Distinctiveness of annual-ring and its relationship with altitudinal and life zones, and climate type

Distintividad de los anillos crecimiento y su relación con las zonas altitudinales y de vida, y el tipo de clima

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Abstract

Costa Rica has a tropical climate composed by diverse life zones with large quantity of tree species. This study aims to establish different types of the annual rings (AR) distinctiveness, and dendrochronological potential (DP) of 320 wood data for Costa Rica, a neotropical and central America country. Besides it was established the relation among distinctiveness and DP species type, growing condition, altitudinal level and life zones, and climate type. So, it can serve as a basis for a proposal of tree species with dendrochronological potential in South America and the neotropics region. The results indicated 70 species (21.9%) did not present AR boundary (with any DP), 104 species (32.5%) presented well-defined (+) AR (with high DP) and the remaining species (146 species or 45.6% of the total) presented more or less distinctive (+/-) AR, then DP varied from medium to low. The 8 species that grow exclusively in dry tropical conditions presented well-defined AR (with high DP), but 137 species (73.3%) that grow in rainy tropical condition presented absent or poor defined AR, then DP varied from medium to low. Many species (67) that grow in low high (basal and premontane) presented null DP and many species presented (+/-) (medium DP) and 41 species shown high DP. Few species grow in high part (montane and subalpine), but barely presented distinctive AR, then high DP are presented. Finally, many species present medium and high DP, the applications of dendrochronology were limited.

Keywords: broadleaved species; dendroclimatology; dendrogeomorphology; tree rings; tropical species.

Resumen

Costa Rica tiene un clima tropical compuesto por diferentes zonas de vida donde crecen muchas especies arbóreas. Este estudio busca establecer diferentes tipos de distintividad de los anillos anuales (AR) y potencial dendrocronológico (DP) de 320 datos de madera para Costa Rica, un país neotropical. Además, se estableció la relación entre la distintividad y el DP con el tipo de especie, condición de crecimiento, nivel altitudinal, zonas de vida, y tipo de clima. Los resultados indicaron que 70 especies (21.9%) no presentaron límite de AR (con ningún DP), 104 especies (32.5%) presentaron AR bien definido (+) (con alto DP) y las especies restantes (146 especies o 45.6% del

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total) presentaron AR más o menos distintivo (+/-), luego el DP varió de medio a bajo. Las 8 especies que crecen exclusivamente en condiciones tropicales secas y presentaron una AR bien definida (con un DP alto), pero 137 especies (73,3%) que crecen en condiciones tropicales lluviosas presentaron una AR ausente o poco definida, por lo que el DP varió de medio a bajo. Muchas especies (67) que crecen en zonas bajas y altas (basales y premontanas) presentaron un DP nulo, mientras que muchas especies presentaron un DP positivo (DP medio) y 41 especies mostraron un DP alto. Pocas especies crecen en zonas altas (cordilleras y subalpinas), pero presentaron una AR poco distintiva, por lo que se presentaron DP altos. Finalmente, muchas especies presentan DP medio y alto, por lo que las aplicaciones de la dendrocronología fueron limitadas.

Palabras claves: especies latifoliadas; dendroclimatología; dendrogeomorfología; anillos de crecimiento; especies tropicales.

Introduction

Dendrochronology constitutes a powerful approach to unravel comprehensive insights into diverse Earth Sciences' fields (Brandes et al., 2022). Amongst the study fields where dendrochronology analysis demonstrated efficiency are climatology (Hughes, 2002), ecology (Fritts and Swetnam, 1989), geomorphology (Shroder, 1980), and archaeology (Kuniholm, 2002). For more than a century, dendrochronology studies have included all the continents but Antarctica, mostly in the Northern Hemisphere (Zhao et al., 2019). These geographics areas predilection is the result of a combination between the availability of trees to record climate and seasonality (Esper et al., 2016).

Tropical forests comprise about 7% of the land surface; however, they store approximately 25% of global terrestrial carbon and make up one-third of global net primary productivity (Amoroso et al., 2017). In addition, tropical forests comprise 56% of the global forest areas (FAO, 2020). Likewise, tropical forests contain almost half of the tree density in the world (Crowther et al., 2015). Tropical regions present seasonal hydric variations which explain the main paradigm for tropical tree annual ring formation (Locosselli et al., 2020, Giraldo et al., 2020). Certainly, dendrochronology in low latitudes is more complex than in temperate regions (Quesada-Román et al., 2022a). Tropical areas present larger number of species, variety of habitats, fluctuating cambial activity, and the complex phenology over the year in absence of well-defined seasons (Silva et al., 2019).

The application of dendrochronological studies in Costa Rica (and Mesoamerica) remains scarce at present, despite the existence of many species with distinctive annual rings. A few studies have identified the potential for climatological, ecological, and geomorphologic approaches in Costa Rica in the last two decades. Most studies have dealt with the formation of annual rings to produce older climatic chronologies. Capparis indica and Genipa americana, considered as high and medium dendrochronological potential, appear to be a source of reliable annual tree rings using macroscopic methods which reflect significant but differing degrees of sensitivity to variation in local rainfall due to the influence of El Niño Southern Oscillation (ENSO) and North Atlantic Oscillation (NAO) in Guanacaste only during the wettest portion of the wet season (Speer, 2010).

Bauch et al. (2006) found that *Podocarpus oleifolius* var. *macrostachyus* with high dendrochronological potential, a tropical conifer, produces annual rings and that their formation is mainly controlled by climatic conditions. Moreover, high-resolution measurements disclose lucid isotope cycles that provide annual chronological control over the last century in mountain cloud forest of Monteverde where climate variability is dominated by the interannual variance in dry season moisture associated with ENSO events (Anchukaitis et al., 2008, Anchukaitis and Evans, 2010). Quesada-Román et al. (2020a) found that *H. irazuense*, an endemic shrub of the Costa Rican Páramo, grows more during La Niña years and mark annual rings.

Other important applications of dendrochronology in different ecology aspects in Costa Rica were reported by Moya-Roque and Tomazelo-Filho (2007, 2009), Gaitan-Alvarez et al. (2019), Worbes and Raschke (2012) and Worbes et al. (2013). Moya-Roque and Tomazelo-Filho (2007, 2009) presented the general and microscopic features of *Gmelina arborea*, an introduced species for commercial purposes, and these authors have identified that tree age, climatic conditions, and plantation management control wood density variability using X-ray densitometry. Gaitan-Alvarez et al. (2019) determined that wood density profiles for Tectona grandis obtained via X-ray densitometry show a lack of annual ring definition during the first eight years of the trees age. Nonetheless, as trees age, annual rings become more clearly defined and wood density profiles become more distinct. Worbes and Raschke (2012) used tree ring analysis in 45 species to show that dry forests have a high potential for carbon sequestration in contrast with studies from other tropical biomes, and that they act as one of the most important terrestrial carbon sinks.

A third branch of dendrochronology applied in Costa Rica is dendrogeomorphology. Studies related to floods using the height of the trees have been developed in Southern Costa Rica in different sites of the Térraba catchment, the biggest basin of the country. Quesada-Román et al. (2020b) found a direct relationship between the geomorphic location of trees in the riverscapes and the peak flow reconstructions uncertainties using trees' heights and hydraulic modelling after a tropical cyclone. More stable landforms such as terraces or cut banks have less mean square errors than straight channels and point bars. Moreover, Quesada-Román et al. (2022a) used dendrogeomorphology, flood-frequency analyses, as well as with vulnerability and exposure calculations to determine flood risk in the Térraba catchment. Quesada-Román (2023) showed that the combination of remote sensing, meteorological assessments, and dendrochronology analyses, hydraulic modelling, and risk assessments can improve the understanding of hydrogeomorphic processes in tropical and developing countries where baseline data is scarce. Quesada-Román et al. (2022b) found that Costa Rica and Central America are tropical regions where dendrochronology has an immense potential for climatological, ecological, and geomorphic applications.

According to previous information, the application of dendrochronology has been limited to few studies dealing with climatic reconstructions in Costa Rica (Anchukaitis et al., 2008, Quesada-Román et al., 2020b, Worbes,1989, Enquist and Leffler, 2001, Fichtler et al., 2003), ecological approaches (Worbes, 2012), or geomorphic assessments (Quesada-Román et al., 2020b, 2022b). Costa Rica's vegetation has the influence of several biogeographic provinces; for example, the Nearctic region, Mexican transition zone, Neotropical region, South American transition zone, and the Andean region (Morrone, 2006). Therefore, dendrochronology can be applied to other similar regions in the neotropics where warming conditions during the last decades have caused droughts, related to ENSO (El Niño-Southern Oscillation) variations in different ecosystems. Moreover, there is a significant time gap in the continuity of climate or extreme events information in the neotropics; thus, that is where dendrochronology could compensate the lack of updated information.

The study collected information about annual ring presence and dendrochrolologial potential in sample in wood collections of Costa Rica. So, it can serve as a basis for a proposal of tree species with dendrochronological potential in Mesoamerica and the neotropics expanding from Mexico to South America. The need to fill large geographic gaps in dendrochronological data has driven rapid expansion of testing in previously unstudied species (Pearl et al., 2020). Increasing and enhancing studies using tropical dendrochronology can help reduce the knowledge gap in regions without enough tree-ring chronologies and thereby support Earth system sciences (Babst et al., 2017). Then, the study aims to establish different types of tree annual rings, distinctiveness, dendrochronological potential (DP) of 320 tree species and establish their relationship species type, growing condition, altitudinal and life zones, and climate type. The selected species were based in commercial and ecological importance of tropical species collected using different references. We performed the literature review and confirmed the selected species using wood samples of the Xylariorum of Biomaterials Laboratory of the School of Forest Engineering at the Instituto Tecnológico de Costa Rica (TECw).

Material and methods

Geographical setting: The country has an extension of 51,100 km² located between 8° and 11° North Latitude and between 82° and 86° West Longitude (Vargas-Ulate, 2012) and is located in southern Central America. Climatically, Costa Rica's territory is divided into five topographic regions Solano and Villalobos (Solano and Villalobos, 2001). Their location and climatic conditions are presented in Figure 1a and Table 1. The regions in the Pacific coast basin normally present a clear dry season, especially in the Northern Pacific (NP) and is less strong in the South Pacific (SP). Moreover, the North Region (NR) located between Central region, and the Nicaragua border, and Atlantic Region (AR) in Caribbean coast basin, precipitation is present during the whole year, and does not present a clear dry period (Pérez-Briceño et al., 2017).

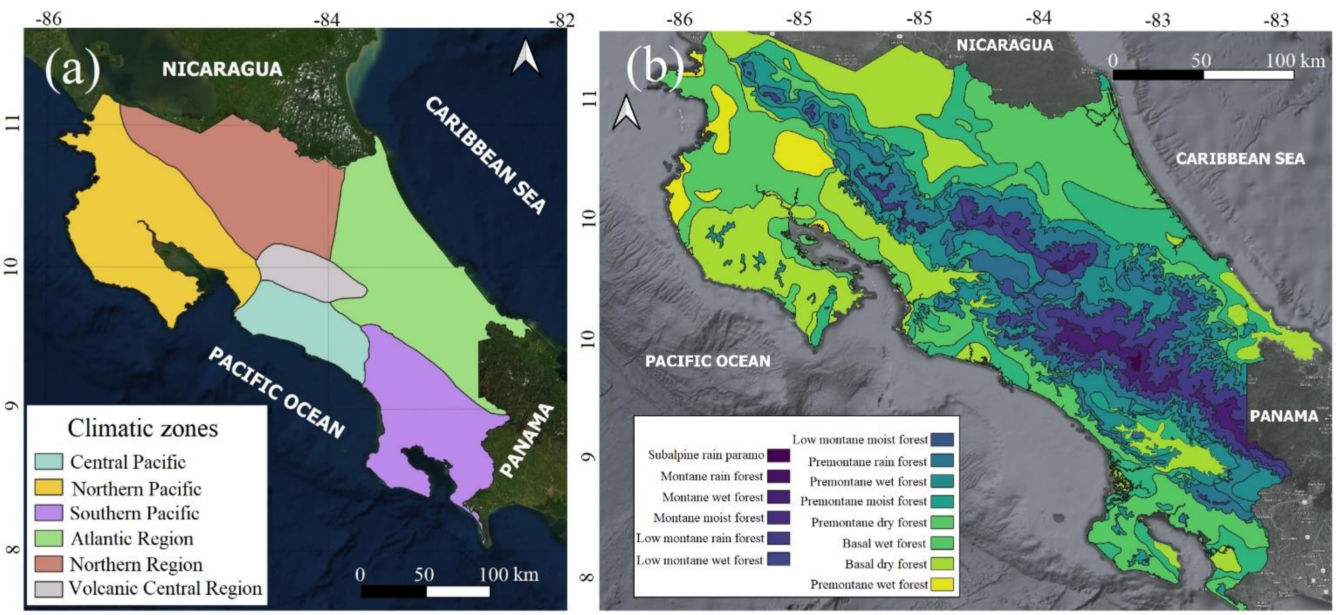

Figure 1. *(a) Costa Rica's climatic zones classification and (b) Costa Rica's Holdridge life zones classification*.

Table 1.
Climatic characterization of the different regions of Costa Rica.

Climatic Region	Annual rainfall average (mm)	Mean temperature (°C)	Months of dry period	Climatic condition
Central Pacific	3578	25	3 (February to April)	Dry
North Pacific	2321	26	4 (January to April)	Dry
South Pacific	3836	25	Without a clear period	Rainy

Atlantic Region	3525	23	Without a clear period	Rainy
Northern Region	3264	25	Without a clear period	Rainy
Central Volcanic Region	2262	19	3 (February to April)	Rainy/Dry

Source: Based on Solano and Villalobos (2001).

The relationship between climate and vegetation are key to understand bioclimatic classifications. The relationship between temperature and precipitation determines many aspects of the distribution of plants. There is a relationship within the climatic zones and the life zones comparing the temperature, precipitation index, and altitude data (Birkel et al., 2022). The criteria to classify life zones in Costa Rica is altitude and vegetation related to climate and temperature, defining five ranges (Holdridge, 1967) and are detailed in Table 2 and Figure 1b.

Table 2.

Distribution and characteristics of life vegetation zones in Costa Rica.

Altitudinal level and abbreviations	Temperature limits (°C)	Altitudinal Ranges (msnm)	Life vegetation zone
Basal (Ba)	< 24 (21)	0-700	Dry forest (B-Df) Wet forest (B-Wf) Moist forest (B-Mf)
Premontane (Pm)	24-18 (26)	700 – 1400	Wet forest (Pr-Wf) Moist forest (Pr-Wf) Rain forest (Pr-Rf)
Lower Montane (Lm)	18-12 (11)	1400 – 3700	Wet forest (Lm-Wf) Moist forest (Lm-Wf) Rain forest (Lm-Rf)
Montane (Mo)	12-6 (13-5.5)	±2400 - 3700	Moist forest (M-Wf) Rain forest (M-Rf)
Subalpine (Su)	6-3 (6.5-2.7)	2800 - 4000	Rain parame (Rp)

Source: Quesada (2007).

Selection of tropical species: We reviewed the studies describing the anatomy of the wood species, which some of them are related with annual ring. However, the description about annual rings was not considered, because the concepts of annual different were different in each study. Forty references were found from 1954 to 2023: We did not consider studies dealing with dendrometer bands in the analysis. Then, 320 tree species were considered (Appendix 1). Species that have been anatomically described were considered because many of them have been of commercial or of ecological importance, so this helps to select the appropriate species. In addition to the importance of species in the literature, it was considered that wood samples of these species were present in the Xylariorum of

Biomaterials Laboratory of the School of Forest Engineering at the Instituto Tecnológico de Costa Rica (TECw). The scientific names, genera, and family of list generated from inventory of tropical species were updated using https://sura.ots.ac.cr/florula4/find_sp2.php?customer=Capparis+indica&busca=Buscar, and http://legacy.tropicos.org/NameSearch.aspx?projectid=66. When the reference indicated only the genera, these were discarded because later it will not be possible to determine the altitudinal zones, life zone, or climatic type where the species grows.

Samples preparation: Wood samples of selected species in the Xylariorum of Biomaterials Laboratory of the School of Forest Engineering at the Instituto Tecnológico de Costa Rica (TECw) were prepared for macroscopic observation. For this, wood samples were polished with sandpaper from 80 to 800. Then, the annual ring and its boundary was observed.

Distinctiveness and type of growth zones: The distinctiveness of annual ring is associated to anatomical markers, which can be macroscopic and microscopic features (Silva et al., 2019). The classification of annual rings was reviewed and widely discussed by Silva et al. (2019) and Ricker et al. (2020). However, despite the fact that there are different types of classifications of annual rings considering different anatomical markers to establish annual ring boundary (Wheeler et al.,1989; 2007, Nath et al., 2016), in the present work was followed the classification proposed by Worbes (1989) and Worbes and Raschke (2012) since this classification is focused in dendrochronologic aspects (Silva et al., 2019), the anatomical markers are observed at a macroscopic level and limited categories are utilized. The classification is based on their distinctiveness and three categories was established:

- Indistinctive or non-defined or boundary non-defined (-): no anatomical elements variation of anatomical in the radial direction was observed, presenting a uniform distribution and dimensions of the vessels, fibers and radial or axial parenchyma (Figure 2a).
- Distinctive or well-defined or boundary defined (+): there are anatomical markers in the growth ring boundary, and they are easily observed, mainly due to density variation (Figure 2b), presence of marginal band parenchyma (Figure 2c-d), recurring patterns of parenchyma and alternating bands of fibers (Figure 2g), size and distribution of vessels (Figure 2e) or well-defined fiber band presence (Figure 2b-d).
- More or less distinctive or poorly defined (+/-): the annual ring boundary was not observed easily, although anatomical markers are observed in the annual ring boundary, its distinctiveness is limited (Figure 2e-h).

Dendrochronological potential: In addition to the previous classification (type of annual rings) of each of the species, a classification of the annual rings was carried out in order to provide more information of the species of Costa Rica, considering the dendrochronological potential following the procedure of Giraldo et al. (2020) proposes four levels (Table 2) and again the authors considered that this classification is focused in macroscopic observation of anatomical aspects of annual rings. This level of dendrochronological potential was assigned using samples from Xylariorum (TECw) samples with cross-section cut with a razor knife and the criteria used in this study are detail in Table 3.

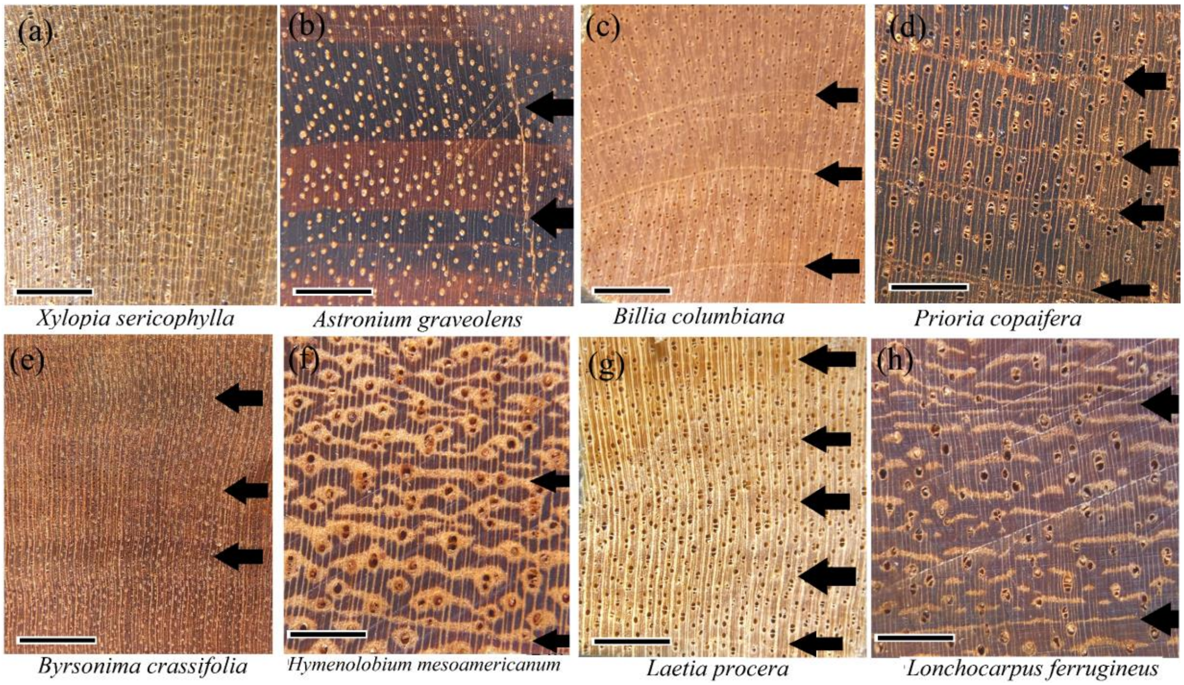

Figure 2. Classifications of distinctiveness of annual tings: (a) without or non-distinctive annual ring in *Xylopia sericophylla*, (b) distinctive or well-defined by density variation in *Astronium graolens*, (c) distinctive or well-defined by marginal parenchyma in *Billia colombiana* and *Cedrela adorata* and (e-h) more or less distinctive or poorly defined.
Note: the arrow (¬) shows annual ring boundary and scale bar: 1 mm.

Table 3.

Criteria considered to establish dendrochronological potential.

Level of dendrochronological potential	Definition by Giraldo et al. (2020)	Criteria in this study
Null potential:	Annual rings are defined by r defined annual ring	This category was assigned to species with indistinctive or non-defined or boundary non-defined (-)
Low potential	Annual ring is catalogued as poorly defined, difficult to observe the annual ring boundary, false annual rings, annual ring too close together, or frequent discontinuity.	The species of this study were poorly defined (+/-) in the distinctive of annual ring, resulting that annual ring in the cross section is difficult to distinguish
Medium	False annual rings are infrequent or more or less	The species of this study presented to more or less distinctive annual ring (+/-), but a difference of above

	distinctive or poorly defined	category the annual ring the distinctive was slightly visible.
High	Annual rings clearly defined in tangential orientation and no presence of false rings	The species with distinctive or well-defined annual ring (+) were assigned this category

Species and growth conditions: The species were classified as: (i) broad-leaved or conifer species, (ii) native, endemic, and exotic and (iii) growing condition in Costa Rica: natural forests, forest plantations, and agroforestry systems.

Altitudinal zones, life zone, and climate type: For species that grow in natural forests, or agroforestry systems, the following three aspects were established for the species:

Altitudinal levels of vegetation zones: four ranges of altitudinal levels were presented in Costa Rica: basal, premontane, lower montane, and subalpine (Table 2) according to Holdridge classification (Holdridge 1967).

Life zones: According to Holdridge (1967) 12 life zones are presented in Costa Rica (Figure 1b) and are detailed in Table 3. However, the classification of 320 species into 12 life zone was difficult, therefore we utilized five main life zone: Basal wet forest (B-Wf), Basal moist forest (B-Mf), Forest rain (Fr), Rain Parame (Rp) and Basal dry forest (B-Df)

Climate type: Although Costa Rica presents many tropical climatic conditions, the National Meteorological Institute of Costa Rica indicated three climatic regions (Solano and Villalobos, 2001) (Table 1) in five areas of Costa Rica (Table 1).

Statistical analysis: Statistical analysis consisted of a multiple correspondence analysis (MCA). It was used because is a statistical technique for qualitative data from multiple data, thus it is possible to separate similarities between the observations of the different studied conditions, which in our case were families, genera, growing conditions, type of climate, altitude levels, and life zones. Then, the dendrochronological potential of the species was associated with these qualitative variables by MCA. The MCA was carried out using the InfoSat statistical software (Di Rienzo et al., 2011).

Results and Discussion

General characterization of the studied species

Although Costa Rica is a small country (51,000 km^2), a high percentage of tree species have been studied (320 species) in relation to the formation of annual rings. Although, these quantity looks high these represented only 19% of total of 1680 species of trees in Costa Rica (Condit et al. 2010). The studied species represent 81 different families and 209 genera (Appendix 1). Only 4 families of coniferous species (1.25% of total) are present in Costa Rica, Podocarpacae, which three species growth naturally in Costa Rica. And other families are introduced and named exotic species (Appendix 1): Araucariaceae (*Araucaria sp.*), Cupressaeceae (*Cupressus lusitanica*), and Pinaceae (*Pinus caribaea* and *P. pseudostrobus*).

The group of species is important to know since the Podocarpacae family is the unique group of species that grows in tropical regions, and other coniferous species that are found in low latitude regions have been introduced or are exotic in this area (Farjon 2010). Another factor is that this type of species is more susceptible to form growth rings (Ricker et al. 2020).

318 species anatomically studied in Costa Rica were focused on trees with commercialization purposes for the production of sawlog, therefore the diameter of the trunk can be bigger and important chronology series can be obtained. *Hypericum irazuense* was the only reported as a shrub species for the study of climatology (Kerr et al., 2018, Quesada-Román et al., 2020a, 2022b). Moreover, another shrub, but a fruit shrub (*Citrus sinensis*) was studied for dendrochronology purpose (Abrams and Hock, 2006).

Type of annual rings and dendrochronological potential

70 species (22.2% of the total) did not present annual rings (-) and the rest of the species (249) presented annual rings, which can be distinctive or well-defined or more or less distinctive and poorly defined. Then, dendrochronological potential of species with non-distinctive annual ring are classified as null. Then, 249 species (77.8% of total species) presented some grade of dendrochronogical potential, and it can be observed or detail Appendix 1.

Endemism and exotic species in relation to dendrochronological potential

Ten (3.1% of total) endemism species (*Eschweilera biflava*, *Guarea aguilarii*, *Huberodendron allenii*, *Lecointea amazonica*, *Pleodendron costaricense*, *Ocotea multiflora*, *O. rivularis*, *Pleurothyrium golfodulcense*, *Pleurothyrium pauciflorum*, and *Sterculia allenii*) were evaluated annual ring distinctiveness and its distribuition in relation to dendrochronological potential were: five endemic species (*E. biflava*, *H. allenii*, *Ocotea multiflora*, *O. rivularis*, and *S. allenii*) did not present distinctive annual rings or non-defined annual rings. Therefore, these species do not present any dendrochronological potential, and the others five species (*G. aguilarii*, *L. amazonica*, *P. costaricense*, *P. golfodulcense*, and *P. pauciflorum*) presented more or less distinctive annual rings, then the dendrochronogical potential of these species was catalogued as medium, considering the criterias used in this study (Table 2).

Eighteen species out of 320 (5.6% of total) were catalogued as exotic species and they were tested in forest plantation (PL) and others in agroforestry systems (AFS) for sawlog production (Rojas-Rodríguez, 2012). Any species presented distinctive annual rings (+), but four species (*Eucaliptus citriodora*, *E. grandis*, *C. equisetifolia* and *Q. cordata*) had non-defined annual ring (-); therefore, these species do not present any dendrochronological potential. More or less distinctive annual rings (+/-) were observed in twelve species, then the dendrochronogical potential of these species is medium. It is important to mention that two species, *Gmelina arborea* and *Tectona grandis* are reported to have high dendrochronological potential (Upadhyay et al., 2021, Islam and Rahman, 2018); however, they were catalogued as medium dendrochronological potential for Costa Rica, due to these species are present in some regions of the country with high rainfall rates and the annual rings were cataloged as more or less distinctive (Gaitan-Alvarez, et. al., 2019, Moya and Tomazelo, 2008). These exotic species were introduced in Costa Rica mainly due to their excellent growth rates. They present excellent adaptability to different sites and climate conditions, resulting in a continuity or lack of seasonality in the vascular cambium, giving as results moderate distinctiveness at the limit of the growth rings (Ricker et al., 2014).

Growing condition: natural forest, plantation, and agroforestry systems

In relation to growing conditions, natural forest (NF) or forest plantation (PL), almost all the species grow in NF (96.9% of total) and their annual ring distinctiveness and dendrochronological potential are detailed Supplementary files. 292 native species growing in NF (91.25% of total species) present annual rings, which 61 species (20.9% of total natives species) presented null potential due to indistinctive annual ring was presented, five species (1.9% of total natives species) was classified as low dendrochronological potential, 133 species (45.5% of total natives species) as medium dendrochronological potential, and 93 species (31.8% of total natives species) was classified as high dendrochronological potential.

32 species (10.0% of total) tested can be grow in NF and can grow on both PL and AFS (Cusack and Montagnini 2004; Piotto et al. 2004; Petit and Montagnini 2006; Obando and Moya 2013). The distribution of annual ring distinctiveness of these are detailed in Table 4. An important aspect of these species planted in forest plantations is that they presented both annual rings: well-defined (+) or more or less distinctive (+/-); therefore, the dendrochronological potential varies from low to high (Supplementary files).

Table 4.
Quantity and percentage of species according to distinctiveness of annual rings for different growing conditions of forest.

Distinctiveness	Growing condition		
	Plantation	AFS	Plantation/AFS
Distinctive (+)	7 (50.0%)	4 (50.0%)	14 (50.0%)
Non-defined (-)	-	-	4 (14.3%)
More or less distinctive (+/-)	7 (50.0%)	4 (50.0%)	10 (35.7%)
Total general	14	8	28

Legend: (+) clearly defined or boundary defined, (-) annual ring non-defined or boundary non-defined, and (+/-) annual ring more or less distinctive or poorly defined.

From used species in AFS conditions, *C. equisetifolia* did not present any dendrochronological potential since annual rings were non-distinctive, but *H. impetiginosus*, *T. rosea*, *B. simaruba,* and *L. leucocephala* presented annual rings catalogued as distinctive; hence, they presented high dendrochronological potential. The rest of the species (*H.*

chryssanthus, *J. copaia*, *J. nigra*, and *E. poeppigiana*) presented annual ring more or less distinctive (+/-), then dendrochronological potential is catalogued as medium.

On one hand, the species growing in PL and AFS conditions (Table 4), *Eucalyptus grandis*, *E. citriodora,* and *Q. cordata* presented null dendrochronogical potential since non-distinctive annual rings were observed. On the other hand, the following species presented distinctive annual rings and, therefore, they are species with high dendrochronological potential: *Alnus acuminata*, *Cedrela odorata*, *C. tonduzii*, *Ceiba pentandra*, *Cordia alliodora*, *Enterolobium cyclocarpum*, *E. schomburgkii*, *Hymenaea courbaril*, *Pachira quinata*, *P. sessilis*, and *Schizolobium parahyba*. The rest of species presented medium dendrochronological potential (Supplementary files).

Climatic type and the dendrochronological potential

Between the studied species forming annual ring distinctiveness, only eight species (2.5% of the total) grow in dry conditions, 187 species (58.4% of total) in rainy conditions, and 125 species (39.1% of total) grow both in dry and rainy conditions. Species with clearly-defined annual rings, or distinctive annual rings were found mostly in dry conditions (Table 5), while 53 species (28.3% of total in this climatic condition) out of 187 species are growing in rainy conditions presented well-defined annual rings (+), and therefore they are classified with high dendrochronology potential. Other 54 species (28.9% of total in this climatic condition) were observed as non-defined (-) annual ring, then they are catalogued as null dendrochronology potential. 80 species (42.8% of total in this climatic condition) with poor defined (+/-) annual rings, three species of them were catalogued as low dendrochronology potential and other 77 species were classified as medium dendrochronology potential (Table 5). In the species growing in rainy/dry climates, 15 species (12.0% of species that growing in rainy/dry condition) lack of annual rings (-) and therefore they were catalogued as null dendrochronology potential. Annual rings well-defined (+) were again low, with 48 out of 125 species (38.4% of species growing in rainy/dry condition). These 48 species were classificated as high dendrochronology potential. Meanwhile, poorly-defined (+/-) annual rings are more frequent in rainy/dry conditions, 61 species (19.1% species growing in rainy/dry condition) and one species was catalogued as low dendronochronology potential (Table 5). The species that grow in different climatic conditions and its dendrochronological potential are detailed in Supplementary files.

Table 5.

Quantity and percentage of species according to distinctiveness of annual rings for climatic conditions and growing conditions.

Type		Climatic condition			
		Dry	Rainy	Rainy/dry	Total
Distinctiveness	Non-defined (-)	1	54	15	70
	Distinctive (+)	7	53	48	108

	More or less distinctive (+/-)	-	80	61	141
	Total	8	187	125	320
Dendro chronolog y potential	Null	1	54	15	70
	High	7	53	48	108
	Medium	-	77	60	137
	Low	-	3	1	4
	Total	8	187	125	320

Legend: (+) clearly defined or boundary defined, (-) annual ring non-defined or boundary non-defined, and (+/-) annual ring more or less distinctive or poorly defined.

Species altitudinal ranges in relation to dendrochronological potential

Costa Rican wood species that have determined the presence of annual rings, when they are located in the different altitudinal zones, 299 species (93.4% of total) grow in the basal category, 186 species (58.1% of total) in the premontane category, 57 species (17.8%) in the lower montane category, 15 species (4.7% of total) in the montane category, and four species in the subalpine category (Figure 3a). Table 6 presents the evaluation of the type of distinctive and the dendrochronological potential of the species growing in the different altitudinal zones.

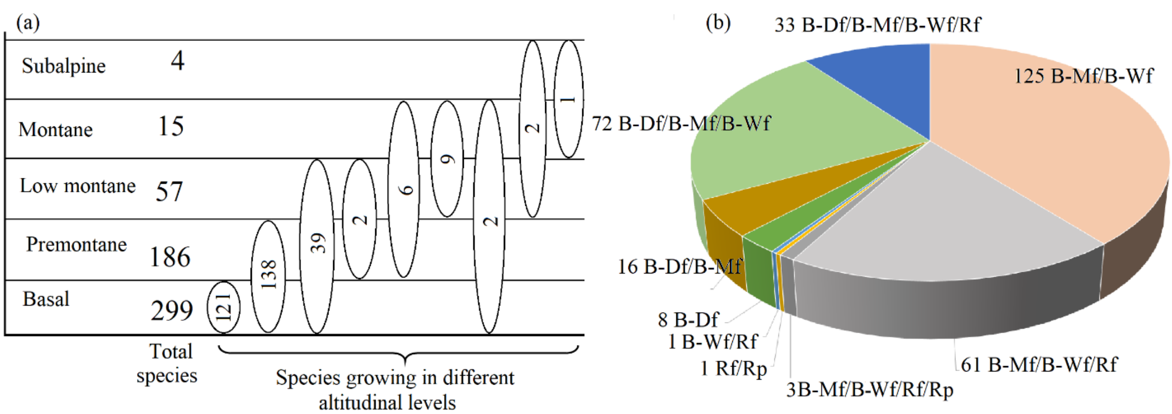

Figure 3. Distribution of species studied in relation to annual rings formation for (a) different altitudinal levels, and (b) life zones of Costa Rica.

Another important aspect to highlight is that some species can grow in different altitudinal levels, which are shown in Figure 3a along with their distinctive and dendrochronological potential in Table 6. 122 species (38.1% of total) grow in the basal zone, the rest of the species are also present in other altitudinal zones and again with the same tendency of the annual ring distinctive, a significant number present null dendrochronogical potential and many species present more or less distinctive (+/-) dendrochronological potential classified as medium, and many species have high potential in these altitudinal zones (Table 6). Only two species, *Quercus bumelioides* and *Ocotea mollifolia*, grow in the four altitudinal zones, they can be found growing in the basal to the montane zones. *Q. bumelioides* is a species with dendrochronological potential (classified as medium potential), since it presents more or less distinctive (+/-) annual ring, while O. *mollioflora*, despite the fact that it can be found in four altitudinal zones, it has the disadvantage that it does not present annual rings, therefore its dendrochronological potential is null.

Table 6.

Quantity of species for different altitudinal levels in relation to distinctive of annual ring and its dendrochronogical potential.

Type of distinctive / Altitudinal zones	Null potential	Distinctive (+)			More or less distinctive (+/-)			
		High	Medium	Total	High	Medium	Low	total
Basal	67	84	16	100	2	126	4	132
Premontane	42	38	15	53	1	86	5	92
Low montane	13	12	7	19		27	1	28
Montane	5	8	2	10		9	1	10
Subalpine		4		4				0

Species growing in different altitudinal levels

Type of distinctive / Altitudinal levels	Null potential	Distinctive (+)			More or less distinctive (+/-)			
		High	Medium	Total	High	Medium	Low	total
Basal	28	46	2	48	1	44		45
Basal/Premontane	29	33	8	41	1	63	3	66
Basal/Premontane/Low montane	9	5	6	11		17	1	18
Basal/Premontane/Low montane/Montane	1					1		1
Premontane/Montano bajo	2	1		1		3		3
Premontane/Low montane/Montane		1		1		1		1
Low Montane/Montane	1	1		1				
Low montane/Montane/Subalpine		1		1		1		1
Montane/Sub alpine		1		1				

Some areas of Costa Rica country presented mountains with elevations above 2500 masl and are referred as cordilleras (Quesada, 2007), but they are not classified as altitudinal areas detailed in Table 2. The dendrochrology potential of the species in these cordilleras were determined its, and it was found that 30 species (9.4% of total) grow in the Costa Rican mountains (elevation level above 2500 m asl) and 12 these species presented high dendrochronological potential, 15 with medium dendrochronological potential, and three with dendrochronological potential.

Life zones in relation to dendrochronological potential

One characteristic of the studied species in relation to life zones is that few species develop in a life zone (Figure 3b). Eight species grow only on B-Df life zone (*Handroanthus impetiginosus*, *Senna atomaria*, *Cordia panamensis*, *Quercus oleoides*, *Chomelia spinosa*, *Randia armata*, *Randia monantha*, and *Jacquinia nervosa*). Seven species presented high dendrochronology potential and only *Q. oleoides* presented null dendrochronology potential (Table 6). Moreover, *Handroanthus impetiginosus* and *Tachigali costaricensis* were the only species with annual rings boundary and they were present in life zones with higher altitudes, rain forest/rain parame (Rf/Rp), and basal wet forest and rain forest (B-Wf/Rf), respectively (Figure 3b). These species are catalogued with high and medium dendrochronological potential, respectively (Table 6). The number of species in relation to life zones is that 125 species (39.1% of total) grow in the B-Mf/B-Wf life zones (Figure 5b), which approximately present a uniform distribution in the three types of distinctive of annual ring and dendrochronology potential (Table 6). Other life zones with high quantity of species were B-Df/B-Mf/B-Wf with 72 species (22.5% of total) and B-Mf/B-Wf/Rf with 61 (19.0% of total) (Figure 5b). In these life zones, most of the species presented distinctive annual rings (+) or more or less distinctive (+/-) and with high or medium dendrochronology potential (Table 6). In relation to species without annual ring types, it means null dendrochronological potential. These characteristics were present in 72 species (22.5% of total). The high quantity of species grows in life zones with B-Mf and few species in life zones with B-Df (Table 6).

Table 6.

Quantity of species for different life zones in relation to distinctive of annual growth rings and its dendrochronogical potential.

Life zone	Type of distinctive				Dendrochronological potential						
					Annual ring clearly defined (+)			Annual ring more or less distinctive (+/-)			
	(-)	**(+)**	**(+/-)**	Null	High	Medium	Total	High	Medium	Low	Total
B-Mf/B-Wf	38	40	46	39	38	2	40	1	44	1	46
B-Mf/B-Wf/Rf	12	15	34	12	11	4	15		32	2	34
B-Mf/B-Wf/Rf/Rp	1	1	1	1	1		1		1		1
B-Wf/Rf			1						1		1
Rf/Rp		1			1		1				
B-Df	1	7		1	7		7				
B-Df/B-Mf		7	9		7		7		9		9
B-Df/B-Mf/B-Wf	12	27	33	12	16	11	27		32	1	33
B-Df/B-Mf/B-Wf/Rf	6	12	15	6	12		12	1	14		15

Total	70	110	139	70	93	16	110	2	133	4	139

Legend: (-) null, annual ring non-defined or boundary non-defined (+) clearly defined or boundary defined, and (+/-) annual ring more or less distinctive or poorly defined.

Dendrochronology potential of Costa Rica tropical species

The behavior of growing conditions, some trends were observed, for example, plantation species, (exotic or natural forest species used for plantations) tended to present a dendrochronological potential (Figure 8a), because these species produced annual rings defined. This probably occurs because plantation conditions are competitive (Obando and Moya, 2013), which produces stress in the tree and favoured the annual rings boundary (Gaitan-Alvarez et al., 2019). All conifer species are considered as high dendrochronological potential, all of them forms a cluster (Figure 4b). Unlike the species growing in AFS condition, that they tend to be located at the level of null or low dendrochronological potential (Figure 4a), due to this condition favored the growth of the trees (Obando and Moya, 2013). In the case of natural forest species, the species are near to medium dendrochronology potential (Figure 4a).

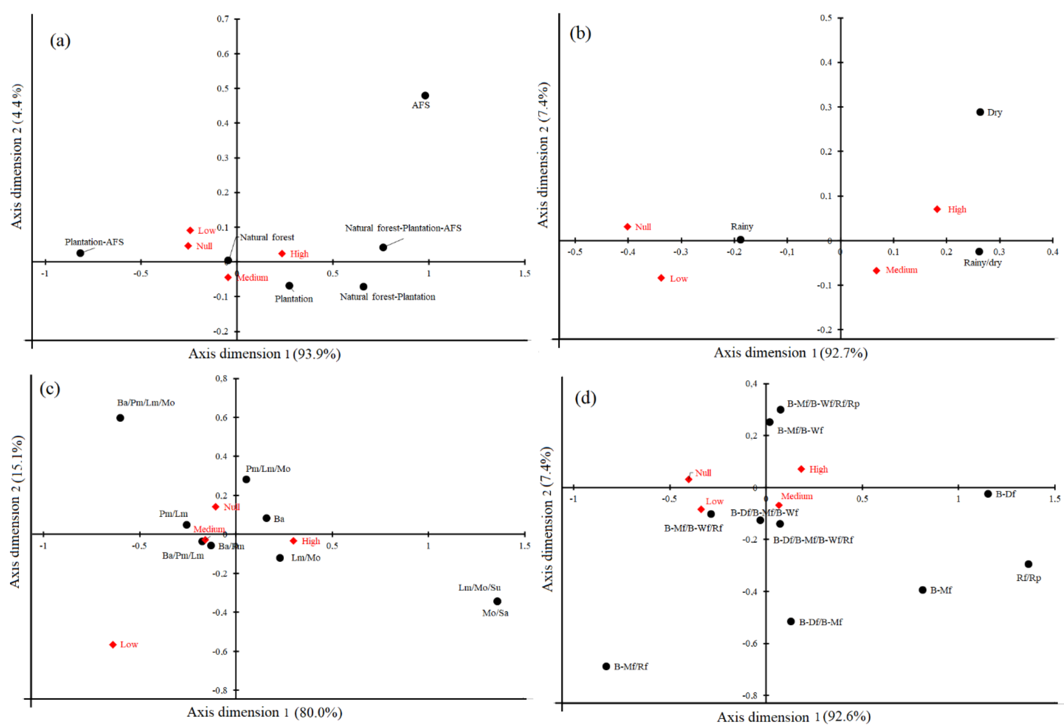

Figure 4. Corresponds analysis between dendrochronological potential and (a) different growing condition, (b) climatic condition, (d) different altitudinal levels, and (b) different life zones of Costa Rica species.

The climatic conditions clearly show the dendrochronological potential of the species (Figure 4b) and confirm with the results showed in Table 6, discussed previously. Species that grow in dry condition tend to have high dendrochronological potential, and species that grow in both rainy and dry conditions are located between high and medium dendrochronological potential, unlike species growing in rainy condition, tend to present low or null potential (Figure 4b).

In relation to the altitudinal levels (Figure 4c), there is no clear tendency to define a dendrochronological potential for species that grow in Mo/Su, Lm/Mo/Su or Ba/Pm/Lm/Mo conditions. But the species that grow in Ba or Lm/Mo condition tend to have high dendrochronological potential. The species growing in Pm/Lm/Mo generally have low dendrochronological potential and species growing in Pm/LM, Ba/Pm and Ba/Pm/Lm condition tend to have medium dendrochronological potential (Figure 4c).

Regarding the life zones, there is less clarity (Figure 4d) in relationship between dendrochronological potential and the life zone. There is only clarity in the species that grow in B-Df/B-Mf/B-Wf and B-Df/B-Mf/B-Wf/Rf levels, which tend to be species of potential dendrochronological medium and the species growing in B-Mf/B-Wf/Rf condition tend to be species with low dendrochronological potential. B-Mf/B-Wf and B-Mf/B-Wf/Rf/Rp species are located very close the point of high dendrochronological potential (Figure 4d).

Finally, although the species in the present study were not classified into deciduous, semi-deciduous, and evergreen groups, this type of species occurs frequently in the regions and typically forms annual rings (Marcati et al., 2006, Marcelo-Peña et al., 2020). Despite a significant number of species being evergreen, it appears that they also form growth rings, as observed in this study. Therefore, based on the results, there are not many associations with the types of forest, life zones, and other studied conditions. Instead, there seems to be a relationship between the formation of rings and whether a species is deciduous or evergreen (Silva et al.,2019).

Conclusions

Despite being a small country, Costa Rica has a remarkable diversity of tree species. Among them, 250 species exhibit annual rings, while 70 species (21.9% of total) do not show annual rings. These species are not limited to natural forests; there is also potential for dendrochronological studies in exotic or native species found in forest plantations, but species growing agroforestry systems presented low potential. It is worth noting that the lower altitude zones, such as the basal and premontane zones, host the majority of species with dendrochronological potential. However, 70 of these species do not form annual rings and therefore have limited dendrochronological potential. On the other hand, a significant number of species do exhibit annual rings, varying in their distinctiveness, ranging from highly distinctive (+) to moderately distinctive (+/-), indicating their medium to high dendrochronological potential. This highlights the considerable opportunities for conducting dendrochronology studies on trees and exploring their various applications, as exemplified by species such as *Capparis indica*, *Genipa americana*, *Podocarpus oleifolius*, *Tectona* *grandis*, *Hypericum irazuense*, and *Citrus sp*. However, as the altitude increases, woody species tend to have more distinctive annual rings and consequently higher dendrochronological potential, albeit with a more limited number of species available for study.

Additionally, researchers in Costa Rica and the Neotropics should expand dendrochronological studies beyond natural forests to include exotic and native tree species in forest plantations and agroforestry systems is crucial for fully exploring Costa Rica's diverse tree population. Focusing research on lower altitude zones, like the basal and premontane areas, provides opportunities to study most species with dendrochronological potential. Lastly, investigating altitudinal variations in dendrochronological potential sheds light on distinctive annual ring patterns in woody species at higher altitudes, despite the limited number of species available for study.

Funding

This research received no external funding

Acknowledgements

The authors thank Vicerrectoría de Investigación y Extensión, of the Instituto Tecnológico de Costa Rica (ITCR, Cartago, Costa Rica). Authors also thank Vice-rrectoría de Investigacón of Universidad de Costa Rica for the project grant C4106: Aplica-ciones geomorfológicas y dendrocronológicas para reconstrucciones climáticas en Costa Rica. We thank Manuel Peralta who assisted with brief sections of the text and figures. We also acknowledge Soll Kracher for her useful corrections which highly improved the syntax and English grammar of the final version of the manuscript

Conflict of Interest

The authors declare no competing interests.

Author contribution statement.

All the authors declare that the final version of this paper was read and approved.

Authors and CRediT Roles: Conceptualization, R.M. and A.Q-R.; methodology, R.M. and R. Q-M.; validation, A.Q-R., and R. Q-M.; formal analysis, A.Q-R. and R.M.; investigation, R. Q-M. and R.M.; resources, R.M.; data curation, R. Q-M. and R.M.; writing—original draft preparation, A.Q-R., R. Q-M. and R.M.; writing—review and editing, A.Q-R. and R.M.; visualization, R. Q-M.; supervision, A.Q-R. and R. Q-M..; project administration, R.M..; funding acquisition, R.M. All authors have read and agreed to the published version of the manuscript.

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The total contribution percentage for this paper was as follows: R.M. 60 %., A.Q-R. 20 % and R.Q-M. 20 %.

Data availability statement

The data supporting the results of this study is available as "supplementary files" on the Uniciencia website.

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