

Article

Tree and Liana Growth in Three Neotropical Dry Forests: Coherent Patterns and Individualistic Responses to Climate Variability

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Abstract: Tropical dry forests (TDFs) are among the ecosystems most threatened by agricultural use and climate warming. However, the long-term growth responses to climate variability of woody plants in TDFs are understudied because not all TDF species form conspicuous annual rings. To address this issue, we sampled trees (26 species) and lianas (2 species) in TDFs subjected to contrasting climate conditions and located in Colombia, Ecuador, and Bolivia. First, we examined the potential to form conspicuous tree-ring boundaries in 22 tree species (*Amyris pinnata*, *Aspidosperma tomentosum*, *Beilschmiedia* sp., *Bursera graveolens*, *Caesalpinia pluviosa*, *Ceiba pentandra*, *Centrolobium microchaete*, *Citharexylum kunthianum*, *Cordia alliodora*, *Croton gossypifolius*, *Cupania cinerea*, *Eugenia* sp., *Genipa americana*, *Guarea guidonia*, *Hymenaea courbaril*, *Machaerium capote*, *Pithecellobium dulce*, *Rapanea guianensis*, *Sapindus saponaria*, *Senna spectabilis*, *Zanthoxylum monophyllum*, *Zanthoxylum rhoifolium*, and *Zanthoxylum verrucosum*) and two liana species (Bignoniaceae and Combretaceae families). Second, we built mean series of ring-width indices in selected tree (*A. tomentosum*, *B. graveolens*, *C. alliodora*, *C. cinerea*, *C. microchaete*, *P. dulce*, *S. spectabilis*, and *Z. verrucosum*) and liana species and related them to climate variables. Wet conditions during the current and prior growing seasons enhanced growth in tree and liana species in different TDFs. Coexisting species showed individualistic responses to climate variability.

Keywords: Bolivia; Colombia; dendroecology; Ecuador; tree rings; Neotropical dry forest



Academic Editor: Guillermo Angeles

Received: 3 March 2025

Revised: 15 March 2025

Accepted: 18 March 2025

Published: 19 March 2025

Citation: Camarero, J.J.; Valeriano, C. Tree and Liana Growth in Three Neotropical Dry Forests: Coherent Patterns and Individualistic Responses to Climate Variability. *Forests* **2025**, *16*, 542. <https://doi.org/10.3390/f16030542>

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1. Introduction

Tropical forests play key roles by supporting biodiversity and modulating global carbon and water cycles [1], but their productivity greatly changes along climate gradients and depending on site conditions [2]. However, insights on how tropical woody plants respond to climate and geographical variability are limited because of the lack of long-term, annually resolved proxies of productivity and growth in many tropical areas. Tree rings can partially fill this research gap by providing estimates of annual woody productivity and measures of vegetation sensitivity to climate variability [3–7]. Recently, several studies have addressed this issue by developing tree-ring chronologies (mean series of cross-date or synchronized ring-width data for a population) for about 500 tree species forming annual tree rings in tropical and subtropical regions [5–8], and 220 of them were found in the Neotropics [6]. However, many tropical regions remain under-represented in global tree-ring studies, which are biased toward temperate and boreal forests where annual ring formation is common [9].

Tropical dry forests (hereafter TDFs) are among the most threatened tropical ecosystems due to agricultural use, cattle ranching, and climate warming [10,11]. TDFs are

subjected to a dry season, lasting from 2 to 7 months, when many tree species lose their leaves [10]. Woody plant species have developed several strategies to withstand such seasonal drought, including seasonal cambial phenology [10]. In TDFs, many woody plant species (tree, shrubs, and lianas) may form annual rings in response to their characteristic dry season [8,12]. Seasonal dry conditions are linked to lower cambial dynamics resulting in the formation of annual rings [13,14]. Nevertheless, identifying tree-ring boundaries in tropical species is not straightforward, because their wood anatomy is complex, and several features (eccentric radial growth, bimodal or multimodal growth patterns, wedging, and false rings) make this task challenging [8]. In addition, conspicuous ring-like boundaries may not correspond to annual growth rings [15], and thus, they are unsuitable for dendrochronology [16]. Therefore, a rigorous visual cross-dating or synchronization of wood samples followed by statistical testing [17] are required to obtain well-replicated chronologies, i.e., mean growth series sharing a common growth pattern among individuals of the same species. A first step to develop such chronologies involves scrutinizing the wood anatomy and intra-annual growth patterns, using dendrometers, for instance, of several species from TDFs subjected to contrasting climate conditions to identify new species with dendrochronological potential [18–27]. A second step is the cross-dating and measurement of ring-width series in a selection of these woody plant species to relate them with climate variability [28–31]. Moreover, such dendrochronological studies could also include other growth forms of woody plants that are abundant in TDFs, such as lianas [32]. Lianas are climbing plants that compete with trees, affecting their growth and regeneration, but also impact TDF dynamics, providing microhabitat and food for many animal and fungi species, thus increasing ecosystem complexity and biodiversity [33]. Some liana species form annual rings, which allow developing dendrochronological studies [34].

In this study, we addressed the following objectives: (i) to examine the presence of tree-ring boundaries in 26 tree species and 2 liana species sampled in three TDFs located in Colombia, Ecuador, and Bolivia; (ii) to develop chronologies in a selection of these species showing dendrochronological potential (8 tree species and 2 liana species); and (iii) to analyze climate–growth relationships in these selected species. Given that seasonal drought is the main climate stressor in TDFs, we expect that radial growth will be limited by low precipitation, particularly in the driest study site located in Ecuador.

2. Materials and Methods

2.1. Study Sites and Field Sampling

We sampled three TDFs located in southwestern Colombia, southwestern Ecuador, and southeastern Bolivia (Figure 1). Their characteristics are summarized in Table 1.

We were interested in analyzing wood anatomy, quantifying growth patterns and responses to climate. We selected dominant or co-dominant trees for sampling. Then, we extracted cores from sampled trees at a height of 1.3 m using 5-mm Pressler increment borers (Haglöf, Långsele, Sweden) and measured their diameters using tapes. In the tree and liana species from Bolivia, we analyzed basal cross-sections taken from stumps after commercial thinning.

The study TDFs were characterized by a dry season when many tree species shed their leaves. The warmest and driest site was the Ecuadorian TDF, where the dry season may last up to seven months, from June to December [35]. The dry season was longer in the Bolivian (June to September) than in the Colombian site (June to August) [25].

In Colombia, the sampled stands corresponded to secondary forests and were located in the “Juan María Céspedes” botanical garden and “El Vínculo” forest, near the city of Tuluá. The studied TDF was situated in a hilly landscape, and it was characterized by a tree species density of 31 tree species ha^{−1} and a basal area of 12.4 m² ha^{−1} [25].

Soils were acid and sandy, with abundant organic matter. There, we followed a mixed approach. First, we sampled 5–10 dominant individuals of the 19 most abundant tree species (*Amyris pinnata* Kunth, *Beilschmiedia* sp., *Caesalpinia pluviosa* DC., *Ceiba pentandra* (L.) Gaertn., *Citharexylum kunthianum* Moldenke, *Cordia alliodora* (Ruiz & Pav.) Cham., *Croton gossypifolius* Vahl., *Cupania cinerea* Poepp., *Eugenia* sp., *Genipa americana* L., *Guarea guidonia* (L.) Sleumer, *Hymenaea courbaril* L., *Machaerium capote* Triana ex Dugand, *Pithecellobium dulce* (Roxb.) Benth., *Rapanea guianensis* Aubl., *Sapindus saponaria* L., *Senna spectabilis* (DC.) H.S. Irwin & Barneby, *Zanthoxylum monophyllum* (Lam.) P. Wilson, *Zanthoxylum rhoifolium* Lam., and *Zanthoxylum verrucosum* (Cuatrec.) P.G. Waterman). Second, we selected five of the species that were dominant and showed conspicuous tree-ring boundaries (*C. alliodora*, *C. cinerea*, *P. dulce*, *S. spectabilis*, and *Z. rhoifolium*), thus having dendrochronological potential. We sampled 65 individuals in total of the five Colombian species.

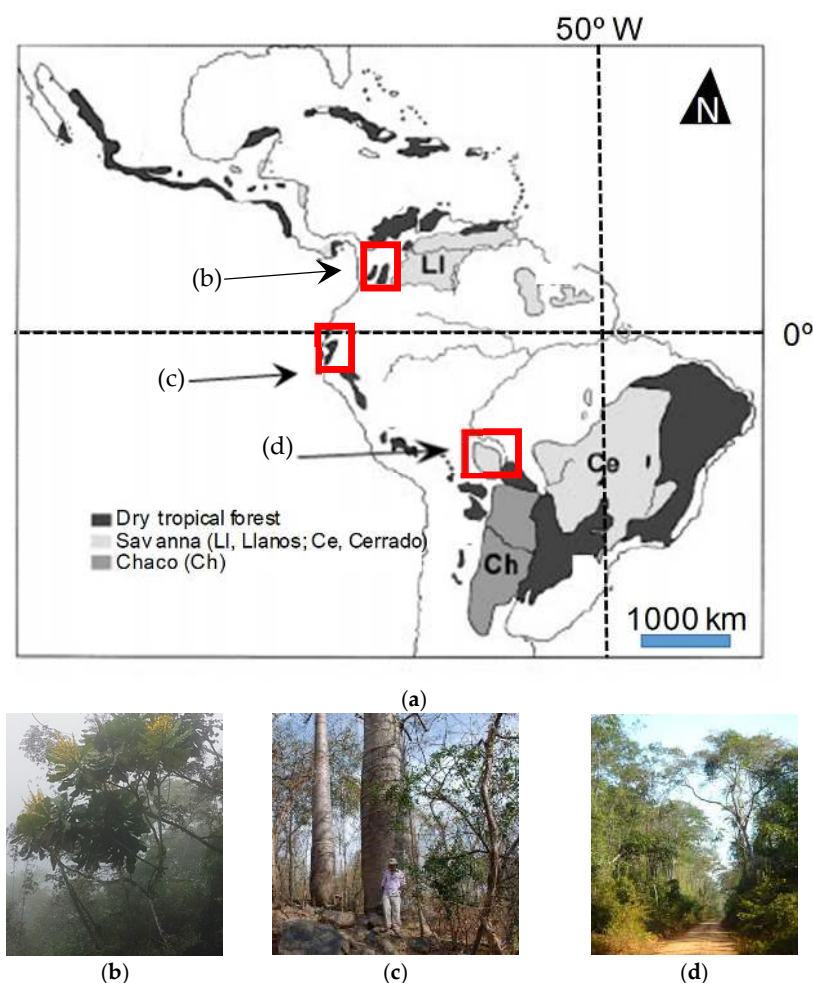


Figure 1. (a) Distribution of seasonally dry tropical forests in America, including savanna (llanos and cerrado) and Chaco biomes. Red boxes indicate the locations of study sites (from N to S): inter-Andean valleys in southwestern Colombia (b), Tumbesian forests near the Pacific Ocean coast in southwestern Ecuador (c) (note the *Ceiba* spp. succulent stems), and the “Chiquitano” forest in southeastern Bolivia (d) (note the road for selective logging). The map was created using Maptive software (<https://www.maptive.com/>, v.1, URL accessed on 13 January 2025), and it was modified from [11]. The map projection is equirectangular.

In the Ecuador site, we sampled 11 trees of the deciduous *Bursera graveolens* (Kunth) Triana & Planch. (“Palo Santo”), which was dominant in the selected site, a well-preserved Tumbesian TDF located in the “Reserva Ecológica Arenillas” [30]. The diameter at 1.3 cm of the sampled trees (mean $\pm$ SD) was 24.4 ± 3.6 cm.

Table 1. Characteristics of the three study sites.

Variable	Characteristics		
Site, country	Tuluá, Colombia	Arenillas, Ecuador	INPA, Bolivia
Latitude	4.33° N	3.52° S	16.12° S
Longitude	76.17° W	80.13° W	61.72° W
Elevation (m a.s.l.)	1220	21	380
Annual temperature (°C)	23.6	25.9	24.3
Annual precipitation (mm)	1193	661	1160
No. tree species (individuals)	19 (151)	1 (11)	2 (38)
No. liana species (individuals)	—	—	2 (30)

Finally, we studied a well-preserved “Chiquitano” TDF located near Concepción, southeastern Bolivia, and sustainably exploited by the INPA Parket Company. The studied TDF was located on gentle slopes, and it was characterized by a tree species density of 34 tree species ha^{-1} and a basal area of 19.7 $\text{m}^2 \text{ha}^{-1}$ [36]. Soils were acid and of sandy-loamy texture [25]. There, we sampled two dominant tree species (*Centrolobium microchaete* (Mart. ex Benth.) H.C. Lima, “tarara amarilla”; *Aspidosperma tomentosum* Mart., “jichituriqui amarillo”). In addition, two liana species belonging to the Bignoniaceae and Combretaceae families were also sampled. The main genera of liana species in the study area were *Clitostoma* and *Pleonotoma*, both belonging to the Bignoniaceae family [37,38]. Regrettably, we were not able to identify the liana species, given the difficulty of their accurate taxonomic identification. Lianas abound in this type of TDF (about 60% of trees with a diameter > 10 cm show some degree of liana infestation), negatively impact the growth of commercial tree species, and increase after disturbances such as logging [37,38]. The diameters of the sampled *C. microchaete* and *A. tomentosum* individuals were 29.0 ± 5.6 ($n = 17$ individuals) and 22.4 ± 2.3 cm ($n = 19$ individuals), respectively. The diameters of the sampled Bignoniaceae and Combretaceae liana species were 5.7 ± 0.7 ($n = 13$ individuals) and 6.1 ± 1.2 cm ($n = 17$ individuals), respectively.

2.2. Climate Data and Indices

Due to the lack of long-term, homogeneous climate series near the study sites, we obtained monthly climate data (TMax, mean maximum temperature; TMin, mean minimum temperature; Prec, total precipitation) from the 0.5°-gridded CRU database v. 4.07 [39]. Year-to-year rainfall variability in the study TDFs depended on El Niño–Southern Oscillation (ENSO), which may have affected their growth rates [35,40]. During warm phases of the ENSO (“El Niño” episodes), precipitation increases and growth is enhanced, as has been observed in Ecuadorian TDFs [41]. To quantify the ENSO variability, we used monthly series of the Southern Oscillation index (SOI), sea surface temperature anomalies in the “El Niño” 3 + 4 area (El Niño 3.4) across the tropical Pacific (lat. 5° N–5° S, long. 120–170° W), and the Pacific Decadal Oscillation (PDO) considering the period 1981–2010 [42,43]. These data were downloaded using the Climate Explorer web portal (<http://climexp.knmi.nl>, URL accessed on 9 January 2025).

2.3. Processing Wood Samples and Ring-Width Measurements

We used dendrochronological methods to process the wood samples, measure growth rates, and quantify climate–growth relationships [44]. The samples were air dried; cores were glued onto wooden supports, and cores and cross-sections were carefully sanded with sandpapers of finer grain until rings were clearly visible. Then, samples were visually cross-dated under the stereomicroscope. In the case of sites sampled in the Southern Hemisphere (Ecuador and Bolivia), we followed the Schulman convention and assigned

to each ring the calendar year in which ring started to be formed [45]. For instance, we assigned the calendar year 1990 to a ring formed from November 1990 to March 1991. Ring widths were measured with a 0.001 mm resolution along two radii per individual on images scanned at a resolution of 2400 dpi (Epson Perfection V19, Epson, Hillsboro, OR, USA). Measurements were performed using the CooRecorder-CDendro software (v. 9.8.1, Saltsjöbaden, Sweden) [46]. The cross-dating of samples was checked using the COFECHA software ver. 6.06P, which calculated moving correlations between individual series of ring-width indices and the mean site series of each species [47].

To compare growth rates between species of the same sites, we converted the ring-width series into basal-area increment (BAI) series, which is a more accurate measure of growth [48]. The BAI series were calculated using the following equation and assuming concentric growth:

$$\text{BAI} = \pi (R_t^2 - R_{t-1}^2) \quad (1)$$

where R_t^2 and R_{t-1}^2 are the radii corresponding to the current (t) and prior ($t - 1$) years, respectively.

To calculate climate–growth relationships, series of ring-width data were detrended and standardized to remove growth trends due to changes in stem size [44]. This was performed using a polynomial spline of 2/3 of the growth series length and a 0.5 response cut-off to preserve annual to decadal growth variability. Autoregressive models were fitted to each detrended series to remove the first-order autocorrelation. The resulting residual or pre-whitened individual series of ring-width indices were averaged by using bi-weight robust means to obtain species' mean series or chronologies. Last, statistics were calculated on this series to characterize them over the common period 1984–2009 [49]. These statistics included the following: the first-order autocorrelation of ring-width series (AR1), the mean sensitivity (MSx) of standardized ring-width indices (a measure of relative changes in ring width between consecutive years), and the mean correlation among indexed ring-width series (Rbar). All the tree-ring width processing and statistics calculations were performed using the package dplR ver. 1.7.8 [50,51] in the R statistical software ver. 4.4.2 [52].

2.4. Statistical Analyses

First, we compared ring-width statistics between sites or between species within the same site using non-parametric Mann–Whitney U tests. Second, to summarize the common variability among the species' chronologies of the same site, principal component analyses (PCAs) were calculated for the groups of Colombian and Bolivian species considering the best-replicated periods. The PCAs were based on the variance–covariance matrix and were obtained with the function rda of the vegan R package ver. 2.6-10 [53]. Third, to calculate climate–growth relationships, we computed Pearson correlations between monthly climate data (TMax, mean maximum temperature; TMin, mean minimum temperature; Prec, total precipitation or indices (SOI and El Niño 3.4)) and the mean species series of ring-width indices. This was performed for the best-replicated common period (1984–2009). The climate–growth relationships were calculated using the treeclim R ver. 2.0.7.1 package [54].

3. Results

3.1. Examining Tree-Ring Boundaries in Species from the Colombian TDF

In 15 of the 19 Colombian tree species, the ring boundary corresponded to parenchyma bands, and two of them also presented semi-ring porous wood (Table 2). In three of the examined species, the ring boundaries corresponded to concurring parenchyma and wall-thickened fiber, whereas in one species, ring limits were not distinct. We selected five of these species presenting distinct growth rings in inner and outer parts of wood samples for building tree-ring width chronologies.

Table 2. Tree species sampled in the Colombian TDF, distinctiveness of tree-ring boundaries, and wood structure. Distinctiveness of growth zones was described in the inner (in) and outer (out) parts of wood samples, and it was classified as follows: good (+), visible (+ −), and poor (−). Wood structure types regarding tree-ring limits were as follows: 1, density variations; 2, parenchyma bands; 3, pattern of concurring parenchyma and fiber; and 4, semi-ring to ring-porous wood. Arrows indicate tree rings or tree-ring limits. The five underlined species were selected to build tree-ring chronologies.

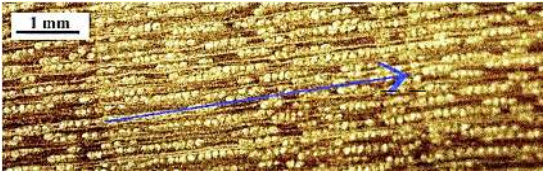
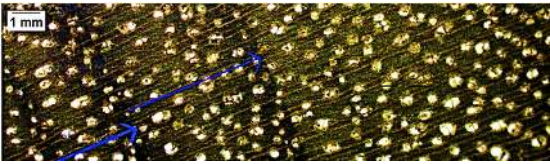
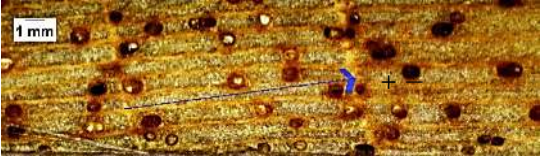
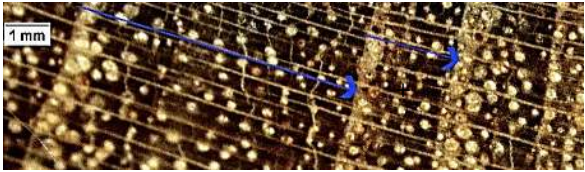
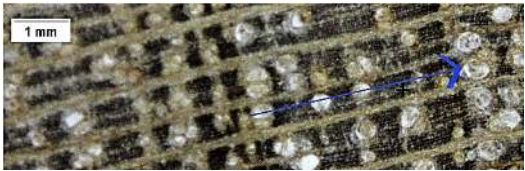
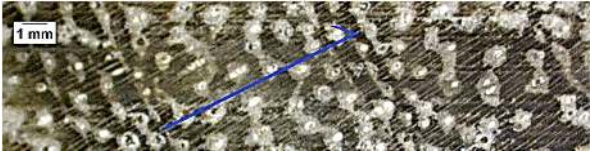
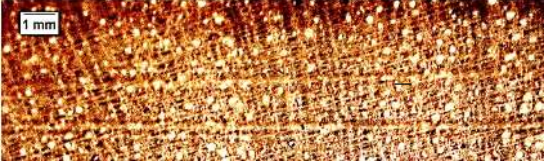
Species	Tree-Ring Detail	Distinctiveness		Wood Structure
		In	Out	
<i>Amyris pinnata</i>			+ −	2
<i>Beilschmiedia</i> sp.			+	1, 2
<i>Ceiba pentandra</i>			+ −	2
<i>Citharexylum kunthianum</i>			+	1, 2, 4
<i>Cordia alliodora</i>			+	2
<i>Croton gossypifolius</i>			+ −	1, 2
<i>Cupania cinerea</i>			+	2
<i>Eugenia</i> sp.			−	2

Table 2. Cont.

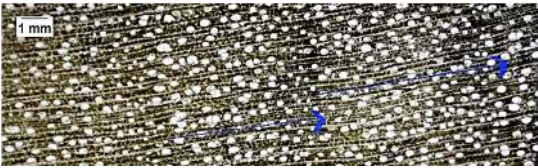
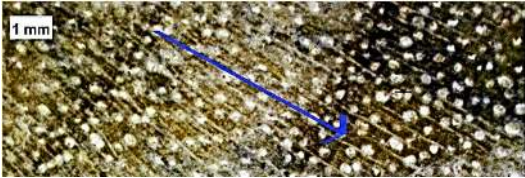
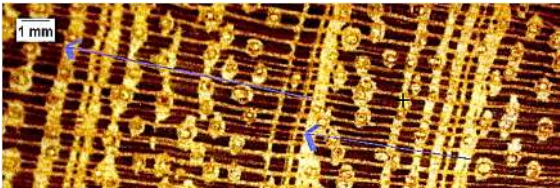
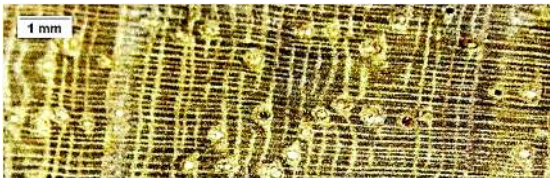
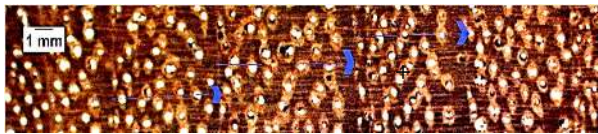
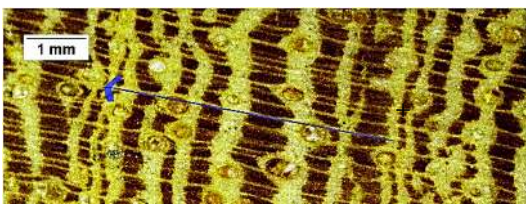
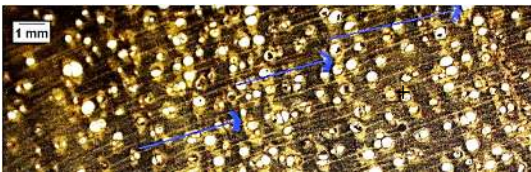
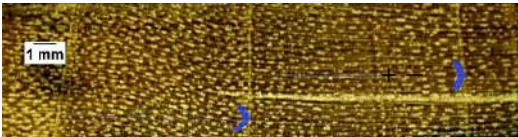
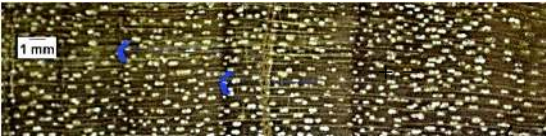
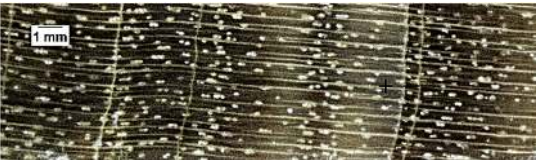
Species	Tree-Ring Detail	Distinctiveness		Wood Structure
		In	Out	
<i>Genipa americana</i>			—	2
<i>Guarea guidonia</i>			—	1, 2
<i>Hymenaea courbaril</i>			+	3
<i>Machaerium capote</i>			+ —	3
<i>Pithecellobium dulce</i>			+	1, 2
<i>Rapanea guianensis</i>			—	—
<i>Sapindus saponaria</i>			+ —	3
<i>Senna spectabilis</i>			+ —	2, 4
<i>Zanthoxylum monophyllum</i>			+ —	2

Table 2. Cont.

Species	Tree-Ring Detail	Distinctiveness		Wood Structure
		In	Out	
<i>Zanthoxylum rhoifolium</i>			+	1, 2
<i>Zanthoxylum verrucosum</i>			+	1, 2

3.2. Ring-Width Data and Growth Patterns in the Three TDFs

The mean growth rate of trees (2.97 mm) was significantly higher ($U = 1$, $p = 0.04$) than that of lianas (0.87 mm) (Table 3). The trees sampled in Colombia showed higher growth rates than those sampled in Bolivia (3.64 vs. 1.34 mm), but the differences were not significant ($U = 2.5$, $p = 0.09$), and this difference was probably related to the shorter (younger age) timespans of Colombian trees. Within sites, we found few significant differences between species. In Colombia, *C. alliodora* showed higher growth rates than the other species, whereas *C. microchaete* was the fastest-growing species in Bolivia. The first-order autocorrelation (AR1) was lower in Colombian than in Bolivian species (0.23 vs. 0.40, $U = 0.1$, $p = 0.016$), whereas the mean sensitivity (MSx) was higher in Colombia than in Bolivia (0.55 vs. 0.45), but the differences were not significant ($U = 2.9$, $p = 0.11$).

Table 3. Statistics obtained in the analyses of ring-width measurements. “Corr” is the mean correlation of individual ring-width series with the site mean series (chronology). Values are means $\pm$ SD. Sample types are as follows: CO, cores; CS, cross-sections. Different letters indicate significant ($p < 0.05$) differences between species within the same site.

Site, Country	Species (Sample Type)	Timespan	No Series	Ring Width (mm)	AR1	MSx	Corr	Rbar
J.M. Céspedes-El Vínculo, Colombia	<i>C. alliodora</i> (CO)	1975–2009	32	4.80 $\pm$ 1.36 ^b	0.21 $\pm$ 0.14 ^a	0.63 $\pm$ 0.15 ^a	0.43	0.24
	<i>C. cinerea</i> (CO)	1976–2009	38	3.43 $\pm$ 1.23 ^a	0.20 $\pm$ 0.12 ^a	0.65 $\pm$ 0.10 ^a	0.53	0.33
	<i>P. dulce</i> (CO)	1971–2009	36	3.57 $\pm$ 1.04 ^a	0.25 $\pm$ 0.18 ^a	0.48 $\pm$ 0.09 ^a	0.42	0.22
	<i>S. spectabilis</i> (CO)	1977–2009	48	3.12 $\pm$ 0.75 ^a	0.23 $\pm$ 0.15 ^a	0.51 $\pm$ 0.13 ^a	0.42	0.19
	<i>Z. rhoifolium</i> (CO)	1970–2009	38	3.27 $\pm$ 1.12 ^a	0.24 $\pm$ 0.16 ^a	0.50 $\pm$ 0.09 ^a	0.38	0.20
Arenillas, Ecuador	<i>B. graveolens</i> (CO)	1965–2014	15	2.89 $\pm$ 0.66	0.31 $\pm$ 0.19	0.52 $\pm$ 0.09	0.37	0.23
	<i>C. microchaete</i> (CS)	1941–2010	26	1.72 $\pm$ 0.44 ^b	0.34 $\pm$ 0.18 ^a	0.37 $\pm$ 0.07 ^a	0.31	0.29
INPA, Bolivia	<i>A. tomentosum</i> (CS)	1936–2011	38	0.96 $\pm$ 0.20 ^a	0.37 $\pm$ 0.19 ^a	0.42 $\pm$ 0.06 ^a	0.30	0.22
	Bignoniaceae # (CS)	1984–2011	26	0.84 $\pm$ 0.21 ^a	0.45 $\pm$ 0.13 ^a	0.47 $\pm$ 0.11 ^a	0.45	0.28
	Combretaceae # (CS)	1982–2011	34	0.90 $\pm$ 0.24 ^a	0.44 $\pm$ 0.17 ^a	0.53 $\pm$ 0.11 ^b	0.48	0.21

Liana species.

The mean correlations of individual ring-width series with the site mean series (variable “Corr” in Table 3) were slightly higher in Colombia (0.44) than in Bolivia (0.39) and Ecuador (0.37). The highest correlation values corresponded to the two liana species from

Bolivia, followed by *C. alliodora*, *P. dulce*, and *S. spectabilis* from Colombia. The R_{bar} values were quite similar between species and sites, with an overall average value of 0.24 and a maximum value of 0.33 for *C. cinerea* from Colombia, followed by *C. microchaete* and the Bignoniaceae liana species from Bolivia.

The BAI series of Colombian tree species showed rising trends corresponding to young trees of secondary forests (Figure 2). The highest and lowest BAI values corresponded to *C. alliodora* and *C. cinerea*, respectively.

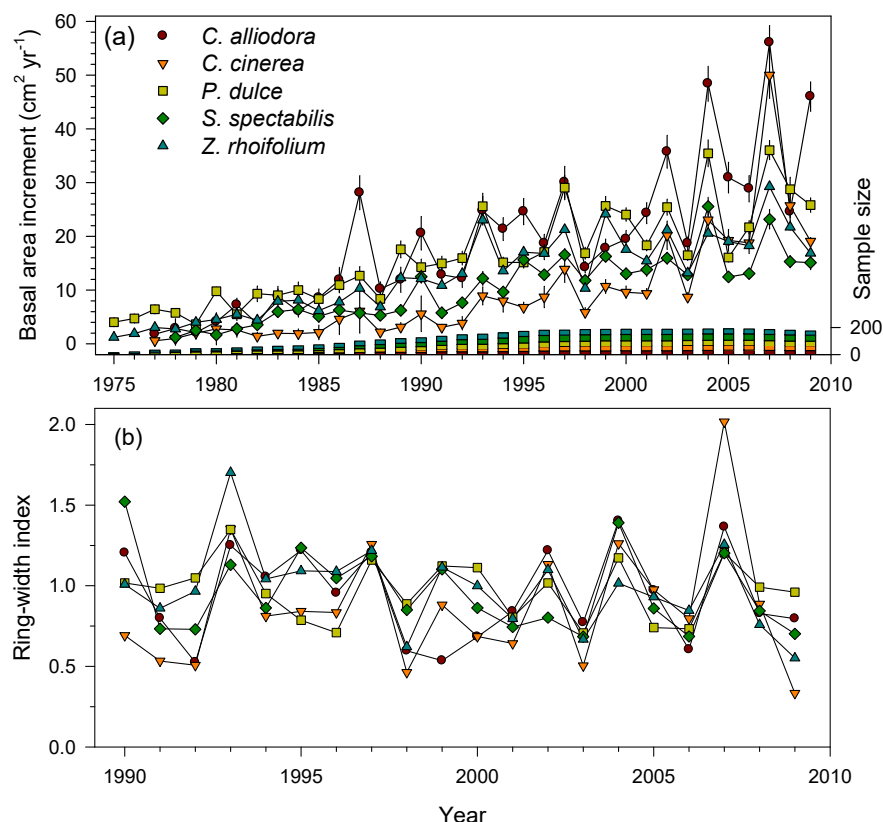


Figure 2. Mean series of basal area increment (BAI) (a) and ring-width indices (b) (best-replicated period) for each tree species measured in the Colombian TDF. In plot (a), bars show the number of samples measured each year (right y axis). BAI values are means $\pm$ SE.

In the PCA based on the series of ring-width indices of Colombian species, the first (PC1) and second (PC2) components of the PCA accounted for 71.9% and 11.3% of the common variance, respectively. The species with the highest PC1 and PC2 loadings were *C. cinerea* and *S. spectabilis*, respectively. This indicated that the sampled species showed high year-to-year growth coherence (Figure 2) as correlations confirmed (Table 4). These analyses showed that the *C. cinerea* chronology was strongly related to the chronologies of *C. alliodora* and *Z. rhoifolium*, whereas the *P. dulce* chronology showed the lowest correlation (the only one that was not significant) with *C. alliodora* growth indices.

The BAI series of *B. graveolens* sampled in Ecuador also showed the ascending phase typical of young trees, with a high year-to-year growth variability (Figure 3).

The BAI series of the tree species sampled in the Bolivian TDF showed stable phases corresponding to mature trees (Figure 4). In this case, *C. microchaete* showed a higher growth rate than *A. tomentosum* (Table 3). During the period with the highest replication for tree and liana species, common and coherent growth patterns were observed (e.g., low growth indices in 2004), indicating similar responses to climate variability.

Table 4. Pearson correlations calculated between the species' chronologies (mean series of ring-width indices) of the tree species sampled in the Colombian TDF considering the best-replicated period (1990–2009). Correlation coefficients are values below the diagonal, and significance levels are values above the diagonal.

	<i>C. alliodora</i>	<i>C. cinerea</i>	<i>P. dulce</i>	<i>S. spectabilis</i>	<i>Z. rhoifolium</i>
<i>C. alliodora</i>		0.001	0.119	0.001	0.008
<i>C. cinerea</i>	0.711		0.015	0.016	0.001
<i>P. dulce</i>	0.360	0.534		0.049	0.004
<i>S. spectabilis</i>	0.687	0.529	0.445		0.010
<i>Z. rhoifolium</i>	0.573	0.712	0.617	0.559	

In the PCA based on the series of ring-width indices of Bolivian species, the first (PC1) and second (PC2) components of the PCA accounted for 66.0% and 20.0% of the common variance, respectively. The species with the highest PC1 and PC2 loadings were the Bignoniaceae liana and *A. tomentosum*, respectively. Correlations showed that the two tree species shared a common inter-annual growth pattern, whereas the liana species shared a different pattern, which was more similar to that of *A. tomentosum* (Table 5).

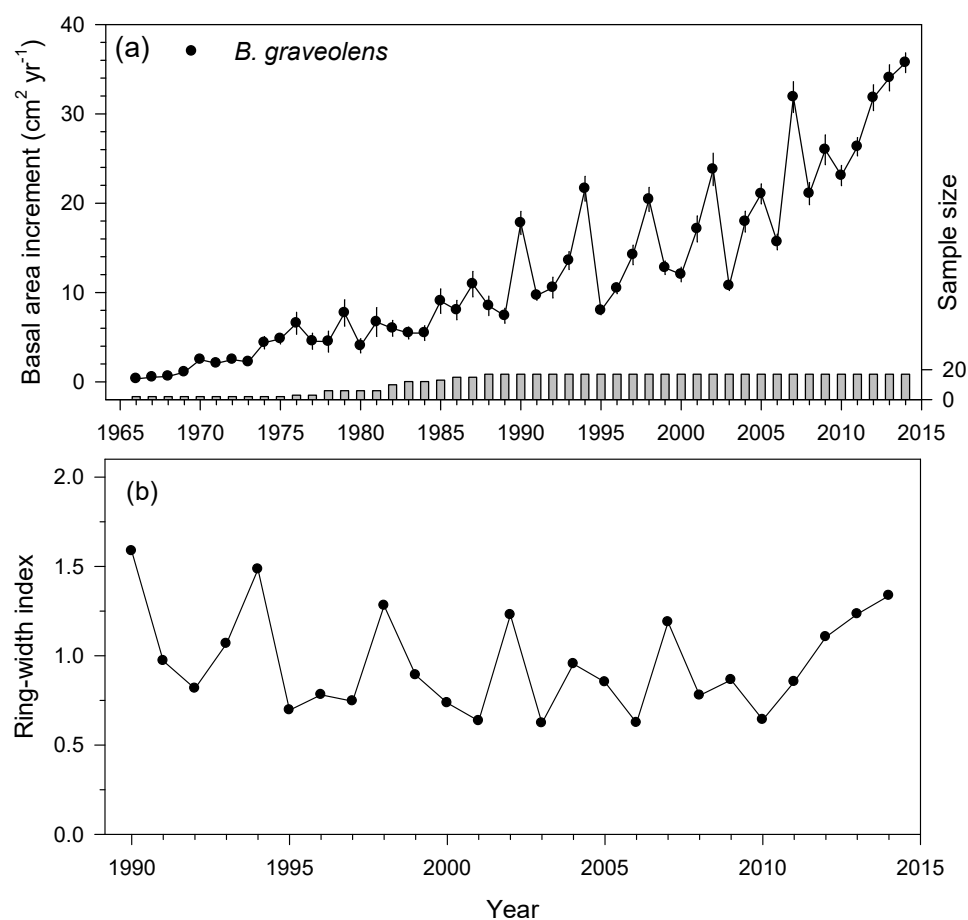


Figure 3. Mean series of basal area increment (BAI) (a) and ring-width indices (b) for the tree species measured in the Ecuadorian TDF. In plot (a), bars show the number of samples measured each year (right y axis). BAI values are means $\pm$ SE.

Table 5. Pearson correlations calculated between the species' chronologies (mean series of ring-width indices) of the tree and liana species sampled in the Bolivian TDF considering the best-replicated period (1987–2010). Correlation coefficients are values below the diagonal, and significance levels are values above the diagonal.

	<i>C. microchaete</i>	<i>A. tomentosum</i>	Bignoniaceae	Combretaceae
<i>C. microchaete</i>		0.000	0.454	0.275
<i>A. tomentosum</i>	0.716		0.079	0.045
Bignoniaceae	0.160	0.365		0.000
Combretaceae	0.232	0.413	0.687	

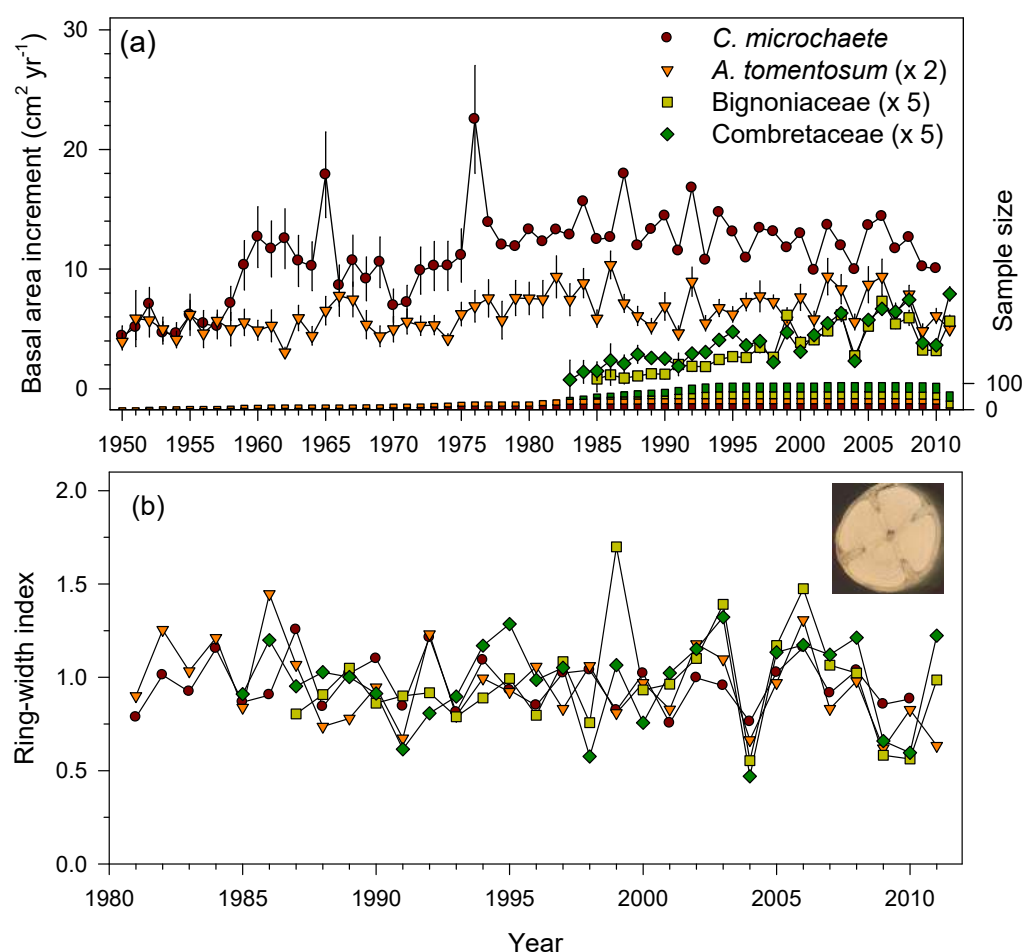


Figure 4. Mean series of basal area increment (BAI) (a) and ring-width indices (b) for the tree and liana species measured in the Bolivian TDF. In plot (a), bars show the number of samples measured each year (right y axis). BAI values are means $\pm$ SE. Some series were multiplied by 2 ($\times 2$, *A. tomentosum*) or by 5 ($\times 5$, liana species) to improve visibility. In plot (b), the image shows a liana cross-section.

3.3. Relationships Between Growth Indices and Climate

In the species from the Colombian TDF, growth was enhanced by low maximum temperatures combined with high minimum temperatures in the previous July (*C. cinerea* and *P. dulce*), warm conditions in the current July (*C. alliodora*), and high April precipitation (*C. cinerea*) (Figure 5).

In the case of the tree species studied in Ecuador, elevated precipitation from December to January significantly increased growth (Figure 6).

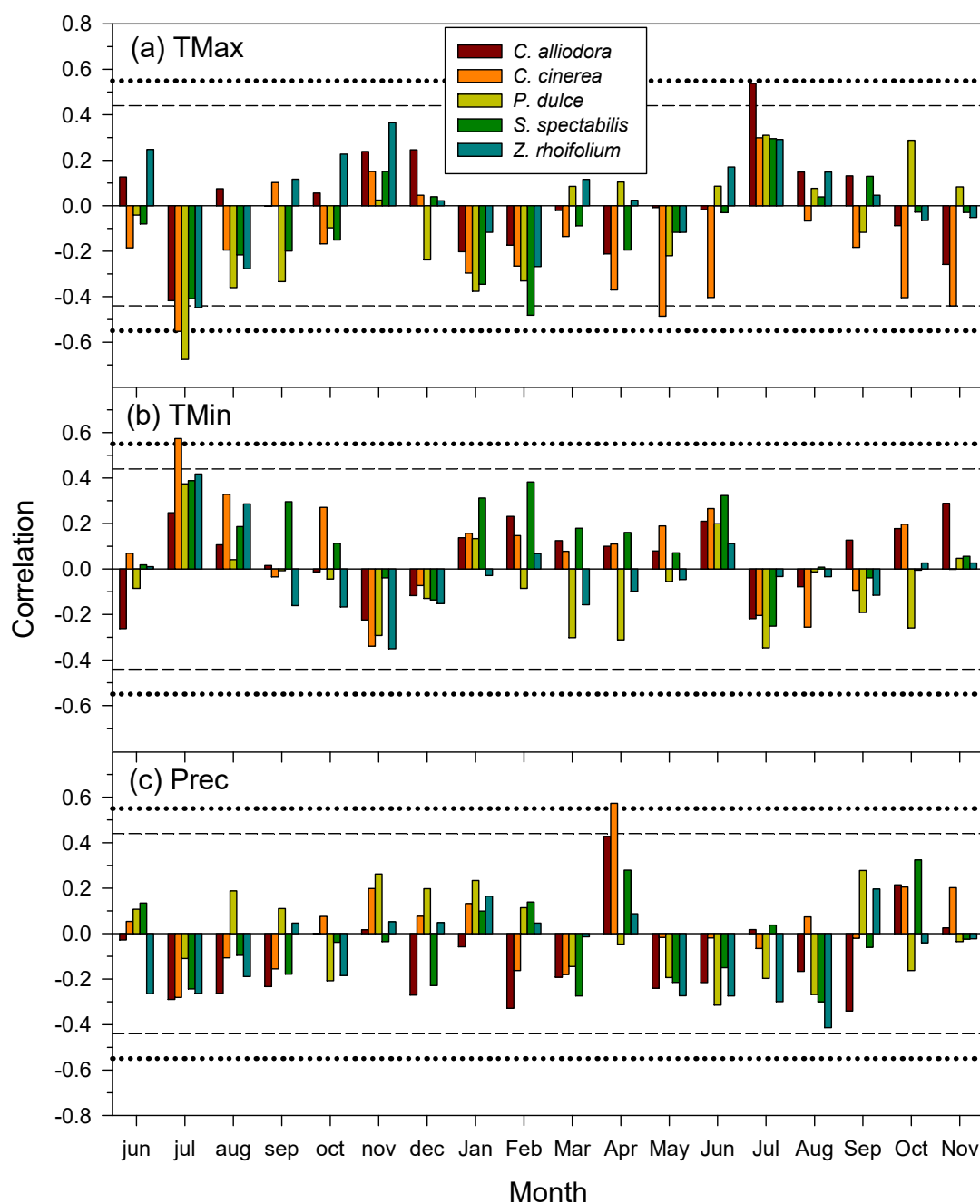


Figure 5. Climate–growth relationships calculated for the tree species measured in the Colombian TDF. The bars are Pearson correlations computed by relating the species’ series of ring-width indices with monthly climate variables ((a) TMax, mean maximum temperature; (b) TMin, mean minimum temperature; and (c) Prec, total precipitation). Correlations were calculated from the previous (months abbreviated by lowercase letters) to the current (months abbreviated by uppercase letters) year. Dashed and dotted horizontal lines indicate the 0.05 and 0.01 significance levels, respectively.

Finally, in the tree and liana species sampled in the Bolivian TDF, growth increased in response to cool and wet conditions during the growing season in October and November in the case of *C. microchaete*, *A. tomentosum*, and the Bignoniaceae liana species (Figure 7). Cool wet conditions in the previous January also enhanced the growth of these species. Low minimum temperatures in June improved the growth of the Bignoniaceae liana species.

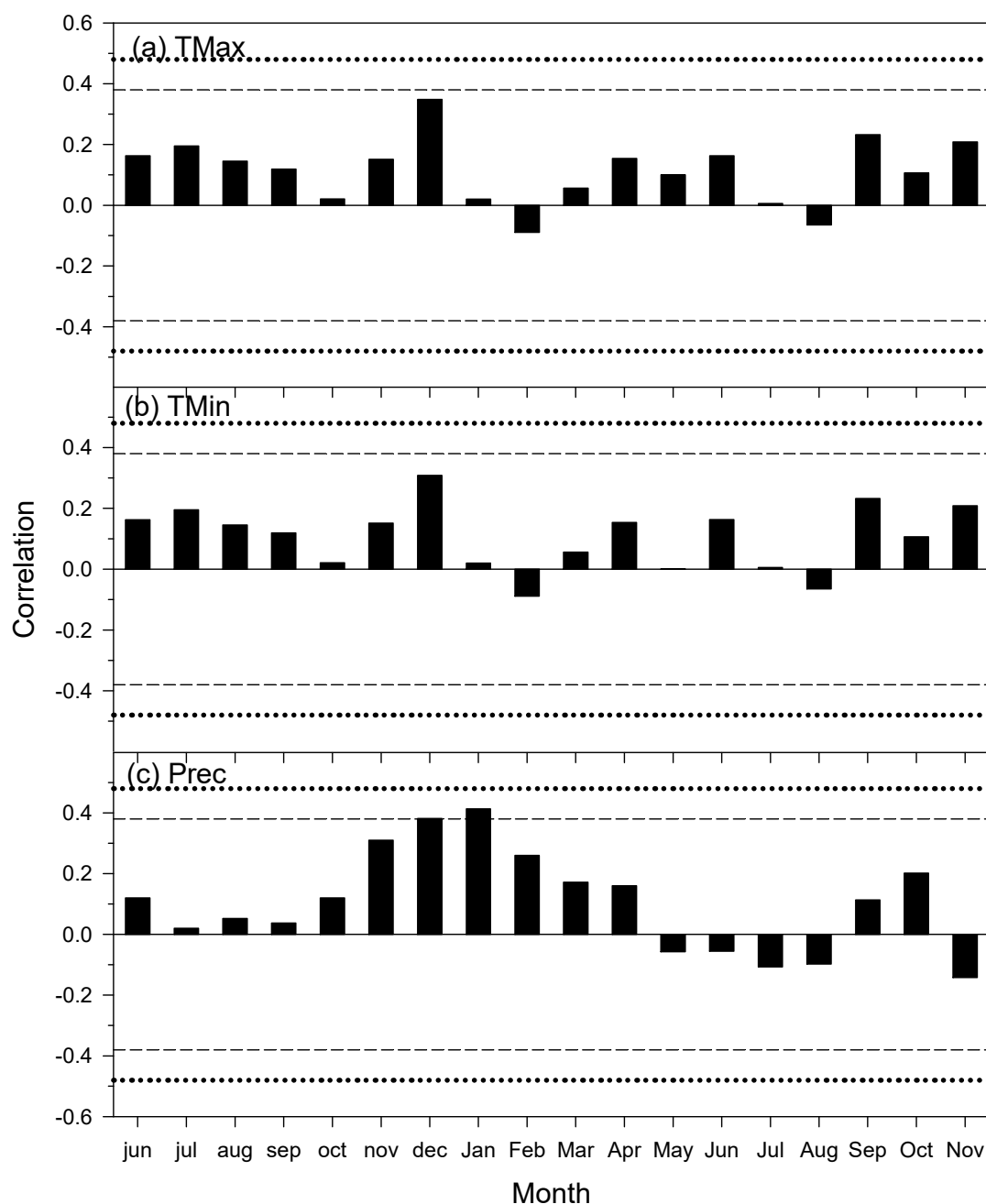


Figure 6. Climate–growth relationships calculated for the tree species measured in the Ecuadorian TDF. The bars are Pearson correlations computed by relating the species’ series of ring-width indices with monthly climate variables ((a) TMax, mean maximum temperature; (b) TMin, mean minimum temperature; (c) Prec, total precipitation). Correlations were calculated from the previous (months abbreviated by lowercase letters) to the current (months abbreviated by uppercase letters) year. Dashed and dotted horizontal lines indicate the 0.05 and 0.01 significance levels, respectively.

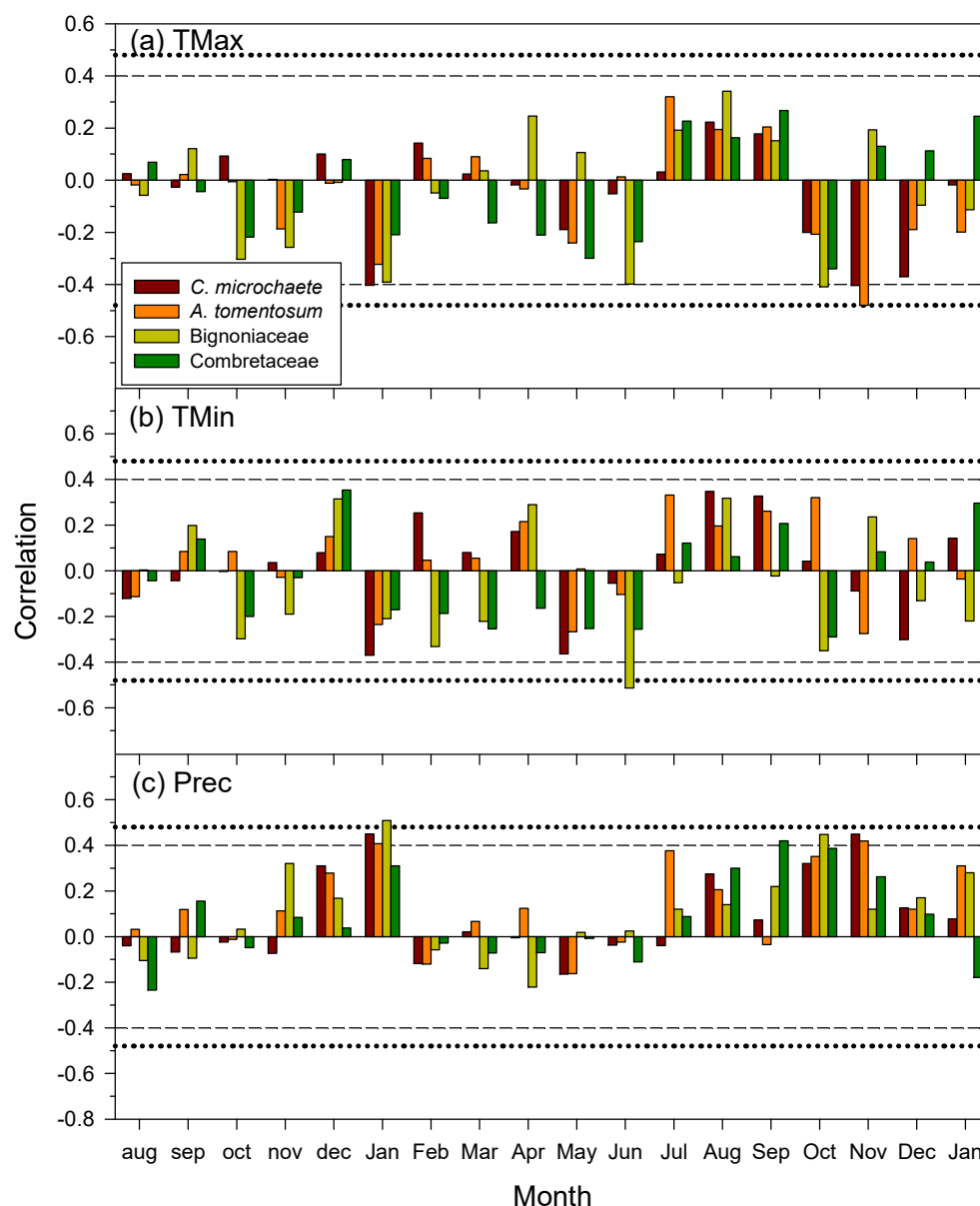


Figure 7. Climate–growth relationships calculated for the two tree and two liana species measured in the Bolivian TDF. The bars are Pearson correlations computed by relating the species’ series of ring-width indices with monthly climate variables ((a) TMax, mean maximum temperature; (b) TMin, mean minimum temperature; (c) Prec, total precipitation). Correlations were calculated from the previous (months abbreviated by lowercase letters) to the current (months abbreviated by uppercase letters) year. Dashed and dotted horizontal lines indicate the 0.05 and 0.01 significance levels, respectively.

3.4. Relationships Between Growth and Teleconnection Indices

Regarding correlations between growth indices and ENSO-related climate indices (SOI, El Niño 3.4, and PDO), we found a positive correlation between the PDO of the previous February and the *C. cinerea* growth indices ($r = 0.59$, $p = 0.006$) and between the PDO of the current August and *Z. rhoifolium* growth indices ($r = 0.50$, $p = 0.015$) in the case of Colombian species. In contrast, the SOI and *Z. rhoifolium* growth indices showed a negative correlation ($r = -0.46$, $p = 0.028$). In Ecuador, the SOI in March showed a negative correlation with *B. graveolens* growth indices ($r = -0.40$, $p = 0.040$), whereas the El Niño 3.4 in May showed a positive but not significant correlation ($r = 0.33$, $p = 0.090$). In the case of Bolivian tree and liana species, a negative correlation was found with prior December SOI ($r = -0.41$, $p = 0.023$) and a positive correlation with January PDO in the case of *A.*

tomentosum ($r = 0.62$, $p = 0.0002$; Figure 8). In the Bignoniaceae liana species, a positive correlation with January SOI was found ($r = 0.47$, $p = 0.010$), while in the Combretaceae liana species, positive correlations were found with the January ($r = 0.44$, $p = 0.027$) and March ($r = 0.43$, $p = 0.029$) SOI series.

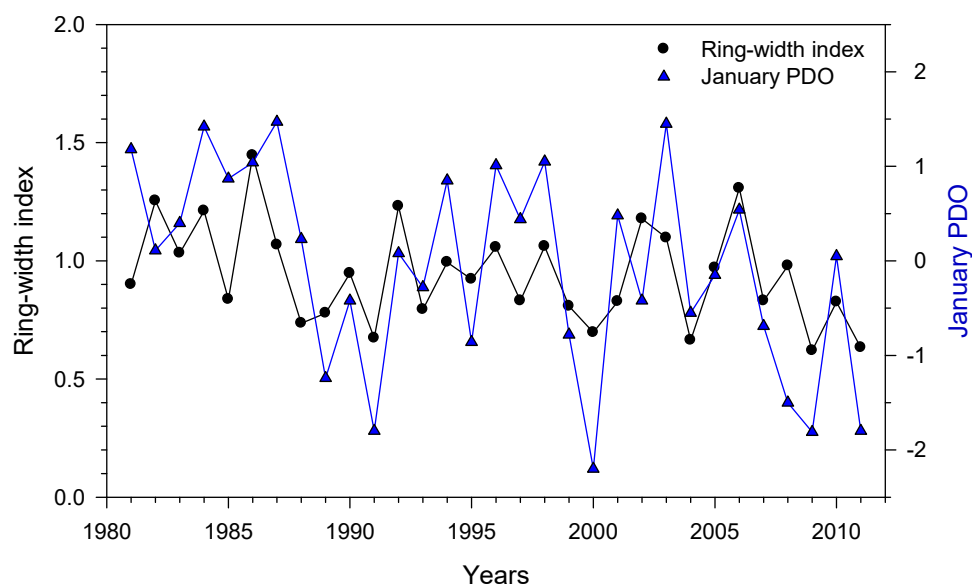


Figure 8. Positive correlation found between January PDO and growth indices of *A. tomentosum* trees sampled in the Bolivian TDF.

4. Discussion

We examined 22 tree species and 2 liana species from Neotropical dry forests and determined that at least 14 tree species and the 2 liana species showed good dendrochronological potential. In addition, two liana species were shown to present datable ring series and showed dendrochronological potential in the study of the Bolivian TDF. Our findings supported the main hypothesis that growth was mainly driven by seasonal water availability, particularly in the driest TDF from Ecuador, although precipitation signals were also evident in the ring series of some Bolivian species (*C. microchaete*, *A. tomentosum*, and the Bignoniaceae liana species).

Overall, our findings concurred with previous studies on the same sites and species but also with pantropical tree-ring studies [2,7]. First, we confirmed that seasonality contributed to the formation of apparently annual rings, as has been shown in tree [3–9] and liana [32–34] species. Most species presented distinct boundaries formed by marginal parenchyma bands, and only two of them showed semi-ring porous wood, in agreement with previous studies [8]. In the Colombian TDF, 11 out of the 19 tree species examined presented distinct ring boundaries in inner and outer parts of wood samples. This finding stressed the importance of careful species selection in dendrochronological studies. In studies on TDFs from Mexico and Amazonia, about 35%–40% of the examined species presented rings and showed dendrochronological potential [8,18,55,56]. Several factors explain tree-ring formation in TDF species including climate seasonality, functional traits, phenology, and phylogeny [8]. For instance, tree species of the Fabaceae, Meliaceae, and Boraginaceae families tend to form distinct annual rings in American TDFs [18,19,27–31]. In addition to ring-limit identification inferred from wood anatomy inspection, a careful validation of annual periodicity of rings should be performed using complementary approaches including the following: xylogensis and phenology [12,13], dendrometer data [23–26,57], periodic cambial wounding [58], high-precision ^{14}C measurements [15,59], or counting rings in trees from known ages such as those from plantations [60].

The growth patterns corresponded to very different tree ages and stand structures with rapidly ascending BAI curves in the secondary Colombian and Ecuadorian TDFs dominated by young trees and more stable BAI curves in the case of older trees of sustainably exploited timber tree species in the Bolivian TDF. Long-term climate trends leading to higher water availability and increased atmospheric CO₂ concentrations could also explain the growth increase observed in the tree species sampled in Colombian and Ecuadorian TDFs [4,7], albeit this should be better assessed measuring long-term changes in wood C and O isotope composition. The role played by different stand structures should be also considered in future studies, given that tree species from TDFs show diverse shade- and drought-tolerance strategies (e.g., facultative to obligate deciduousness, sapwood water storage, and rooting depth), which may be modulated by stand structure [61–64].

In the case of growth variability, Colombian species showed a higher year-to-year coherence (higher variance explained by PC1) than Bolivian species. This may be explained by the older trees sampled in Bolivia or by the comparison of different growth forms (tree vs. liana species) in this case. Nevertheless, the correlations between indexed ring-width series indicate a reliable cross-dating in most of the studied species. In liana species, ring distinctiveness is improved by the presence of several wood anatomical markers, such as the presence of marginal parenchyma and ring- to semi-ring porosity [32]. This was the case of the study of Bolivian liana species, suggesting they form annual, datable rings.

Regarding the climate–growth correlations, our analyses concurred with previous research carried out in similar TDFs from Colombia [65], Ecuador [35,40,41,66–68], and Bolivia [29–31,69–71]. In general, wet conditions improved radial growth, whereas warm, dry conditions constrained it. These effects were evident during the growing season in the case of the Bolivian tree species, particularly during the onset of the rainy season (October to January), as was found for *Amburana cearensis* in seasonally dry TDFs [71]. In addition, wet conditions during the prior growing season were also important for the growth of some Bolivian tree (*C. microchaete*) and liana (Bignoniaceae) species. This was also observed in the same study site [31]. Site conditions could also enhance these responses as found in Brazilian TDFs, where the most responsive *A. cearensis* individuals were growing in sites with shallow and dry soils [72]. Moreover, our findings reinforced the results of previous studies showing the dendrochronological potential of liana species in TDFs [34,73]. It seems that liana radial growth positively responded to precipitation during the early rainy season, which may be explained by their growth habit and their large xylem vessels providing high hydraulic conductivity [74]. This response was stronger for the Bignoniaceae than for the Combretaceae species, highlighting individualistic growth responses to climate variability [75]. Such individualistic responses of sympatric tree or liana species may contribute to their coexistence through temporal segregation of the climate windows for radial growth. In addition, these individualistic responses may reflect different functional traits of the compared species (e.g., leaf and shoot phenology, rooting depth, hydraulic conductivity, sapwood capacitance, soil water uptake, etc.).

The ENSO has clear implications for South American climate conditions. In general, a negative correlation between the SOI and November–December rainfall over most of southern America was found by previous studies [76]. During negative SOI phases (“El Niño” events), there is an increase in precipitation in Ecuador, Bolivia, southern Brazil, and Peru, whereas positive SOI phases (“La Niña” events) have been linked to droughts across Colombia and Argentina and wetter conditions during the austral summer (from December to February) [77]. In the Bolivian lowlands, high PDO values are associated with wetter conditions [78]. These atmospheric circulation patterns and their related precipitation regimes were recorded by some of the study species but with different intensities. In particular, *C. cinerea* in Colombia responded to the PDO, whereas *B. graveolens* in Ecuador

and the Bignoniaceae liana species in Bolivia showed strong responses to the SOI. Again, a careful selection of sensitive species with long lifespans forming annual rings and suitable sites is recommended if the aim is to reconstruct ENSO variability. The complex topography of many TDF sites may distort or reverse ENSO impacts on local climate variability posing additional difficulties to develop ENSO-sensitive ring-width chronologies.

We identified at least four sources of limitations in our study. First, the cross-dating should be further checked using complementary methods indicated previously to check the annual periodicity of rings (records of aboveground phenology, xylogenesis, and dendrometers). Second, given that many tropical tree species tend to form wedging rings or present missing rings, the complementary study of cross-sections and cores is also highly recommended. Third, these results must be taken with caution given the limitations imposed by using short and heterogeneous local climate records of many tropical areas, which often lack data of relevant drivers (solar radiation, soil moisture, evaporation). Nonetheless, the use of gridded climate datasets is widespread and allows partially solving this shortcoming at regional to global scales (e.g., [7]). However, local climate records should be used in mountain areas (e.g., Colombian TDFs located in inter-Andean valleys) where gridded datasets cannot substitute them. Fourth, stand variables related to tree-to-tree competition could be considered in future studies to quantify the amount of growth variability they account for.

5. Conclusions

A careful selection of woody plant species is recommended when performing dendroecological studies in seasonal TDFs to detect those forming distinct annual rings. In the Colombian TDF, 11 out of the 19 examined tree species presented distinct ring boundaries in inner and outer parts of the wood samples. The three tree species sampled in the Ecuadorian and Bolivian TDFs also showed dendrochronological potential. The mean ring widths were 2.97 mm and 0.87 mm in tree and liana species, respectively. Wet conditions during the current and prior growing seasons enhanced radial growth of trees and lianas. Species coexisting in the same TDF showed coherent growth patterns but also presented individualistic responses to climate variability. Lastly, two liana species showed dendrochronological potential, and their growth series could be compared with coexisting trees in TDFs.

Author Contributions: Conceptualization, J.J.C. and C.V.; methodology, J.J.C. and C.V.; software, J.J.C. and C.V.; validation, J.J.C.; formal analysis, J.J.C.; investigation, J.J.C. and C.V.; resources, J.J.C. and C.V.; data curation, J.J.C. and C.V.; writing—original draft preparation, J.J.C.; writing—review and editing, J.J.C. and C.V.; visualization, J.J.C. and C.V.; supervision, J.J.C.; project administration, J.J.C.; funding acquisition, J.J.C. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by a BBVA-foundation project (Análisis retrospectivos mediante dendrocronología para profundizar en la ecología y mejorar la gestión de los bosques tropicales secos -DENTROPICAS) and by the Spanish Ministries of Foreign Affairs (“Regeneración, crecimiento y modelos dinámicos de bosques tropicales secos: herramientas para su conservación y para el uso sostenible de especies maderables”, ref. AECID 11-CAP2-1730) and Science and Innovation (grants PID2021-123675OB-C43 and TED2021-129770B-C21).

Data Availability Statement: The dataset is available on reasonable request from the authors.

Acknowledgments: We thank H.A. Mendiavelso, C.I. Espinosa, M. Toledo, Vincent Voos, W. Devia, A. Castaño-Naranjo, and R. Corria for their help during field sampling and to get sampling permissions. We thank Carme Pedrol for organizing the analysed samples. We also thank the personnel of the “Juan María Céspedes” botanical garden (INCIVA, Tuluá, Colombia), Reserva ecológica “Arenillas” (Ecuador), Instituto Boliviano de Investigación Forestal, and P. Roosenboom (INPA, Bolivia).

Conflicts of Interest: The authors declare no conflicts of interest.

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