

Identifying the impact of climate extremes on radial growth in young tropical trees: A comparison of inventory and tree-ring based estimates

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Viktoria Dietrich, Georgios Skiadaresis, Florian Schnabel, J. M. Leban, Catherine Potvin, et al.. Identifying the impact of climate extremes on radial growth in young tropical trees: A comparison of inventory and tree-ring based estimates. Dendrochronologia, 2024, 86, pp.126237. ⟨10.1016/j.dendro.2024.126237⟩. ⟨hal-04676020⟩

HAL Id: hal-04676020

https://hal.inrae.fr/hal-04676020v1

Submitted on 23 Aug 2024

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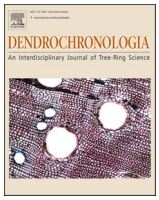
Dendrochronologia 86 (2024) 126237



Contents lists available at ScienceDirect

Dendrochronologia

journal homepage: www.elsevier.com/locate/dendro



Original article



Identifying the impact of climate extremes on radial growth in young tropical trees: A comparison of inventory and tree-ring based estimates

Viktoria Dietrich [a,b,1,*], Georgios Skiadaresis [a,2], Florian Schnabel [a,c,3], Jean-Michel Leban [d,4], Catherine Potvin [e,f,5], Jürgen Bauhus [a,6], Julia Annick Schwarz [a,g,7]

[a] Chair of Silviculture, Faculty of Environment and Natural Resources, University of Freiburg, Germany
[b] Chair of Applied Vegetation Ecology, Faculty of Environment and Natural Resources, University of Freiburg, Germany
[c] Systematic Botany and Functional Biodiversity, University of Leipzig, Leipzig, Germany
[d] French National Institute for Agriculture, Food, and Environment (INRAE), France
[e] Department of Biology, McGill University, Montreal, Quebec, Canada
[f] Smithsonian Tropical Research Institute, Panama City, Panama
[g] Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland

ARTICLE INFO

Keywords:
Tree-rings
Dendrochronology
Dendroecology
Juvenile trees
Tropical forest
Climate change

ABSTRACT

The loss of tropical forest resilience has been linked to increased climate variability and associated droughts, but the response of tropical trees to climate extremes remains poorly understood. This limits our ability to design effective forest adaptation strategies in the tropics. Here we analyse the potential of using young trees to analyse climate variability and extremes, which opens new avenues given the increasing area of secondary forests and tree plantations. We used annual tree diameter measurements and stem discs from 139 16-year-old trees belonging to five native species planted in the Sardinilla tree diversity experiment in Panama and compared three methods to determine annual radial growth. Employing inventory measurements, visual stem disc analysis, and wood density measurements, series of radial growth were calculated to compare relative growth during wet and dry extreme events, and to compute continuous climate-growth correlations. Our results show that annual radial growth data derived from wood density profiles are best suited for climate-growth relationships, as they could capture a common growth signal within the high intraspecific variability of young trees to seasonal climatic variables. Annual radial growth data derived visually and from inventories are still useful for quantifying growth responses during extreme drought. The highest similarity among methods to determine annual radial growth, combined with the strongest climate-growth relationships, were found for *Cedrela odorata*, a species that shows a pronounced decrease in water use and cambial dormancy during the dry season. Stem discs from young trees planted in tropical forest plantations may thus offer a suitable source for dendroecological analyses.

1. Introduction

Regional climate in the tropics is differentially affected by climate change, and obervations range from an increase in extreme events including both intensive rainfall associated with flooding as well as droughts in the Amazon (Gloor et al., 2013; Boisier et al., 2015; Duffy et al., 2015) to an overall decrease in precipitation in the area affected by the North American monsoon (Pascale et al., 2019). Although little is known about the response of tropical tree species to changes in rainfall regimes, reduced precipitation and increased temperatures in the dry

* Correspondence to: Chair of Silviculture, University of Freiburg, Stefan-Meier Str. 76, Freiburg im Breisgau D-79104, Germany.
E-mail address: viktoria.dietrich@ecology.uni-freiburg.de (V. Dietrich).
[1] https://orcid.org/0000-0003-1545-2459
[2] https://orcid.org/0000-0002-2385-0476
[3] https://orcid.org/0000-0001-8452-4001
[4] https://orcid.org/0000-0002-8998-6472
[5] https://orcid.org/0000-0002-5640-9329
[6] https://orcid.org/0000-0002-9673-4986
[7] https://orcid.org/0000-0003-2610-3588

https://doi.org/10.1016/j.dendro.2024.126237
Received 14 February 2024; Received in revised form 3 July 2024; Accepted 8 July 2024
Available online 14 July 2024
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season are known to lead to reductions in woody biomass production in the following wet season (Zuidema et al., 2022). In addition, tree responses to seasonally dry climates are amplified in regions that are drier, hotter, and more climatically variable (Fontes et al., 2018; Zuidema et al., 2022). Furthermore, drought was found to be a key driver of increasing mortality rates in moist tropical forests (McDowell et al., 2018). Based on remotely sensed vegetation indices for major forest biomes including the tropics, a recent global analysis reported significant declines in forest resilience attributing it to increased water limitations and climate variability (Forzieri et al., 2022). Yet more information is needed to identify forest responses to climate extremes and to develop effective adaptation strategies to future global changes (Corlett, 2011), especially for young tropical trees as secondary forests and plantation forests increase in area (Dockendorff et al., 2022). Several methods based on annually resolved data are potentially suitable for analysing tree performance in response to past climate extremes, which can be used to assess and predict forest responses to climate change.

Commonly, tree performance is derived from radial growth series, that can for example be calculated from forest inventories based on annual recurring measurements of diameter at breast height (DBH) (Blundo et al., 2021). This method has been successfully applied to analyse tree productivity responses to climatic extremes in a young mixed-species plantation (e.g. Schnabel et al., 2019). However, it requires annual inventory data sets, which are available almost exclusively in experimental settings due to high labour demands. In addition, the suitability of this type of datasets for climate-growth analyses depends on the overall quality of the DBH inventories. Frequent changes of personal conducting the inventories and inconsistent measurement locations on the stem are common sources for potentially large measurement errors. Where the radial growth rates are low, the measurement errors may easily exceed the annual radial growth.

Alternatively, tree-rings are known to be a reliable archive of growth responses to climate variability for a large number of tree species across all forest biomes including tropical ones (e.g. Schöngart et al., 2017; Brienen et al., 2016; Worbes, 2002). Several studies in the tropics have successfully correlated growth series based on visually detected tree-ring widths to climatic data (Stahle, 1999; Worbes, 1999; Brienen and Zuidema, 2005; Schöngart et al., 2006; Soliz-Gamboa et al., 2011, Aragão et al., 2019; Zuidema et al., 2022), and to a lesser extent also with other forest stand characteristics such as soil water capacity and species identity (López et al., 2019; Aragão et al., 2022). Although not all studies could confirm the annual nature of tree-rings in tropical species (Worbes, 1999; Brienen and Zuidema, 2005; Dünisch et al., 2003), it is now acknowledged that distinct annual growth rings are commonly formed by tree species growing in tropical regions that exhibit a distinct dry season (Brienen et al., 2009; Borchert, 1999; Aragão et al., 2019). For example, for *Cedrela odorata*, one of the most intensively studied tree species in tropical dendro-ecology, two months with total rainfall below 50 mm are sufficient to cause strongly reduced growth rates or even complete cambial dormancy (Worbes, 1999). Therefore, many tree species in tropical regions with a distinct dry period are particularly suitable for dendroecological analyses.

A third way to produce annually resolved growth series that may be used for determining tree responses to climatic variability is the analysis of radial variation in wood density at the annual or intra-annual tree-ring level using micro densitometry (Jacquin et al., 2017). This method is normally used either for ringless species or to facilitate identification of unclear tree-ring boundaries (Quintilhan et al., 2021; Rodriguez et al., 2022). The different types of wood formed during wet and dry periods are characterized by differences in vessel size and related wood anatomical properties leading to intra- and inter-annual differences in wood density (Domec, Gartner, 2003). Wood density is also sensitive to environmental variability, such as temperature fluctuations (Camarero et al., 2014; Zeller et al., 2017). Several studies found density related variables to be good indicators of extreme climate events (Rozenberg et al., 2002; Martinez-Meier et al., 2008; Zeller et al., 2017), sometimes exhibiting even stronger responses to climate than ring width (Camarero et al., 2014; Toïgo et al., 2015). In addition to growth rates and tree size, wood density is also related to a tree's hydraulic properties and drought tolerance (Hoeber et al., 2014; Poorter et al., 2019) by reflecting changes in cell division due to soil water deficit or reduced precipitation (Bouriaud et al., 2005). Therefore, wood density data contain additional information compared to traditional analyses of annual ring widths (Polge, 1967). Radial density profiles can be used to derive annually resolved ring width series, but to our knowledge no study has yet compared the suitability of density vs. visually and from inventory derived tree-ring and radial growth series when determining drought responses of trees.

Long series of tree performance are usually obtained from mature trees. However, tree-ring series of juvenile trees have also been successfully correlated with climate variables (Worbes, 1999; Brienen and Zuidema, 2005; Schöngart et al., 2006; Soliz-Gamboa et al., 2011). If data from young trees can be successfully used for assessing drought responses, this would permit the analyses of the impact of climatic extremes in large areas of the tropics and subtropics that are now covered by secondary forests and plantations (Chazdon, 2019). The increasing area of young secondary forests and tree plantations in the tropics (Dockendorff et al., 2022) could thus offer a unique opportunity to study the impact of climate variability on tree performance.

In this context, the overall aim of this study was to identify the most suitable method(s) to generate annually resolved series of radial growth for the purpose of assessing responses of young tropical trees to climatic variability with a focus on extreme events. We sampled tree disks from five tropical species growing in a planted tree diversity experiment in Panama to compare the suitability of three approaches to generate annual radial growth chronologies: DBH inventories, visual tree-ring analyses and density profiles (hereafter referred to as inventory, visual and density data). Although visual tree-ring analysis and wood density measurements are derived from similar procedures, both analyses were conducted independently in our study, allowing for an unbiased comparison of both approaches. For the species sampled, transpiration differs significantly between the wet and dry season for the majority of tree species (Kunert, 2016) and gross primary production of all five species declined slightly in the dry season compared to the wet season in Sardinilla (Kunert et al., 2019). Therefore, we expected that all five species exhibited visible differences in wood anatomical characteristics that lead to the formation of annual growth rings and addressed the following research questions, focusing on young tropical trees:

1. How comparable are the detected changes in annual radial growth due to climate extremes among the three methods: DBH inventories, visual tree-ring analyses, and density profiles?

2. Do radial growth series from all three methods capture climate-growth relationships?

2. Materials and methods

2.1. Study site and data collection

The Sardinilla planted forest was established in 2001 in Central Panama 9°19`N, 79°38`W in an area previously used as pasture (Scherer-Lorenzen et al., 2005). Tree seedlings were planted in monocultures and mixtures using six native species (*Anacardium excelsium*, *Cedrela odorata*, *Cordia alliodora*, *Hura crepitans*, *Luehea seemannii* and *Tabebuia rosea*), for more detail about the experiment see: (Scherer-Lorenzen et al., 2005; Potvin et al., 2009). In 2017, a destructive harvest of 167 trees for the five species growing in monocultures and mixture was carried out (Guillemot et al., 2020). Stem discs were obtained at breast height (1.3 m), except for *Cordia alliodora* because of its extensive dieback across the experiment (Potvin et al., 2008, 2009). Harvested stem discs allowed us to compare radial growth series derived from tree-level DBH-inventories and tree-ring based

variables identified visually or derived from wood density profiles.

Monthly temperature and precipitation data from 2001 to 2016 for our study site were obtained from the meteorological station in Barro Colorado Island (BCI) (Physical Monitoring Program of the Smithsonian Tropical Research Institute (STRI)), located at a distance of ca. 30 km from the Sardinilla experiment. The prevailing climate at the study site is characteristic for a moist tropical forest (Vitousek and Sanford, 1986) with average annual rainfall sums of 2665 mm and an average annual temperature of 26°C (in the period 2001–2016) including a pronounced dry season from January to the beginning of May.

2.2. Inventory data

The diameter at breast height (1.3 m, DBH) of all trees in the plantation above a total height of 2 m was measured once a year for each trunk during the dry season (January-March) starting in 2003. For our analysis, we used diameter measurements from 2006 onward as at this time 85 % of all trees in the plantation were at least 2 m of height (Schnabel et al., 2019), resulting in 11 years of continuous data available for all the samples. To allow for comparison with the data obtained from stem discs, annual measurements of the main trunk (in presence of multiple stems per tree) from all harvested trees were selected from the inventory data set. Subsequently, the selected DBH measurements were transformed into annual radial growth. Negative annual increments, likely due to measurement inaccuracies, were set to zero ring width, as is common practice. Annual radial growth values over 50 mm obtained from the inventory data were treated as measurement errors and were therefore excluded from the analysis because the maximum ring width obtained with the other two methods did not exceed 50 mm (max. visually derived data: 36.5 mm; max. density data: 39.0 mm; still allowing subsequently higher measurement values in the inventory dataset due to bark growth).

2.3. Visual tree-ring width characterization

All discs were sanded with increasingly finer sandpaper to a grain size of 120 μm. Subsequently, samples were scanned at high resolution of 1200 up to 2400 dpi (depending on disc size) using a flatbed scanner (EPSON Expression, 1640 XL, Model EU22). The scanning contrasts were increased manually for three species (*A. excelsium*, *H. crepitans*, *T. rosea*) to improve the visibility of ring limits (see also A.2, Figure A.1). For each tree, the visual identification of ring boundaries started with the examination of the anatomical characteristics, such as vessel size, wood colour or (alternation of) parenchyma bands, visible in recent years (near the bark; see also A.3, Table A.2), because of high variation of anatomical characteristics in the first years (Fritts, 2001). To assess the overall likelihood of the five tree species to form distinct annual rings, we used available information on several physiological characteristics from the existing literature (see also A.1, Table A.1). In addition, we compared the number of annual rings visible on the stem disc of each tree with the expected number of annual rings inferred from inventory data. After the identification of the ring limits, the ring width was measured using the WinDENDRO^{TM} software (Regent Instruments Canada Inc., Reg 2014a, Copyright 1989–2014) on four to six radii per disc depending on its circularity/ovality.

2.4. Wood density measurements

Measurements of wood density were conducted on the stem disks that were also used for the visual analysis of ring width, but at two randomly selected radii per disc. Wood density in tree-rings was determined by X-ray densitometry using an automated system (Decoux et al., 2004; Jacquin et al., 2017). Two 2.1 mm thick strips were cut from each disk in the radial plane using a twin blade saw. Following conditioning of the cut samples at a temperature of 20 °C and a relative air humidity of 60 %, X-ray CT scanning of the wood strips was performed at a resolution of one measurement each 20 microns in radial direction. This yielded high resolution density profiles that were used to identify ring limits using the software CERD (Mothe et al., 1998).

2.5. Dendrochronological analysis

Quality control, detrending and chronology development were performed using the dplR-package in R (Bunn, 2008). Each radial growth series per tree, method and species was averaged and detrended to remove age-related trends in tree growth using the regional curve standardization (RCS; Helama et al., 2017). A mean chronology per species and method was then developed, and we used the bi-weight robust mean to develop residual chronologies. Given the variability in short time series of young trees, we decided to use as the longest possible radial growth series of single trees to compute detrended chronologies.

Common dendrochronology descriptive statistics were calculated to assess the quality of the detrended chronologies separately for each species. The expressed population signal (EPS), which varies between zero and one, is used to assess how well a chronology represents a theoretically infinite population (Buras, 2017; Wigley et al., 1984). Commonly, EPS-values over the threshold 0.85 are considered to express common variation in the growth signal of the analysed tree population (Wigley et al., 1984). Lower EPS-values than 0.85 can still be referred to as approximate explanatory power (r^2) of a calculated chronology (Buras, 2017). In addition, the Rbar ($\bar{r}$) (average correlation between all series in a chronology) is used to quantify the signal strength (common variance) of each chronology. The signal-to-noise-ratio (SNR) is the ratio of desired information (signal) to unwanted information (noise) in tree-ring chronologies (Speer, 2010). The mean 'Gleichläufigkeit' (Glk, mean synchronicity) was calculated to assess the similarity of detrended growth series among trees for each species via computing all possible comparisons among individual radial growth series per species (Schweingruber, 1988; Eckstein and Bauch, 1969). These statistics (EPS, Rbar SNR, and Glk) were also computed as a first indication of whether detected tree-ring boundaries were formed annually (Soliz-Gamboa et al., 2011). To quantify the influence of growth in the year prior to ring formation, the first order autocorrelation (Ar1) was calculated (Fritts, 2001).

For each species and method, mean, median, and standard deviation of annual radial growth were calculated over the entire period of available radial growth data (maximum: 2001–2016). Finally, we computed Spearman correlation coefficients (r) between pairs of average radial growth series, determined using the three different methods, per species, to assess their similarity.

2.6. Extreme events

Based on BCI's precipitation and temperature data, we calculated the Standardized Precipitation Evapotranspiration Index (SPEI) for 2001–2016 (Vicente-Serrano et al., 2010). Monthly series of the SPEI index were calculated for different accumulation periods (1, 3, 6 and 12 months). The most extreme dry and wet years in our observation period were identified based on the annual values of SPEI 12 of December ($SPEI12_{Dec}$), which summarizes information on water availability throughout the year, as the rainy season runs from May to December (BCI, Physical Monitoring Program of STRI). The highest value of $SPEI12_{Dec}$ was observed in 2010, characterized by an exceptionally wet La Niña period, whereas the lowest $SPEI12_{Dec}$ value was observed in 2015 (Fig. 1), a year that was characterized by a strong and prolonged El Niño drought (Detto et al., 2018). To evaluate and compare the suitability of inventory, visual and density data for capturing growth responses during these climate extremes, radial growth in the respective extreme year (wet = 2010 and dry = 2015) was divided by the mean radial growth in the two years preceding the extreme year (hereafter called "relative growth"). The period of two years preceding the extreme event was used, as no other extreme event should be included in the

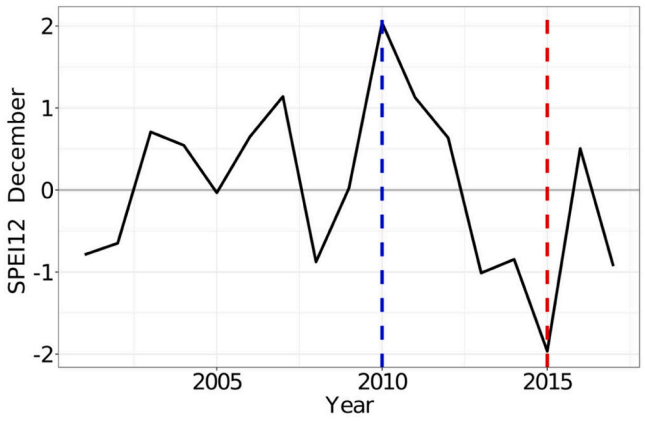


Fig. 1. Standardized precipitation index (SPEI) calculated over 12 months shown for December and therefore, representing annual climatic conditions, blue line: wet extreme, red line: dry extreme (BCI, Physical Monitoring Program of STRI).

recent estimate of average growth. Therefore, the year 2007, as another wet extreme event ($SPEI12_{Dec} > 1$, Fig. 1), limited the number of years before the extreme event in 2010 to two. Values of relative growth above and below one represent greater and lower growth, respectively, than the average growth observed in the two years before the extreme events. For each species, differences in relative growth among radial growth quantification methods were tested using the Wilcoxon-Rank-Sum-Test.

2.7. Climate-growth correlations

We compared correlation coefficients between the three species-specific (inventory, visual and density data) detrended chronologies and climate variables. Correlations between climatic parameters (monthly temperature, precipitation, SPEI 1, 3, 6 and 12) and detrended radial growth chronologies were computed using the *treeclim*-package in R-studio (Zang and Biondi, 2015). Correlation coefficients (Pearson`s *r*) were estimated using the 95 % quantile range method based on a standard bootstrapped procedure for significance testing. Climate-growth correlations were calculated over an 11-year period, as inventory data were available from 2006 onwards, resulting in an analysis period of 2006–2016. Therefore, standard bootstrapping had to be performed to compute confidence intervals, and climate growth correlations of no more than ten consecutive months could be computed at a time. We then ran the analysis separately with multiple periods of ten months and excluded the month with the least effect on radial growth across all three methods from the final analysis (January and February at the beginning of the dry season).

3. Results

3.1. Method comparison

Mean annual radial growth was comparable across all three methods for four tree species, but for *L. seemannii* we found differences of at least 1 mm among methods (Fig. 2). The median annual radial growth was lower than its mean across species and methods, with the inventory-derived radial growth showing the greatest deviation across species. In addition, the standard deviation of the visual and density-derived radial growth was comparable, but the inventory-derived radial growth had a higher standard deviation (Fig. 2). Mean radial growth series derived visually and from density were most highly correlated for each species (Table 1, see also A.4, Figure A.2). In contrast, correlations of either visually or density derived increment growth series with inventory derived growth series were lower. Among species, correlations across all methods were highest for *C. odorata* and lowest for *H. crepitans* and *L. seemannii* (Table 1).

3.2. Capturing responses to climatic extreme events

For years with extreme climatic conditions (extremely wet and dry years), the similarity of relative growth responses amongst methods was higher in extremly dry than in extremly wet years (Fig. 3). The comparison of relative growth responses among methods revealed overall similar magnitudes of changes in radial growth for both density and visually derived data. Only for the species *H. crepitans*, growth responses in the extreme wet year (2010) were significantly lower when using

Table 1
Spearman correlation coefficients between pairs of series of average radial growth per species, determined using the three different methods. Levels of significance: (*)$P \leq 0.10$, *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$.

Species	Methods correlated	Coefficient
Anarcadium excelsium	Inventory ~ Visual	0.35 ***
	Inventory ~ Density	0.39 ***
	Visual ~ Density	0.71 ***
Cedrela odorata	Inventory ~ Visual	0.58 ***
	Inventory ~ Density	0.53 ***
	Visual ~ Density	0.82 ***
Hura crepitans	Inventory ~ Visual	0.25 ***
	Inventory ~ Density	0.37 ***
	Visual ~ Density	0.57 ***
Luehea seemannii	Inventory ~ Visual	0.27 ***
	Inventory ~ Density	0.15 **
	Visual ~ Density	0.47 ***
Tabebuia rosea	Inventory ~ Visual	0.44 ***
	Inventory ~ Density	0.33 ***
	Visual ~ Density	0.62 ***

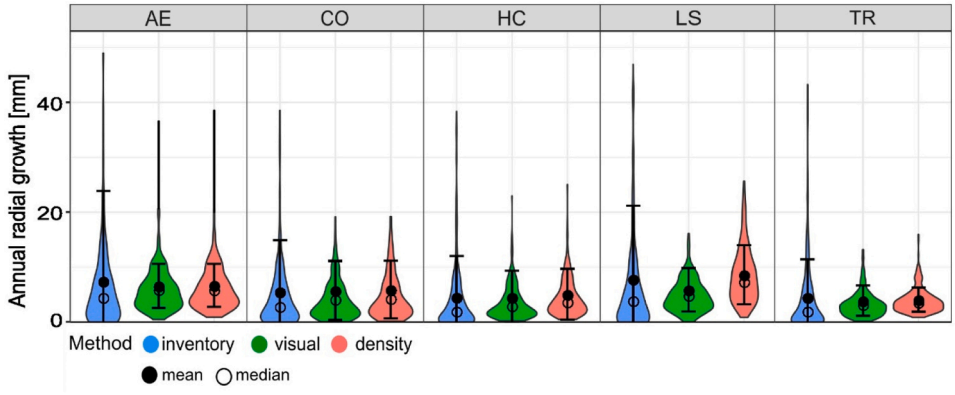


Fig. 2. Violin plot of mean and median radial growth with standard deviation per species and method. Coloured areas represent data distribution, filled dots represent the mean, unfilled dots represent the median, bars represent the standard error. Number of trees: N_{AE}=29, N_{CO}=27, N_{HC}=27, N_{LS}=26, N_{TR}=30.

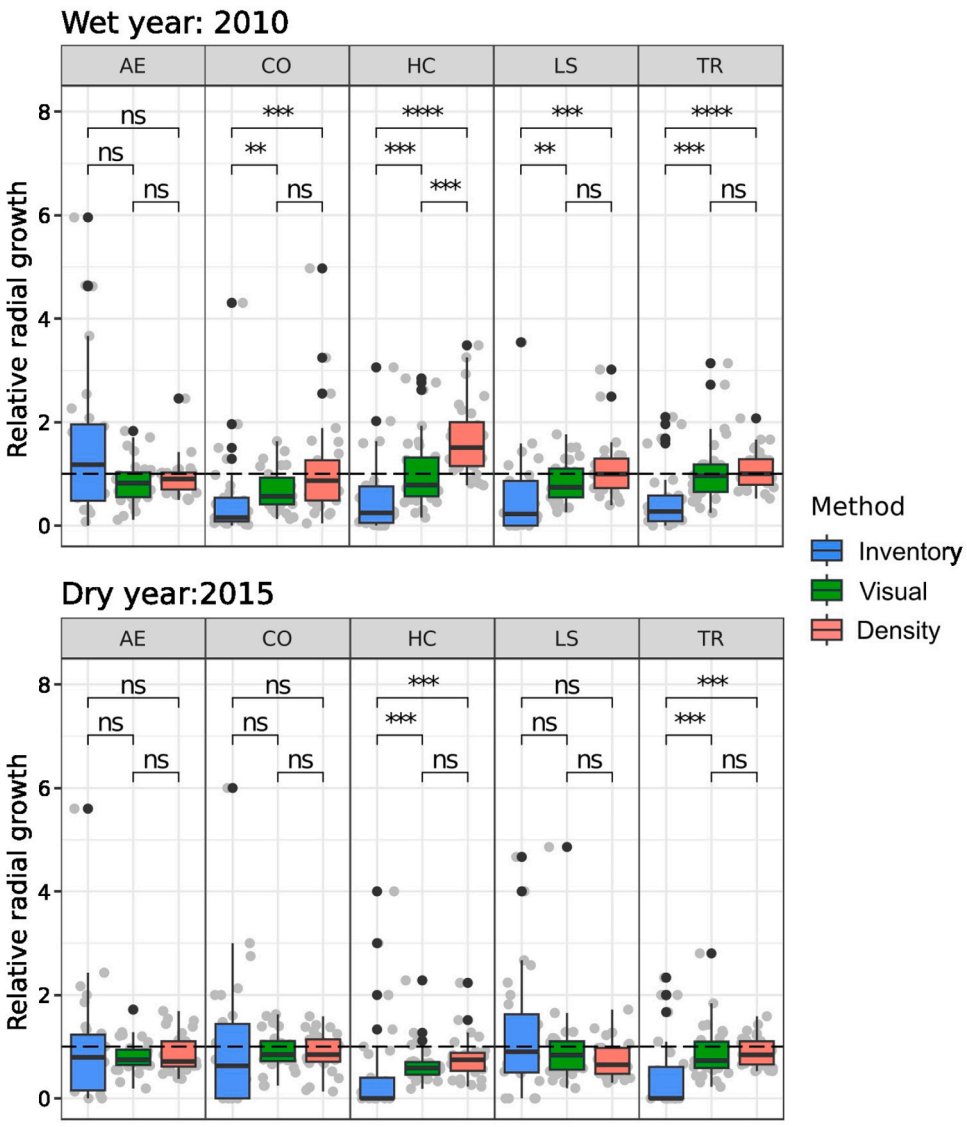


Fig. 3. Comparison of relative radial growth during extreme events among Density, Visual and Inventory per species (AE= *Anarcadium excelsium*, CO= *Cedrela odorata*, HC= *Hura crepitans*, LS= *Luehea seemannii*, TR= *Tabebuia rosea*). Relative radial growth was calculated as tree-ring width in the year of the extreme event divided by the mean tree-ring width in the two years before the extreme event (N_{AE}=29, N_{CO}=27, N_{HC}=27, N_{LS}=26, N_{TR}=30). Pairwise comparisons were performed using Wilcoxon-Rank-Sum-Tests (ns $p>0.05$, * $p\leq0.05$, ** $p\leq0.01$, *** $p\leq0.001$, **** $p\leq0.0001$).

visually derived data than those observed based on density data (Fig. 3). Overall, relative radial growth calculated using inventory data differed significantly from the other two methods. Particularly in the wet year, the magnitudes of changes in radial growth calculated with inventory data were significantly different from and more variable than the magnitudes captured with density and visually derived data (except for *A. excelsium*), while this pattern was only visible for two species in the dry year (*H. crepitans*, *T. rosea*; Fig. 3).

3.3. Quality of radial growth chronologies

Radial growth chronologies were calculated for the longest period of years available for each method. The expressed population signal (EPS) of the developed chronologies ranged from 0.3 to 0.98 (Table 2, compare with method section), with the lowest EPS of any species (except *C. odorata*) calculated from chronologies derived from either inventory or visually derived data, but not from density-derived chronologies. The mean inter-series correlation among individual chronologies ($\bar{r}$) increased from < 0.15 for chronologies derived from inventory data, to < 0.21 for visually derived data and to < 0.32 for density data (Table 2). Mean Gleichläufigkeit (Glk) of chronologies was rather similar across species and methods and ranged from 0.51 to 0.57. For most chronologies, the autocorrelation was low after detrending (Table 2). Only for the species *L. seemannii* using the visually derived data, no meaningful chronology could be developed (e.g. SNR below 1, negative $\bar{r}$ and EPS values, Table 2).

3.4. Climate-growth relationships

To further test whether the three methods employed could be used to quantify annual growth and its sensitivity to climate variability we computed bootstrapped correlation functions between the detrended species chronologies per radial growth detection method and monthly climate variables. Among all tested climatic variables, SPEI series calculated for relatively short accumulation periods (three and six months) correlated best with annual growth of the different species (Fig. 4). Correlations between growth and SPEI series were positive, revealing a crucial role of water availability at the beginning (May) or the middle of the wet season for annual growth of all species (Fig. 4). Across all species, the use of density data provided the highest number of

Table 2
Comparison of chronologies obtained from different methods measuring tree-rings up to the last year 2016 detrended with the regional curve standardization (RCS); Density= tree-rings derived from density measurements, Visual= visually detected tree-rings, Inventory= tree-rings calculated from the inventory data set, stdev=standard deviation, EPS= expressed popul-ation signal, Glk= Gleichläufigkeit, SNR= signal to noise ratio, Ar1= first-order autocorrelation, $\bar{r}$: mean inter-series correlation.

Species	Method	First Year	EPS	$\bar{r}$	Glk	SNR	Ar1
Anarcadium excelsium (N=29)	Inventory	2006	0.33	0.13	0.53	0.49	-0.13
	Visual	2002	0.64	0.21	0.52	1.79	0.12
	Density	2001	0.65	0.14	0.51	1.82	0.19
Cedrela odorata (N=27)	Inventory	2006	0.73	0.15	0.52	2.76	-0.10
	Visual	2003	0.52	0.18	0.54	1.07	0.34
	Density	2001	0.49	0.14	0.52	0.95	0.31
Hura crepitans (N=27)	Inventory	2006	0.90	0.03	0.53	8.66	-0.04
	Visual	2003	0.45	0.15	0.53	0.83	0.00
	Density	2003	0.80	0.32	0.57	4.04	0.11
Luehea seemannii (N=26)	Inventory	2006	0.98	0.09	0.54	51.04	-0.07
	Visual	2002	-1.39	-0.14	0.51	-0.58	0.30
	Density	2002	0.76	0.27	0.53	3.12	0.26
Tabebuia rosea (N=30)	Inventory	2006	0.98	0.15	0.53	83.04	-0.10
	Visual	2001	0.30	0.05	0.53	0.43	0.20
	Density	2000	0.41	0.06	0.52	0.69	0.20

significant climate-growth correlations with SPEI3 and SPEI6 (total: 39 with *A. excelsium*: 10; *C. odorata*: 8; *H. crepitans*: 9; *L. seemannii*: 2; *T. rosea*: 11) when compared to inventory (total: 17) and visually derived data (total: 8) (Fig. 4). Significant correlations between radial growth series and SPEI series were found for 3-months periods ending at the beginning of the wet season (March to July), and shifted to the middle of the wet season (June to September) when correlated with SPEI series calculated for a period of six months. This pattern was visible for radial growth data derived from density and inventory data, but more species exhibited significant correlations based on density data, while no comparable or clear pattern could be observed in the radial growth data based on visual assessment (Fig. 4). Monthly precipitation, temperature, and SPEI1 and SPEI12 showed no clear pattern of significant climate-growth correlations with radial growth across the five species and three methods (see also A.5, Figure A.3). Including January and February in the analysis of the ten months' sequence showed no significant climate-growth correlations (results not shown).

4. Discussion

4.1. Comparison among methods and responses to climatic extreme events

A main objective of this study was to determine how comparable the detected changes in radial growth due to climate extremes are among the three methods: DBH inventories, visual tree-ring analyses, and density profiles. If annual radial growth responds to drought, then it is promising to determine the drought resistance of tree species as droughts become longer and more frequent in subtropical regions (Boisier et al., 2015; Duffy et al., 2015; Pascale et al., 2019). Together with visual and density-derived ring width, radial growth data from inventory measurements captured comparable tree growth responses during extreme droughts for three of the five species studied (*A. excelsium*, *C. odorata*, *L. seemannii*, Fig. 3). However, for species *H. crepitans* and *T. rosea* relative growth measured during extreme dry years based on inventory data was not comparable to relative growth estimates derived from density or visually derived data (Fig. 3, Table 3). Therefore, we conclude that inventory measurements are less suitable for detecting a common growth signal for species with thorns on their bark (*H. crepitans*) when using small sample sizes as in this study (N=30), which makes reproducible circumference measurements more difficult. Likewise, growth data from DBH inventories are less suitable for determing growth responses to climatic extremes for slow-growing species (*T. rosea*, Schnabel et al., 2019) because these are also susceptible to the risk of negative radial growth measurements. In addition, by

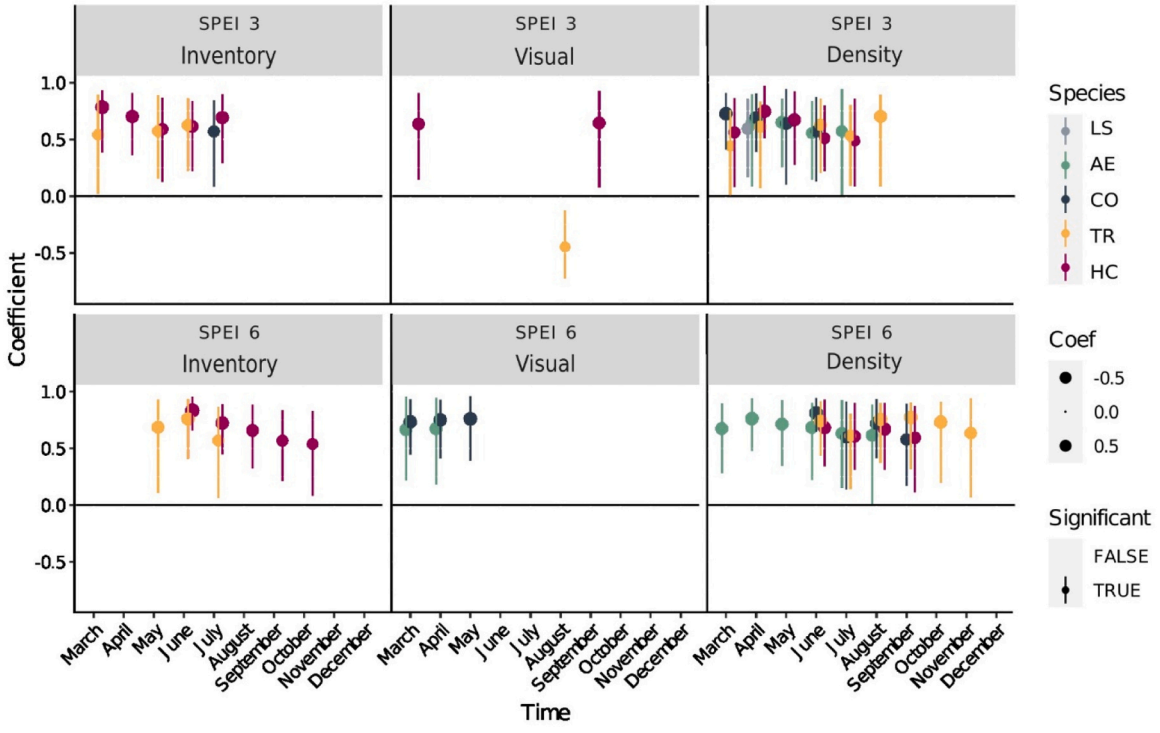


Fig. 4. Correlation coefficients based on standard bootstrapping between chronologies detrended with regional curve standardization computed using Density, Visual and Inventory and climatic variables during the growing season of the current year for each species, over the period: 2006 – 2016. Bars denote upper and lower confidence intervals. Only significant correlations are shown ($p \leq 0.05$), (N_{AE}=29, N_{CO}=27, N_{HC}=27, N_{LS}=26, N_{TR}=30; AE= *Anarcadium excelsium*, CO= *Cedrela odorata*, HC= *Hura crepitans*, LS= *Luehea seemannii*, TR= *Tabebuia rosea*).

Table 3
Summary of the potential for using the different tree species to 1) capture similar growth responses to climatic extremes across methods, and 2) compute climate-growth relationships. Listing corresponds to our research questions. Ability ranked from high (++) to low (–).

	1) Responses to climatic extremes across methods	2) Climate-growth relationships
Anarcadium excelsium	++	+
Cedrela odorata	+	+
Hura crepitans	–	+
Luehea seemannii	+	-
Tabebuia rosea	-	+

setting all negative radial growth measurements to zero, there is also a risk of underestimating the true median of growth responses in dry years but not in wet years due to a higher chance of obtaining negative measurements when growth is reduced during droughts.

Our results show that radial growth series from both density and visually derived data were only weakly correlated with inventory data for each species. We conclude that the inventory method is at risk of over- or underestimating radial growth due to sapwood swelling and shrinkage caused by daily or seasonal changes in moisture and temperature, which can cause circumference changes of up to 0.5 mm in large trees (Scholz et al., 2008; Herrmann et al., 2016; Butz et al., 2017), and might be of greater relative importance in young trees with a smaller radius. Additional growth changes in the phloem and/or bark, which have also been suggested to have a stronger relative effect on tree radius in smaller (young) trees (Biondi, 1999), might be another explanation. In *Cedrela fissilis,* a close relative of *C. odorata*, seasonal phloem growth with distinguishable phloem growth rings have been found (Angyalossy et al., 2020), and this phloem growth variability may have been added to the DBH measurements of *C. odorata*. These explained shortcomings of inventory data compared to the other methods are likely to result in a constant measurement error in radial increment, the relative importance of which increases as growth itself decreases (during drought), and thus could lead to an underestimation of growth depressions.

4.2. Ability of the different methods to quantify annual tree growth variations

Using standard dendrochronological methods, we established radial growth chronologies for all five species and quantified tree growth with annual resolution (except for *L. seemannii* when using visually derived data). The development of chronologies with comparable quality measures for at least two radial growth quantification methods was an indication that the correct boundary structures were identified either visually or from wood density profiles. However, the EPS of the dendroecologically derived chronologies (density and visually derived data) were comparatively low (0.3–0.8) and did not exceed the commonly used threshold of 0.85 (Wigley et al., 1984). This suggested lack of common variation could be due to differences in soil microsites within the planted tree diversity experiment, characterized by different water tables, carbon and nitrogen stocks, and pH values (Healy et al., 2008), likely combined with different nutrient dependencies among species, which are known to influence species distributions in tropical forests (John et al., 2007). This might have caused variation in tree growth among individuals, independent of growth responses to the common climatic signal. In addition, as observed in our study, ring widths formed in young trees are also expected to have high variability within individuals (Soliz-Gamboa et al., 2011). The Glk per species reported here (0.51–0.57) was only slightly lower than previously reported values in other tree-ring-width studies conducted in (sub)tropical regions (0.56–0.76, Pucha-Cofrep et al., 2015; Sanogo et al., 2022).

We observed clear differences in the quality of the developed radial growth chronologies among the five tree species, probably due to species-specific differences in tree-ring appearance related to their patterns of leaf abscission. Quality parameters for series of density and visually derived data showed comparable values for *A. excelsium*, *C. odorata* and *T. rosea*, which indicates that visual detection of ring-width was as successful as detection via density measurements. Two of these three species, *C. odorata* and *T. rosea*, are leafless for at least three months per year (Menalled and Kelty, 2001; Newell et al., 2002; Sapijanskas et al., 2014), which results in significant and visible changes in wood morphology (see also A.1, A.3, Table A.1, A.2). In the past, many studies underlined the good suitability of *C. odorata* and other species of the family *Meliaceae* for tree-ring analysis (Brienen and Zuidema, 2005, 2006; Rozendaal et al., 2010; López et al., 2012), which we could confirm with our analysis (Table 3). The high similarity between density, visual and inventory data for *A. excelsium* was not expected, as this species has high water use and sap flow rates, and only a short leafless period during the dry season (Meinzer et al., 2001; Sapijanskas et al., 2014). Nevertheless, the peak of leaf abscission of *A. excelsium* in January (Meinzer et al., 1999) might have resulted in visually detectable changes (tree-rings), such as a possible decrease in fibre lumen size in the dry season. However, for the remaining two species, *H. crepitans* and *L. seemannii*, the series of density data showed the highest values for EPS, $\bar{r}$ and SNR. Because *H. crepitans* has an irregular pattern of leaf abscission and *L. seemannii* only sheds leaves for a few days twice a year (Sapijanskas et al., 2014), the distribution of vessels and wood anatomy between ring width boundaries may not be suitable for visual detection due to less distinct wood morphology, although they could be detected with density data.

4.3. Climate-growth relationships

Ring width data from density measurements allowed us to calculate significant climate-growth relationships for the majority of species over a short 11-year period (four out of five, Fig. 4, Table 3). In contrast, we observed less significant climate-growth correlations for visual and inventory data probably because these data are based on coarser measurements than micrometer-scale changes in wood density. For visual detection, stored water in the soil acting as a buffer during periods of lower rainfall at the end of the rainy season or even during the early dry season (Brienen and Zuidema, 2005; 2006), and intrinsic species-specific irregularities in leaf abscission (Meinzer et al., 1999; Menalled and Kelty, 2001; Newell et al., 2002; Sapijanskas et al., 2014) might have resulted in less clear tree-ring boundaries, obscuring the small-scale variability potentially needed to calculate climate-growth relationships over a short period of time. By using the standardized precipitation index and monthly precipitation in our analysis, soil water reserves, their variability and influence on climate-growth relationships are ignored in our analysis. However, soil water reserves are often strongly related to the ongoing dry El Niño or wet La Niña climate extremes (Detto et al., 2018).

The annual resolution of ring width measurements based on density data was further confirmed as detrended growth was strongly and positively correlated with monthly series of SPEI6 and SPEI3 (Schöngart et al., 2006). The consistently observed positive relationships of radial growth with the SPEI3 and SPEI6 series at the beginning of the rainy season were to be expected, as they coincide with the emergence of leaves. They are also consistent with results that found positive correlations between growth and precipitation either during the transition from the dry to the rainy season or at the beginning of the rainy season (Brienen and Zuidema, 2006; 2005; Buckley et al., 2007). Furthermore, the strong synchrony of climate-growth correlations among individuals for each species is likely to be because stem discs were obtained from trees growing in a designed experimental plantation without competition for light from overstorey trees (Brienen and Zuidema, 2005; Soliz-Gamboa et al., 2011), and thus may be a good reflection of common climate-growth relationships. In general, the overall suitability of

young trees for climate response analyses may depend on the vertical structure of the sampled stand. Young trees growing in the forest understorey are probably unsuited for such analyses, because in this situation tree growth is strongly influenced by competition from larger trees in their vicinity, microclimate and site-specific variables, rather than regional climate patterns (Chhin and Wang, 2008).

Using ring width data from density measurements, we calculated the strongest climate-growth relationships for four of the five species (except *L. seemannii*). Therefore, we focus on density data for the remainder of this discussion to relate the pattern of wood production and water usage to the observed growth variations with climate: Models of radial growth in *C. odorata* showed the strongest climate-growth relationships and highest explanatory power in models describing climatic conditions over time and independence of model residuals from observed climatic values. In our sampling design, *C. odorata* is the only shallow rooting species (Schwendenmann et al., 2015) with the cambial activity taking place exclusively during the wet season (Dünisch et al., 2003) and with the most distinct sap flux decline in the dry season (Sapijanskas et al., 2014). In contrast, *T. rosea* takes up most water from deep soil layers below 70 cm (Schwendenmann et al., 2015), and hence may experience a more stable water supply throughout the whole year. Another difference in physiology is shown by the species *A. excelsium* and *H. crepitans*, as *A. excelsium* maintains sap flux even during the dry season while in *H. crepitans* sap flux commences before the beginning of the wet season (Sapijanskas et al., 2014). Therefore, these species, *A. excelsium*, *H. crepitans* and *T. rosea*, might show lower growth reductions during droughts. However, the continued water demand of *A. excelsium* during and of *H. crepitans* at the end of the dry season is in line with the finding of significant positive climate-growth correlations of density data. For the multi-stemmed species *L. seemannii*, only the main stem could be analysed, which might have resulted in a diluted growth signal because the growth variation with climatic conditions could also be distributed to the smaller stems. These reasons may explain the weaker climate-growth relationships of the significant models of density data for species other than *C. odorata* (Table 3).

5. Conclusion

Our results demonstrate that radial growth data from wood density profiles were the most suitable for assessing tree growth and climate-growth relationships in (young) tropical tree species. For the species *A. excelsium*, *C. odorata* and *L. seemannii*, radial growth data from all methods analysed (DBH inventories, visual tree-ring analyses, and density profiles) were suitable to detect growth responses to dry climate extremes such as the herein examined extremely dry El Niño phenomena in 2015. As droughts become longer and more frequent, our results indicate that growth data obtained from young tropical trees may be a good source of information to understand how different tree species respond to such extreme events. To date, dendroecological studies conducted in the tropics often rely on obtaining disc samples from ecologically and/or economically valuable mature trees that are either felled or which recently died in (natural) forests (e.g. Brienen and Zuidema, 2005). Our results indicate that stem discs from (young) trees planted in tropical forest plantations may offer a promising and under-utilized source for samples suitable for dendroecological analyses. Primary old-growth forests are becoming scarce in many regions of the (sub) tropics. Therefore, for most regional studies such as this one, we have to use young trees from secondary native forests and plantation forests. In addition, due to the active promotion of forest landscape restoration, such as in the 20×20 initiative in South America (Initiative 20×20, 2014), the area covered with young (often mixed and native) secondary forests and tree plantations is currently increasing worldwide. This development paves the avenue for establishing novel databases, including growth data from these new forests, which will allow future studies to validate our findings against data from large-scale ecological gradients. A priority in this context would be collecting data from species highly suitable for dendroecological research, such as *C. odorata*.

Compliance with ethical standards

Conflict of Interest: Viktoria Dietrich, Florian Schnabel, Georgios Skiadaresis, Jean-Michel Leban, Jürgen Bauhus, Catherine Potvin and Julia Schwarz declare that they have no conflict of interest.

Human and Animal Rights and Informed Consent: This article does not contain any studies with human or animal subjects performed by any of the authors.

Funding

Deutsche Forschungsgemeinschaft (DFG, German Research Foundation, grant no. BA2821/18-1); Natural Science and Engineering Council of Canada; Canada Research Chair Programme to CP; Smithsonian Tropical Research Institute

CRediT authorship contribution statement

Jean-Michel Leban: Writing – review & editing, Resources, Methodology, Investigation. **Julia A. Schwarz:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Catherine Potvin:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization. **Jürgen Bauhus:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Viktoria Dietrich:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Conceptualization. **Georgios Skiadaresis:** Writing – review & editing, Visualization, Supervision, Methodology, Investigation, Conceptualization. **Florian Schnabel:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

We thank José Monteza, Lady Mancilla and their fieldworkers, who worked on the Sardinilla plantation for the past 16 years. The harvesting, drying, packaging and shipping of all the stem disks to Germany was a particularly challenging exercise. We are grateful for their persistence. The maintenance of the Sardinilla plantation was funded from the Natural Science and Engineering Council of Canada, and Canada Research Chair Programme to CP, as well as by site support from the Smithsonian Tropical Research Institute. The laboratory work was supported through a Research Grant (Sachbeihilfe) provided by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) to Jürgen Bauhus [grant number BA2821/18–1].

Authors' contributions

Julia Schwarz and Jürgen Bauhus conceived and designed the study and Jürgen Bauhus obtained the financial resources. Catherine Potvin initiated and managed the Sardinilla tree diversity experiment. Data collection and material preparation were performed by Viktoria Dietrich, Georgios Skiadaresis, Jean-Michel Leban, Florian Schnabel and Catherine Potvin. The data was analysed by Viktoria Dietrich and

Georgios Skiadaresis. The first draft of the manuscript was written by Viktoria Dietrich and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2024.126237.

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