaker negative effects (βstd = −0.07 and −0.04, respectively). Model diagnostics are shown in Supplementary Figure S5. Individual-level analyses showed consistent patterns with the main models, although some variation in effect sizes and predictor importance was observed (Supplementary Table S4, Supplementary Figure S6).

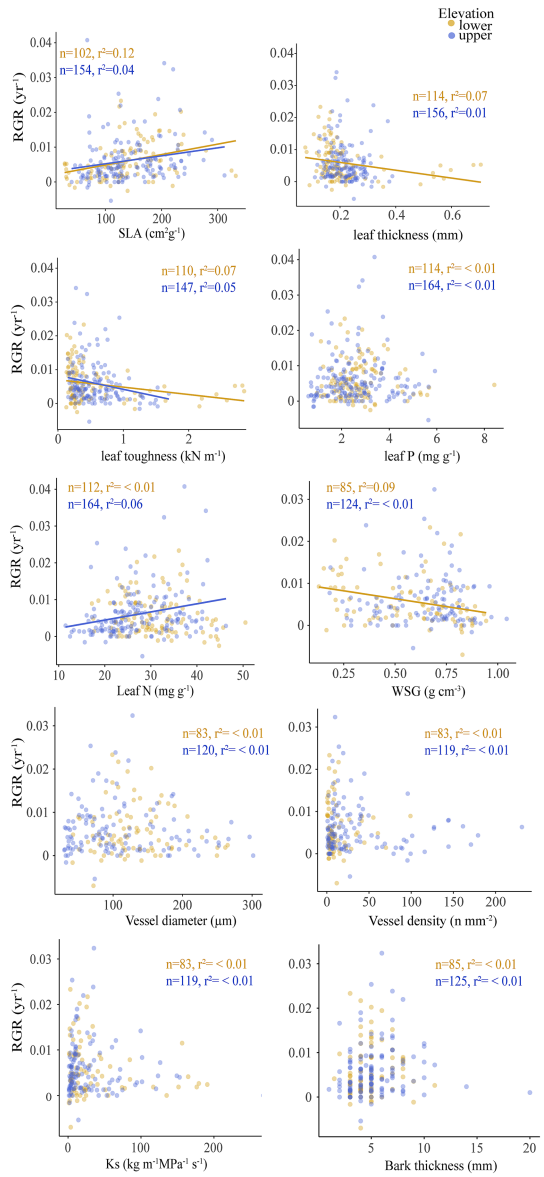

FIGURE 4
Pearson correlations between RGR and 10 functional traits for forest formations at lower and upper elevations in the Reserva Natural Laipuna. Lines indicate significant correlations ($p < 0.05$).

4 Discussion

4.1 Tree growth patterns in the Laipuna dry forest

Here, we used growth rates of 2,883 stems from two tropical dry forest formations to determine key predictors of RGR, including functional traits and soil properties. Mean annual diameter increment across both elevations was 2.6 mm yr^{-1}, consistent with values reported for other tropical dry forests (1–4.5 mm yr^{-1}) (Murphy and Lugo, 1986; Villegas et al., 2009; Carvajal-Vanegas and Calvo-Alvarado, 2013; Rodríguez-Alarcón et al., 2024).

Our multi-model analysis revealed a clear hierarchy of drivers of tree diameter growth in the Laipuna dry forest, with tree size (DBH) emerging as the strongest predictor (βstd = −0.34). This pattern is consistent with other studies (Gibert et al., 2016; Prado-Junior et al., 2016) and is in line with the view that tree height and diameter growth in TDF are constrained by harsh environmental conditions, particularly seasonal water limitation. It is important to note that the RGR of a tree necessarily declines as it transitions from a smaller to a larger diameter. This general trend of RGR to decrease with increasing size is referred to as ontogenetic drift (Pommerening et al., 2023), implying that larger trees may have a higher absolute diameter increment despite a smaller RGR.

The strong, positive effect of the first functional trait axis (βstd ≈ 0.33) highlights the positive effect of plant strategies related to resource acquisition on RGR (Díaz et al., 2016; Reich, 2014), whereas conservative traits, such as elevated wood density, showed a strong negative influence on growth (βstd = −0.30 to −0.39). Together, these patterns are consistent with the growth–survival trade-off, whereby species investing in resource acquisition achieve faster growth, whereas species investing in structural strength and hydraulic safety grow more slowly (Poorter et al., 2008; Chave et al., 2009; Wright et al., 2010; Báez and Homeier, 2018).

In addition, the most parsimonious model (DBH + WSG + pH + C/N) revealed that soil chemical properties play only a secondary role in growth regulation. Soil pH, P_{av}, and soil C/N explained only a minor portion of variation in RGR (βstd ≤ 0.07; Table 3), suggesting that soil fertility is not a major driver of tree diameter growth in the study area. Instead, variation in growth appears to be primarily associated with intrinsic factors, notably tree size and species-specific functional strategies, which regulate carbon gain and hydraulic performance and ultimately determine how trees survive in these water-limited ecosystems. This result aligns with patterns observed in Bolivian tropical forests, where rainfall fluctuations were a stronger determinant of growth than soil fertility (Toledo et al., 2011). However, it contrasts with tropical moist forests where variation in water availability is often of secondary importance and soil fertility may be more important for forest productivity (Homeier and Leuschner, 2021).

4.2 Associations between RGR and functional traits

As expected, deciduous species exhibited higher RGRs than semi-deciduous and evergreen species. This pattern aligns with the fast–slow economics spectrum: most deciduous species are associated with acquisitive traits that maximize carbon gain during the rainy season (Fu et al., 2012; Krishna and Chandra Garkoti, 2022; Yan et al., 2025), while evergreen species prioritize hydraulic safety and structural persistence at the cost of slower growth (Poorter, 2009; Rodríguez-Alarcón et al., 2024).

Our results revealed a pronounced functional shift with elevation at our study site. In the lower-elevation forest where water availability is more limited, RGR was primarily related to investment in conservative traits (thick, tough leaves, high wood density). Conversely, in the upper-elevation forest, where water availability is higher and temperatures are lower, RGR was more strongly associated with acquisitive leaf traits (high SLA, leaf N, and leaf P) and traits related to hydraulic efficiency (larger vessel diameters, higher K_s).

Nevertheless, the community-weighted trait means suggest a more acquisitive strategy in the drier lower-elevation forest formation. Given that harsher environments are generally assumed to favor conservative resource-use strategies, it is unexpected that the trait CWMs found in the lower-elevation forest were assessed as more acquisitive than in the upper-elevation forest. Furthermore, a positive SLA–RGR relation was observed at both

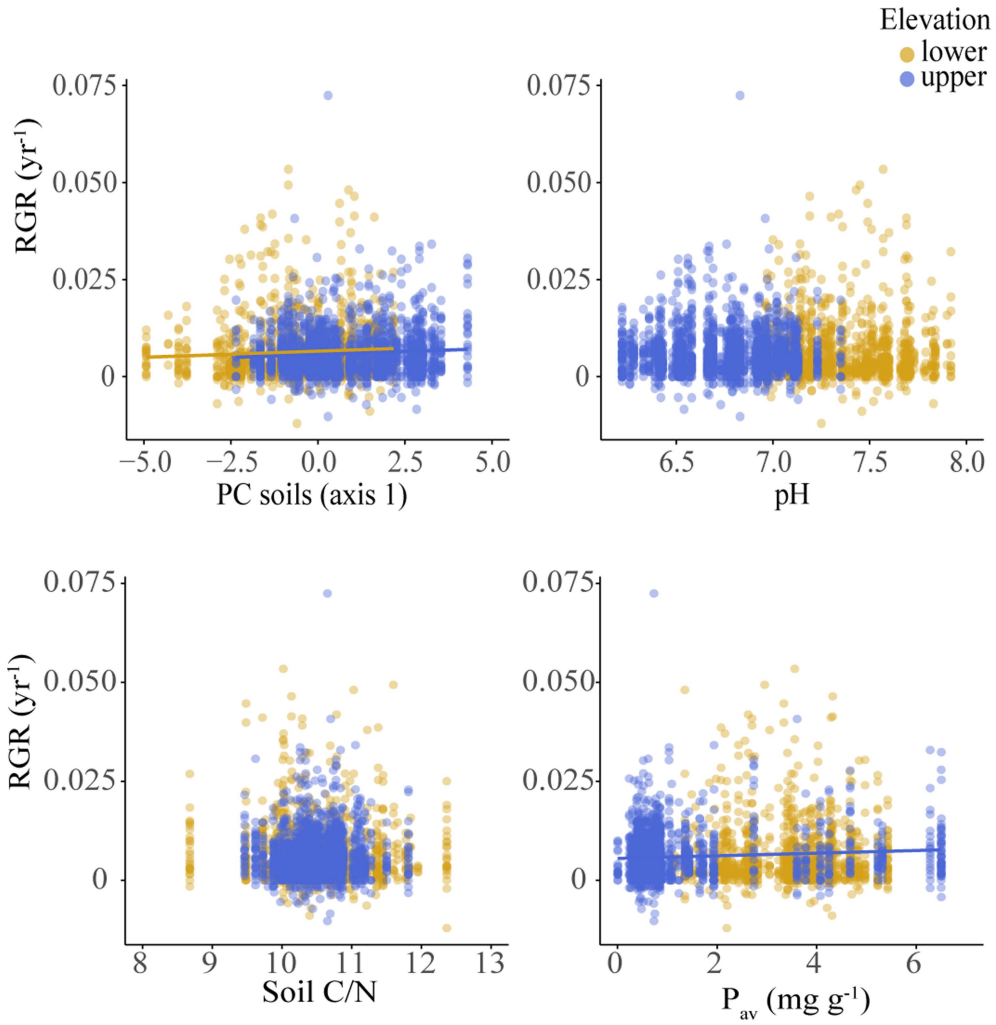

FIGURE 5
Pearson correlations between relative growth rate (RGR) and soil properties in the lower- and upper-elevation forests in the Laipuna reserve. Lines indicate significant correlations ($p < 0.05$).

TABLE 3 Results of linear mixed-effects models comparing the relative contributions of tree diameter, functional traits, and environmental variables to explain RGR.

Model	Fixed factors	Standardized effect size (βstd)	AIC	R^2 marginal	R^2 conditional
1. DBH + PCAs + environment	DBH + traits (PC1 & PC2) + soil (PC1 & PC2) + elevation	DBH (−0.33), traits PC1 (0.33), trait PC2 (−0.05), soil PC1 (0.07), soil PC2 (0), elevation (0)	−14,646	0.13	0.32
2. DBH+ PCAs (traits & soil, 1. axis)	DBH + traits (PC1) + soil (PC1)	DBH (−0.33), traits PC1 (0.31), soil PC1 (0.07)	−14,651	0.13	0.31
3. DBH + traits	DBH + WSG + tough+ SLA+ Vdia	DBH (−0.33), WSG (−0.30), tough (−0.08), SLA (0.02), Vdia (0.02)	−14,643	0.16	0.32
4. DBH + soil	DBH + pH + P_{av} + C/N	DBH (−0.33), pH (−0.07), P_{av} (0), C/N (−0.04)	−14,630	0.11	0.38
5. DBH + traits + soil	DBH + WSG + tough + SLA + Vdia + pH + P_{av} + C/N	DBH (−0.33), WSG (−0.31), tough (−0.08), SLA (0.01), Vdia (0.02), pH (−0.07), P_{av} (0), C/N (−0.04)	−14,645	0.15	0.33
6. DBH + WSG + soil	DBH + WSG + pH + C/N	DBH (−0.33), WSG (−0.39), pH (−0.07), C/N (−0.04)	−14,652	0.16	0.33

Fixed effects are shown with standardized coefficients (β). Models included species and plot as random effects.

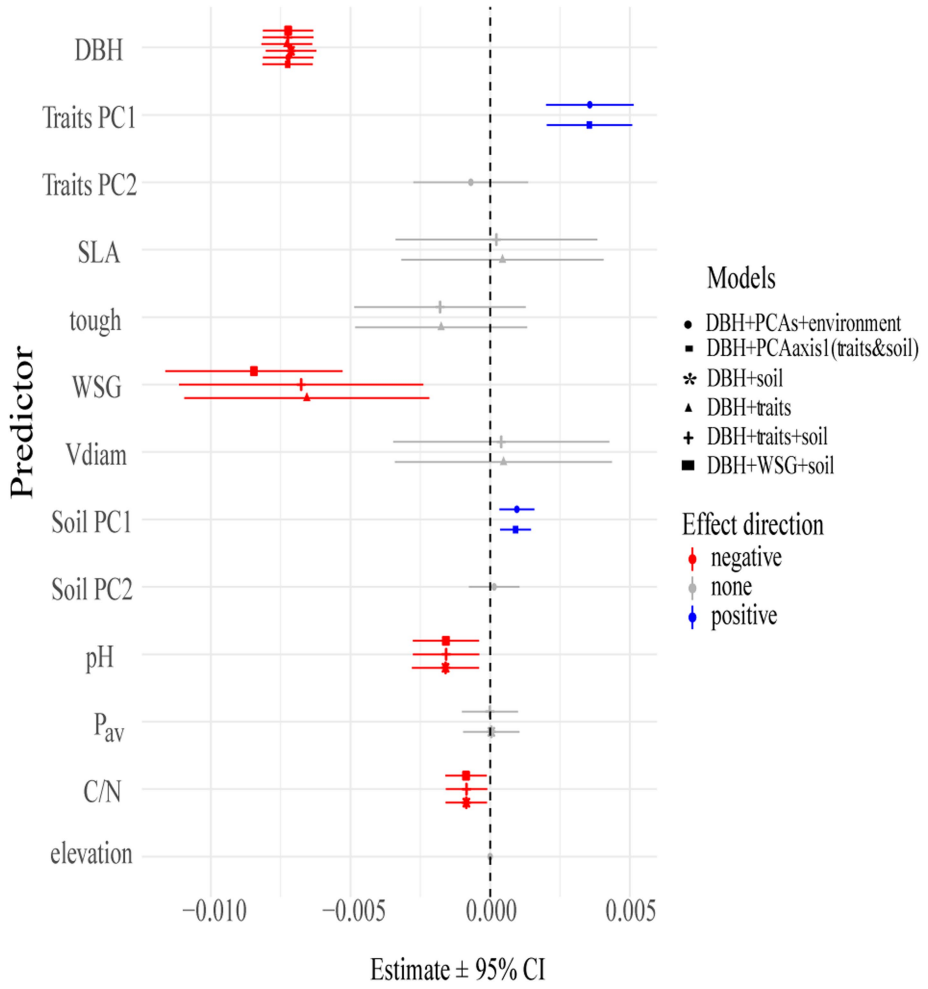

FIGURE 6
Standardized regression coefficients (± 95% CI) for six models testing the effects of functional traits, soil properties, and elevation on tree RGR. Significant effects are shown in blue (positive) or red (negative), whereas gray indicates non-significant effects. Models included species and plot as random effects.

elevations, with a stronger relationship in the lower-elevation forest, despite stronger drought and heat stress compared to the upper-elevation formation. It appears that the key factor determining elevation differences in trait means is the proportion of drought-deciduous trees in the communities, which decreased from the lower- to the upper-elevation forest, while the proportion of evergreen species remained unchanged. These deciduous species with thinner, short-lived leaves shift community-weighted trait means towards more acquisitive values.

A closer look at traits other than SLA suggests that several species in the lower-elevation forest prioritize long-term survival and cavitation resistance by allocating resources away from rapid stem growth (Givnish, 1995; Poorter et al., 2014; Mangini et al., 2025) and thereby pursue a stress-resistance strategy associated with reduced resource acquisition. In fact, WSG was, after stem diameter, the most influential factor associated with relative growth rate in the tree sample. This pattern is also indicated by negative relationships of RGR with leaf thickness and toughness, as well as a lacking dependence of RGR on foliar N and P.

This demonstrates that community-weighted means of the studied traits can give misleading impressions of the prevailing strategies for acquiring or conserving resources in a drought-limited community. In the lower-elevation dry forest, traits such as fine root drought resistance, xylem embolism resistance, and the capacity for damage repair after severe drought may be more decisive for growth than the conventionally measured traits SLA and leaf N. However, these traits were not studied here and are not considered in most other plant trait studies. The positive relationship between SLA and RGR, even in a strongly water-limited environment, may be due to the importance of maximizing carbon gain during the short moist growth periods, a pattern widely documented in tropical forests (Wright et al., 2004; Poorter et al., 2009; Silva et al., 2015).

As expected, RGR was negatively related to conservative traits (high WSG and leaf toughness). This pattern is consistent with the trade-off, whereby slower-growing species with denser wood invest more in mechanical stability and strength, resulting in slower growth, while species with lighter wood grow faster because they invest less biomass in structures enabling stress tolerance (Putz et al., 1983; Poorter et al., 2014; Gray et al., 2019). Likewise, tougher leaves reduce RGR because they are associated with a conservative strategy focused on leaf longevity rather than high photosynthetic rates, compared to the more N-rich and thinner leaves of the deciduous tree species that enable higher carbon gain (Kitajima and Poorter, 2010; Onoda et al., 2017; Harenčár et al., 2024).

Some traits (e.g., high WSG, tough leaves) and growth respond to the same underlying developmental and physiological processes.

Reduced cambial activity, smaller cell expansion, and greater proportional investment in cell walls can simultaneously produce slower radial growth, denser wood, and tougher leaves. Under this framework, WSG and leaf toughness are not necessarily causal drivers but rather consequences of growth-related anatomical processes.

4.3 Associations between RGR and soil chemical factors

Nutrient limitation can strongly influence plant growth, especially in regions with ample water supply. However, Neotropical dry forest soils are characterized by a predominantly negative water balance and are typically more fertile than soils of humid tropical forests at similar elevations (Gei and Powers, 2013; Homeier and Leuschner, 2021; Rivero-Villar et al., 2022). Moreover, the soil pH gradient was small in our study. Consequently, variation in soil nutrient availability plays only a secondary role in controlling RGR in our dataset, as reflected in the weak and inconsistent soil-RGR relationships observed.

Although the first principal component of soil variables captured a gradient of base-cation concentration and alkalinity, its correlation with RGR was weak at both lower- and upper-elevation sites. Among individual nutrients, only soil P_{av} showed a small positive correlation ($p < 0.05$) with RGR at the upper-elevation site. The absence of a stronger P-RGR association at the lower elevation suggests that, under more pronounced seasonal drought, water limitation overrides nutrient limitation, thereby reducing the sensitivity of growth to soil fertility. In these water-limited tropical dry forests, species-specific functional traits and related physiological mechanisms that confer conservative and efficient water use seem to exert far greater control on tree growth performance than soil nutrient availability (Baker et al., 2003; Quintero-Vallejo et al., 2015; Sandoval-Granillo and Meave, 2023).

Our results are only partly supportive of our hypotheses: Trees of the drier lower-elevation forest possess on average more acquisitive traits and have slightly higher growth rates than trees in the cooler upper-elevation forest. However, RGR was positively related to SLA at both elevations, while other trait–growth relationships differed between elevations. At lower elevation, RGR was negatively related to WSG, leaf thickness, and leaf toughness, whereas at the upper elevation, RGR was positively related to foliar N and negatively related to leaf toughness. These contrasting relationships, together with differences in community-weighted trait values, suggest that different functional strategies may contribute to tree growth under the environmental conditions prevailing at each elevation.

Models combining functional traits and soil variables did not outperform those based on functional traits and tree size alone. This indicates that variation in tree growth in this tropical dry forest is primarily driven by species-specific functional strategies and plant size, while soil properties add little explanatory power beyond these factors.

5 Conclusion

We found a wide variety of trait combinations and thus strategy types in the studied drought-exposed tropical dry forests. They range from fast-growing deciduous tree species with a more acquisitive strategy during the wet season, such as *Ceiba trischistandra* and *Erythrina velutina*, which maximize carbon gain during a 3–4 month period (Würzberg et al., 2026), to evergreen, drought-tolerant species such as *Morisonia scabrida*, which produce persistent, long-lived leaves and deep roots, while exhibiting relatively low growth rates. Between these two strategies, a continuum of semi-deciduous species does exist which adjust their leaf lifespan in response to water availability. In both forest formations, evergreen, semi-deciduous and drought-deciduous tree species are present. Since the deciduous species with higher SLA and foliar N content are more common in the lower drier forest, the community-weighted trait means shift from more conservative to more acquisitive in downslope direction. However, wood specific gravity was far more influential on growth rate than SLA, foliar N or other traits.

Our study is based on species mean traits, thus not taking into account intraspecific trait variation which could also influence individual growth responses. While this approach is commonly used in community-level trait studies, it may underestimate the contribution of within-species variability to growth dynamics. Future studies incorporating trait measurements at the individual level would help refine these relationships and better quantify within-species variation.

Increasing evidence shows that most trees in tropical forests are sensitive to sustained warming and increasing drought and heat stress, which will ultimately lead to alterations in species composition, loss of diversity (Fadrique et al., 2018, 2026; Ortega et al., 2024; Restrepo et al., 2025), and shifts in the tree growth strategies prevailing in the forest communities. We have identified WSG, a trait important for stress tolerance, as a main predictor of tree growth in TDFs. However, the high abundance of a few deciduous tree species in the drier and warmer forest formation at lower elevation points in a different direction, namely that in tropical dry forests under a hotter and drier climate, these drought-avoiding species with low WSG will eventually dominate.

Data availability statement

The datasets analysed during the current study are available at the RESPECT project database "FOR816 data warehouse (FOR816dw)" http://www.tropicalmountainforest.org/data_pre.do?citid=2067.

Author contributions

JM-G: Formal analysis, Visualization, Methodology, Investigation, Writing – review & editing, Data curation, Funding acquisition, Validation, Writing – original draft. KG-V: Investigation, Methodology, Writing – review & editing. FM: Investigation, Writing – review & editing. KC: Investigation, Writing – review & editing. CF: Investigation, Writing – review & editing. DP-C: Writing – review & editing, Investigation, Resources, Validation, Methodology. SB: Writing – review & editing. CL: Writing – original draft, Resources, Supervision, Writing – review & editing. JH: Formal analysis, Data curation, Writing – original draft, Methodology, Project administration, Resources, Validation, Writing – review & editing, Conceptualization, Funding acquisition, Supervision, Investigation.

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Conflict of interest

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