A global review on wood growth rings in lianas

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ABSTRACT

Lianas (woody vines) have a critical role in ecosystem dynamics, especially in the tropics. At present, there is an increasing need to develop reliable methods to measure liana's growth and age, given their suggested increase in abundance following deforestation events and climatic changes. Dendrochronological analyses offer powerful tools that provide temporal information for ecological studies at different scales, with the first step being the detection of distinct growth rings and compiling a list of species with this feature. Hence, this study offers a thorough list of lianas with distinct growth ring markers across both gymnosperm and angiosperm lianas, with and without cambial variants, from both north and southern hemispheres, based on global surveys, bibliographical references and our own collections. Lianas with distinct growth rings are common in species from both temperate and tropical regions. We found 530 lianas with distinct growth rings belonging to 74 families. Bignoniaceae, Celastraceae, Malpighiaceae, Menispermaceae, and Leguminosae are the families with more species listed. Thick-walled and/or radially flattened latewood fibres, semi-ring-porosity, marginal parenchyma, ring-porosity were the main anatomical markers delimiting growth rings in lianas. Future analyses evaluating the periodicity of growth ring formation, mainly in species with cambial variants, are the next step to advance dendroecological application in lianas.

1. Introduction

Growth rings are detectable by the presence of tangential anatomical markers in the secondary xylem (wood). These markers are generated by differences in cell arrangement, types, or wall thicknesses produced during radial growth by direct alterations in vascular cambium activity (Coster, 1927; IAWA Committee, 1933, 1989; Silva et al., 2019, 2021). The formation of these differences can result from environmental, physiological, and genetic factors (Silva et al., 2019, 2021). However, growth rings are not as simple a concept, since there is a broad variation on growth ring markers and degrees of distinctiveness. Given that the pioneer wood anatomical works started with researchers from temperate regions, where growth rings are clearly distinct, tropical species and other growth forms where growth rings distinctiveness is more subtle were frequently described as having indistinct growth rings,

even though for a tropical botanist they may be evident, which led to an underestimation of their potential (Nath et al., 2016; Silva et al., 2019, 2021; Wheeler et al., 2007). Previously, based on the global analysis from the InsideWood database, distinct growth rings were shown to occur in 34% of the "dicots" (magnoliids + eudicots), being more common in the temperate than in the tropical regions (Wheeler et al., 2007). In contrast, more recent global analyses scored a much higher number of distinct growth rings in woody plants, being present in 77% of the seed plants (spermatophytes), 78% of the angiosperms, and 65% of the gymnosperms, with a similar proportion both in temperate and tropical regions (Silva et al., 2021). Several studies corroborated that growth rings in tropical species are common (Nath et al., 2016; Roig et al., 2005; Schöngart et al., 2017; Tarelkin et al., 2016; Worbes, 1995, 2002). For example, a broad study with Brazilian species found that 48% presented distinct growth rings associated with mild and medium

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mesothermal climates (Alves and Angyalossy-Alfonso, 2000). Other studies showed higher values of distinct growth rings occurrence, as in species from Brazilian savanna (61%) (Marcati et al., 2006) and moist tropical forests (79%) (Silva et al., 2017). Distinct growth rings are well-known in trees and shrubs, but are also present in other habits as dwarf shrubs, herbs with some secondary growth, and lianas (Angyalossy et al., 2015; Brandes et al., 2011; Büntgen et al., 2014; Schweingruber and Poschlod, 2005; Schweingruber and Büntgen, 2013; Silva et al., 2019), although to date no studies have shown either how frequent this feature is in these habits or provided with a list of species with distinct growth rings.

In a strict definition, lianas are climbing plants that grow up from the ground, require external physical support to reach the canopy, and present woody stems (Acevedo-Rodríguez, 2005; Cabanillas and Hurrell, 2012; Gentry, 1992; Gerwing et al., 2006; Sperotto et al., 2020). However, a broad definition would include herbaceous vines, such as climbing monocots, including Araceae, climbing bamboos and rattan palms (Acevedo-Rodríguez et al., 2015; Gerwing et al., 2006). The climbing plants evolved independently in several lineages and display numerous morphological convergences related to attachment structures and a very similar vascular system (Angyalossy et al., 2015; Isnard and Feild, 2015; Rowe et al., 2004; Schenck, 1892). This habit has a fundamental role in the ecosystem functioning and is a key component in tropical forests, which are known to be the ones that contain the bulky of woody plant's diversity (DeWalt et al., 2015; Schnitzer et al., 2015). Lianas compete with trees, reducing tree recruitment, growth, reproduction, survival, and carbon uptake (Álvarez-Cansino et al., 2015; Cai et al., 2009; Schnitzer and Carson, 2010). As a consequence, they can affect the trees diversity and community species composition (Cai et al., 2009; Schnitzer and Carson, 2010). Liana abundance and species diversity are highly variable across the ecosystems, regions, climates, and environments; but are higher in tropical than temperate forests. Liana density shows a negative relationship with annual precipitation, while a positive relationship with seasonality in precipitation (DeWalt et al., 2015). In addition, liana diversity displays a bivariate relationship with annual precipitation (hump-shaped), but no relationship with the length of the dry season (DeWalt et al., 2015). Complementing these findings, some studies indicate that liana abundance, biomass, and productivity have been increasing in the Neotropics (Schnitzer et al., 2015; Schnitzer and Bongers, 2011; Schnitzer and Carson, 2010; van der Heijden et al., 2015), while other studies indicate a stasis (Gerolamo et al., 2018). Either way, understanding the growth of lianas is fundamental to understand tropical ecosystem dynamics.

There is a substantial taxonomic diversity of lianas in the world (ca. 133 families), especially in the neotropics (ca. 119 families, 977 genera, 10,966 species) (Acevedo-Rodríguez et al., 2015; Gentry, 1992). Associated to this taxonomic abundance, an enormous anatomical diversity in vascular stem patterns have evolved correlated to the habit, a phenomenon coined the "lianescent vascular syndrome" (Angyalossy et al., 2015; Brandes and Barros, 2008; Carlquist, 2001; Luizon Dias Leme et al., 2021). Among the characters related to the lianescent habit, the most remarkable are likely the cambial variants, which result either from a single vascular cambium with different activities across its girth or multiple cambia, both generating stems with various alternative anatomical architectures (Angyalossy et al., 2015; Carlquist, 2001).

Studies dealing with the age and growth of lianas are sparse and mostly applying indirect methods (Gerwing, 2004; Nabe-Nielsen, 2002; Putz, 1990). Methods for assessing lianas' age and growth can greatly advance ecological studies (Ladwig and Meiners, 2015). Within this scenario, growth ring analysis is an invaluable source of temporal data and can help understand growth and forest dynamics, population age structure, forest succession, liana-tree interactions, forest management, conservation, and restoration (Bräker, 2002; Brienen and Zuidema, 2006; Godoy-Veiga et al., 2018; Grau et al., 2003; Ichihashi and Tateno, 2011; Nola, 1997; Venegas-González et al., 2020; Worbes et al., 2003). Nevertheless, the first step is to search for liana species with distinct

growth rings and ascertain their growth rings are annual (Stahle, 1999). In spite of the anatomical complexity of lianas stems, a few previous studies have demonstrated well-delimited annual growth rings in some species, including species with cambial variants (Angyalossy et al., 2015; Brandes and Barros, 2008; Brandes et al., 2011, 2015; Lima et al., 2010; Schenck, 1893). In some of these studies, the annual periodicity of the growth rings allowed dendrochronological studies (Brandes et al., 2011; Ichihashi and Tateno, 2011), especially with species of the temperate region, such as *Hedera helix* and *Vitis vinifera* (Castagneri et al., 2013; Davis and Evert, 1970; de Micco et al., 2018; Esau, 1948; Garfi and Ficarrotta, 2003; Heuzé et al., 2009; Manzanedo et al., 2018; Maxwell et al., 2016; Munitz et al., 2018; Nola, 1997; Roig-Puscama et al., 2021; Schnitzler and Heuzé, 2006; Shtein et al., 2017; Tyminski, 2013; Verheyden et al., 2006). These studies helped to understand liana-tree interactions, rootstock effects, hydrological, edaphic and climatic conditions on lianas growth, and evaluate responses to future climatic scenarios.

Despite the increasing information on liana ecology (Schnitzer et al., 2015), we still ignore how frequent are distinct growth rings in lianas and possible candidate species for dendroecological studies. Providing a species list will certainly advance and stimulate growth rings and dendroecological research with lianas, as previous lists did for other plant groups and vegetational types under-investigated, but with potential for growth ring analyses (Ferrero et al., 2014; Marcati et al., 2006; Reis-Avila and Oliveira, 2017; Roig et al., 2005; Schöngart et al., 2017; Silva et al., 2017; Tarelkin et al., 2016; Worbes, 2002). Therefore, this review aims to (i) provide a global overview of lianas with distinct growth rings, (ii) to describe the most common growth ring markers in lianas, and (iii) to provide with a thorough list of liana species with distinct growth rings.

2. Materials and methods

First, we performed a survey of liana species with distinct growth rings in the InsideWood database (InsideWood, 2004; Wheeler, 2011) for quantitative occurrence analyses. The InsideWood stores wood anatomical data from over 10,000 species of 200 families and has a global coverage (Wheeler et al., 2020). The features used in the descriptions follow the codes of the "IAWA list of microscopic features for hardwood identification" (IAWA Committee, 1989). The search was conducted first using the feature "vine/liana" (IAWA code 191) to know the total of lianas in the database and then added the feature "growth ring boundaries distinct" (1) to calculate the proportion. We found duplicated records for lianas species. We also double-checked the distinctiveness of growth rings and anatomical markers for all liana species with images available in this database. The results were filtered by other anatomical features for interpretation (wood ring-porous (3), wood semi-ring-porous (4), axial parenchyma in marginal or in seemingly marginal bands (89), concentric included phloem (133), diffuse included phloem (134), and other cambial variants (135)) and by geographical distribution (164–188). We did not perform a search for gymnosperm lianas in the InsideWood database, which follows the "IAWA list of microscopic features for softwood identification" (IAWA Committee, 2004). This list was designed mainly for conifers and not for other gymnosperm groups where lianas are, such as Gnetales. Therefore, the habit feature is not available to be used as a filter in this context.

Second, we performed a survey in the species list provided as Supplementary material by Silva et al. (2021) for quantitative occurrence analyses and comparison. Silva et al. (2021) investigated growth ring presence and markers in 4790 species belonging to 301 families obtained from 456 published studies. We sorted the lianas species from these 4790 species using three methods. First, we checked the orders in which lianas occur based on Isnard and Feild (2015). Within these selected orders, the families were checked on the Plants of the World platform (KEW) (http://www.plantsoftheworldonline.org/) (POWO, 2021) looking for information that suggested lianas in that group. If no

information or description were encountered, we assumed the possibility of liana occurrence. The final and third method was checking the GBIF (Global Biodiversity Information Facility) (https://www.gbif.org/) (GBIF.org, 2021). All the remaining species were one by one searched on the platform and at least three exsiccates of each were observed in order to confirm any registers of climbing habit. The species that occur in Brazil were all checked in the Flora do Brasil 2020 platform (http://floradobrasil.jbrj.gov.br/) (Flora do Brasil, 2020, 2021). Having that sorted, we identified the lianas species, lianas with distinct growth rings, and calculated the proportions. The anatomical markers of the growth rings and climatic occurrence (tropical and temperate) were used in data analysis.

Third, we used the data from The Xylem Database (https://www.wsl.ch/dendropro/xylemdb/) provide by the Swiss Federal Research Institute WSL (WSL, 2014) to expand the quantitative analysis. The Xylem Database represents the diversity of extra-tropical dicots and growth forms (Büntgen et al., 2014), with 3993 species from 139 families. This database uses the standard anatomical features proposed by IAWA for hardwood identification (IAWA Committee, 1989). Based on this database we calculated the proportion of lianas/climber species with distinct growth rings (IAWA code 1). We filtered the data by the same IAWA features used to filter the data from InsideWood database (IAWA codes 3, 4, 89, 133, 134, 135). Geographical distribution analyses were not performed with these data because it is mostly restricted to the temperate region.

Fourth, we performed a bibliographical search for wood descriptions or mentions about growth rings in lianas to produce a list of lianas with distinct growth rings. Several academic databases and web search engines (e.g., Google Scholar, Web of Science, Scopus, Scielo) were used in the search. We also consulted specialised bibliographies (e.g., journals, books, manuals, thesis, dissertations, and monographs) that appeared in search engines or were known to the authors, but we are aware that non-publicly available references might have been missed. We recorded, when available, the growth ring anatomical markers and cambial variant type, when the latter was present. For standardisation, the growth ring markers terminology followed Silva et al. (2019) and the cambial variant terminology followed Angyalossy et al. (2015). We also proceeded with a search in the cross-section image database of "Lianas and climbing plants of the Neotropics" (https://naturalhistory.si.edu/research/botany/research/lianas-and-climbing-plants-neotropics/lia

nas-cross-sections) (Acevedo-Rodríguez et al., 2015). We evaluated the presence and absence of growth rings using macroscopic images to classify the growth ring markers (Silva et al., 2019). In addition to the databases available online and the literature, we have also revised our own collections of lianas. All information on species collector, collector number, locality and where the vouchers are deposited can be found in Appendix S1.

The lianas with distinct growth rings were listed in Table S1, which was evaluated to find the main growth ring anatomical markers, the presence of cambial variants, and the main plant families. We verified the species names obtained from literature in "The Plant List" (http://www.theplantlist.org/) and provided the accepted scientific species names.

3. Results

The InsideWood database contains 259 lianas descriptions (3% of the species in the database) (IAWA character 191p). Among them, 129 lianas have distinct growth rings (1p), representing 50% of the total (Fig. 1). Thirty-one (24%) of the liana species with distinct growth rings have ring-porous wood (3p), 41 (32%) have semi-ring-porous wood (4p), and 26 (20%) have axial parenchyma in marginal or in seemingly marginal bands (89p) (Fig. 1). Cambial variants occur in some species; 8 (6%) have concentric included phloem (133p), 4 (3%) diffuse included phloem (134p), and 16 (12%) other cambial variants (135p) (Fig. 1).

Based on the InsideWood database, 81% of the lianas in Europe and temperate Asia (Brazier and Franklin region 75) (164p) have distinct growth rings, 50% in Central South Asia (Brazier and Franklin region 75) (168p), 30% in Southeast Asia and Pacific (Brazier and Franklin region 76) (171p), 45% in Australia and New Zealand (Brazier and Franklin region 77) (175p), 26% in Tropical mainland Africa and adjacent islands (Brazier and Franklin region 78) (178p), 50% in Southern Africa (south of the Tropic of Capricorn) (Brazier and Franklin region 79) (181p), 78% in North America, north of Mexico (Brazier and Franklin region 80) (182p), 47% in Neotropics and temperate Brazil (Brazier and Franklin region 81) (183p), 50% in Temperate South America including Argentina, Chile, Uruguay, and S. Paraguay (Brazier and Franklin region 82) (188p) (Fig. 1).

From Silva et al. (2021) list, we sorted 308 liana species (6%), 223 with distinct growth rings (72%). Since lianas are more frequent in the
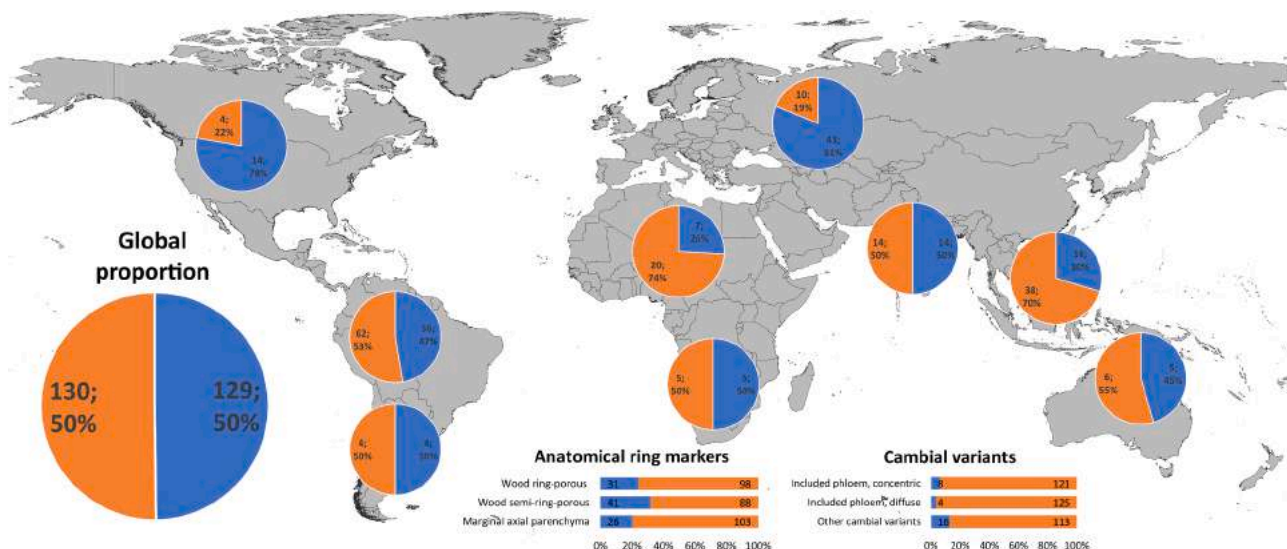

Fig. 1. Map showing proportion of lianas with distinct growth ring by geographical distribution. Bar graphs show proportion of anatomical growth ring markers and cambial variants in lianas with distinct growth rings. Data source: InsideWood database (InsideWood, 2004; Wheeler, 2011). In pie charts, blue = distinct growth rings, orange = indistinct growth rings. In bar graphs, blue = feature present, orange = feature absent. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

tropical than temperate region, we found 142 species of tropical lianas with distinctive growth rings versus 62 species for the temperate region, which represent 67% of the lianas from the tropical region versus 84% from the temperate region (Fig. 2). Ring-porosity is the anatomical marker in 29 lianas (13%), semi-ring-porosity in 79 (35%), marginal axial parenchyma in 52 (23%), fibre zone in 2 (1%), thick-walled and/or radially flattened latewood tracheids in 6 (3%), thick-walled and/or radially flattened latewood fibres in 171 (77%), distended rays in 26 (12%) (Fig. 2).

The Xylem Database has 121 lianas and climbers recorded (3%) and 77 of them (64%) display distinct growth rings (1p). Among them, 43 (56%) have wood ring-porous (3p), 28 (36%) have wood semi-ring-porous (4p), and 14 (18%) have axial parenchyma in marginal or in seemingly marginal bands (89p). Concentric included phloem occurs (133p) in 3 (4%), diffuse included phloem (134p) in 1 (1%), and other cambial variants (135p) in 1 (1%) (Fig. 3).

We prepared a new list with 530 lianas with distinct growth rings (Supplementary material: Table S1), belonging to 74 spermatophytes families (Table 1), obtained from 93 literature references and our own collections (Supplementary material: Appendix S1 and S2). The ten families with more species with distinct growth rings were Bignoniaceae (82), Celastraceae (46), Malpighiaceae (32), Menispermaceae (30), Leguminosae (29), Ranunculaceae (26), Vitaceae (25), Connaraceae (22), Apocynaceae (19), Loganiaceae (15) (Table 1).

Cambial variants occur in 242 species (46%), do not occur in 220 (41%), and they were not informed in 68 species (13%). The cambial variants are the product of single cambium in 194 species (80%) and of multiple cambia in 48 species (20%) (Fig. 4). Phloem arcs/wedges (100 species, 41%), axial vascular elements in segments (46, 19%), successive cambia (44, 18%), interxylary phloem (32, 13%), non-cylindrical stems (16, 7%), intraxylary phloem (6, 2%), fissured stem (4, 2%), and external secondary cylinders (1) were the cambial variants present (Fig. 4).

The main growth ring markers in the listed lianas were thick-walled and/or radially flattened latewood fibres (358 species, 68%), semi-ring-porosity (176, 33%), marginal parenchyma (136, 26%), ring-porosity (105, 20%), fibrous zone (46, 9%), distended rays (32, 6%), and thick-walled and/or radially flattened latewood tracheids (17, 3%) (Fig. 4). Some records in the list of the present study did not give the anatomical markers because they were not reported in the references.

We exemplify with photos five lianas with distinct growth rings (Fig. 5). Two lack cambial variants (Fig. 5A, B), while three have conspicuous cambial variants (Fig. 5C–E). *Dalbergia frutescens* (Vell.) Britton (Leguminosae) is a liana with well-delimited growth rings, marked by

semi-ring porosity, marginal parenchyma and radially flattened fibres (Fig. 5A). *Heladena multiflora* (Hook. & Arn.) Nied. (Malpighiaceae) also has distinct growth rings delimited by radially flattened fibres and marginal parenchyma, but their delimitation is not so evident, especially because of the abundant non-lignified wood parenchyma between lignified cells (Fig. 5B). *Fridericia chica* (Bonpl.) L.G.Lohmann (Bignoniaceae) is a liana with xylem furrowed by four equidistant phloem wedges, with well-delimited growth rings, marked by semi-ring porosity, marginal parenchyma and radially flattened fibres (Fig. 5C). *Wisteria sinensis* (Sims) Sweet (Leguminosae) is a liana from the temperate region with successive cambia, marked by ring-porosity and radially flattened fibres (Fig. 5D). Last, *Pisoniella glabrata* (Heimerl) Standl. (Nyctaginaceae) is a liana with interxylary phloem and growth rings well-delimited by radially flattened fibres and a line of axial parenchyma (Fig. 5E).

We also exemplify the main growth ring markers in four leguminous lianas with photos, which show very clear growth rings under different magnifications (Fig. 6). *Piptadenia micrantha* Benth., *Piptadenia adiantoides* (Spreng.) J.F.Macbr., *Acacia tenuifolia* (L.) Willd., and *Dalbergia frutescens* (Vell.) Britton present growth ring boundaries delimited by thick-walled and radially flattened latewood fibres, semi-ring-porosity, marginal parenchyma, and fibrous zone. The first feature is just detectable under microscopic analysis (Fig. 6E–H), while the others are detectable even in macroscopic view (Fig. 6A–D).

4. Discussion

4.1. Growth rings in lianas from tropical and temperate regions

Growth rings in lianas are here shown to prevail, representing 50% of the lianas recorded on InsideWood (2004), 72% of the lianas recorded by Silva et al. (2021), and 64% of the lianas in The Xylem Database (WSL, 2014). The proportion of this feature in lianas is close to the proportion observed in the global data from seed plants as a whole (77%) (Silva et al., 2021) and much higher than previously reported to "dicot" species (magnoliids + eudicot) (34%) (Wheeler et al., 2007). In addition, we provide with a novel list of 530 liana species with distinct growth rings from our own survey, further emphasising this feature in lianas. This list included lianas with or without cambial variants and belonging to numerous seed plant families.

Distinct growth rings are common in lianas from both tropical and temperate regions disputing previous statements that liana woods typically lack distinct growth rings (Ladwig and Meiners, 2015; Schenck, 1893). Growth rings can be formed when precipitation is
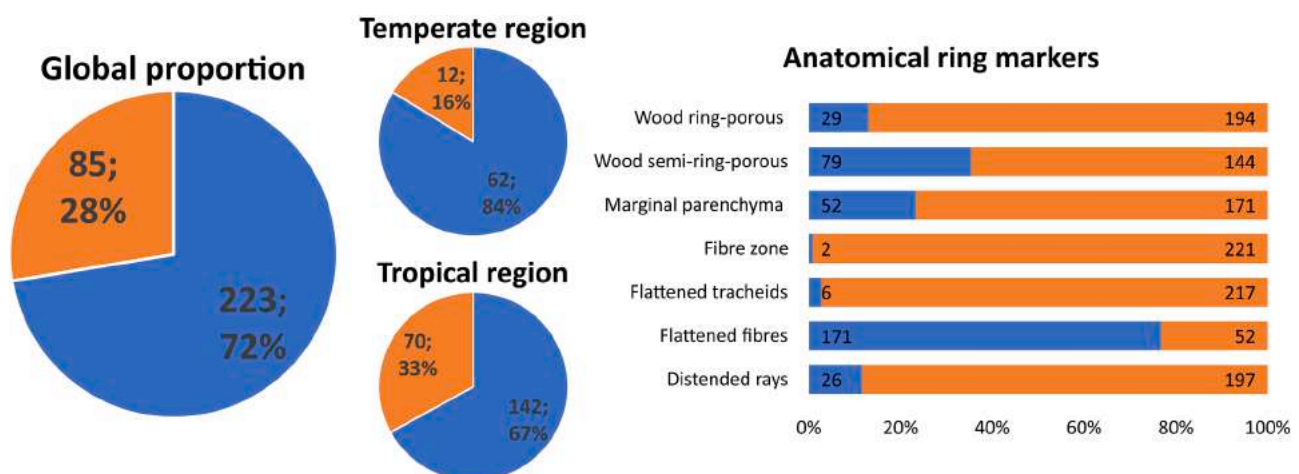

Fig. 2. Proportion of lianas with distinct growth ring by geographical region and anatomical growth ring markers. Data source: Silva et al. (2021). In pie charts, blue = distinct growth rings, orange = indistinct growth rings. In bar graphs, blue = feature present, orange = feature absent. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
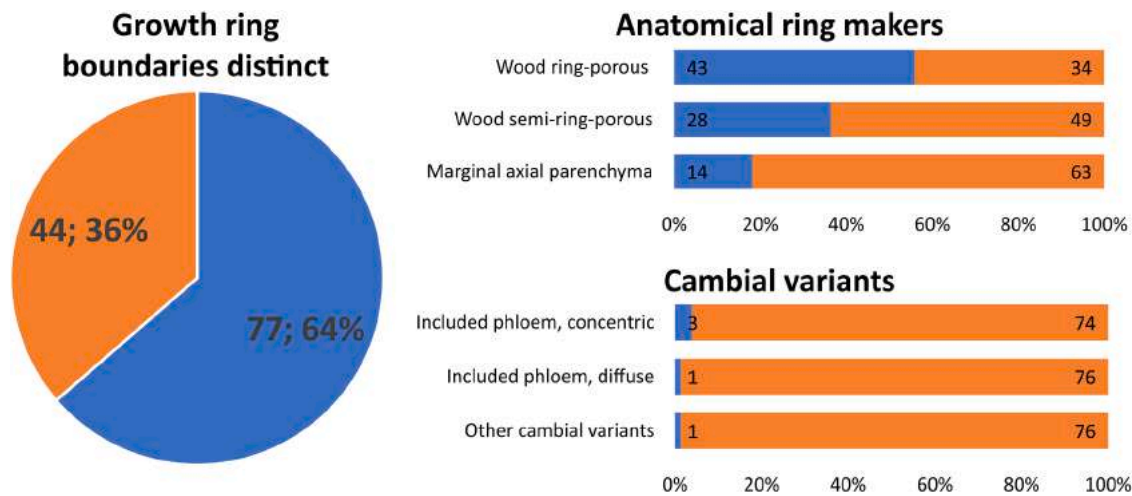
Fig. 3. Proportion of lianas with distinct growth ring, anatomical growth ring markers and cambial variants. Data source: The Xylem Database (WSL, 2014), which represents mainly the temperate region. In pie charts, blue = distinct growth rings, orange = indistinct growth rings. In bar graphs, blue = feature present, orange = feature absent. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Families and total of liana species with distinct growth rings.

Family	Species	Family	Species
Bignoniaceae	82	Ericaceae	2
Celastraceae	46	Euphorbiaceae	2
Malpighiaceae	32	Gnetaceae	2
Menispermaceae	30	Melastomataceae	2
Leguminosae	29	Phytolaccaceae	2
Ranunculaceae	26	Polygalaceae	2
Vitaceae	25	Rosaceae	2
Connaraceae	22	Schlegeliaceae	2
Apocynaceae	19	Amaranthaceae	1
Loganiaceae	15	Ancistrocladaceae	1
Combretaceae	12	Annonaceae	1
Convolvulaceae	12	Aphanopetalaceae	1
Lardizabalaceae	12	Austrobaileyaceae	1
Aristolochiaceae	11	Barbeuiaceae	1
Caprifoliaceae	9	Basellaceae	1
Rhamnaceae	9	Berberidopsidaceae	1
Actinidiaceae	7	Boraginaceae	1
Icacinaceae	7	Caryophylloideae	1
Polygonaceae	7	Coriariaceae	1
Rubiaceae	7	Degeneriaceae	1
Solanaceae	7	Hernandiaceae	1
Araliaceae	6	Marcgraviaceae	1
Schisandraceae	6	Meliaceae	1
Malvaceae	5	Misodendraceae	1
Dilleniaceae	4	Nepenthaceae	1
Ephedraceae	4	Olacaceae	1
Hydrangeaceae	4	Passifloraceae	1
Oleaceae	4	Piperaceae	1
Sapindaceae	4	Pittosporaceae	1
Acanthaceae	3	Sabiaceae	1
Anacardiaceae	3	Salicaceae	1
Lamiaceae	3	Santalaceae	1
Moraceae	3	Styracaceae	1
Nyctaginaceae	3	Talinaceae	1
Opiliaceae	3	Trigoniaceae	1
Asteraceae	2	Urticaceae	1
Cannabaceae	2	Verbenaceae	1

seasonal (Callado et al., 2013; Worbes, 1995) and lianas were shown to be specifically abundant in tropical dry forests where seasonality in precipitation is well-marked (DeWalt et al., 2015).

4.2. The main taxa with distinct growth rings

Five families noticeably showed a higher number of lianas with distinct growth rings: Bignoniaceae, Celastraceae, Malpighiaceae, Menispermaceae and Leguminosae. The higher number in these families might however reflect the fact that these are among the most abundant lianas in floristic surveys (Acevedo-Rodríguez et al., 2015; Gentry, 1992), and also the ones whose wood anatomy has been more heavily studied in the past years (Amorim et al., 2017; Brandes and Barros, 2008; Lima et al., 2010; Pace et al., 2018). In contrast, another family that is in the top 5 more abundant lianas in the neotropics and has been heavily studied recently, the Sapindaceae, indeed show a prevalence of indistinct growth rings (Chery et al., 2020; Gentry, 1992; Pellissari et al., 2018; Tamaio, 2011). While new families with abundant lianas are surveyed, such as the Nyctaginaceae (Cunha Neto et al., 2021), the number of lianas with distinct growth rings is likely to increase.

Bignoniaceae is a family with the potential to advance in growth ring analysis because it has numerous species with well-distinct growth rings and is one of the most abundant and species-rich families in neotropical forests. The high occurrence of ring-porosity and semi-ring porosity in Bignoniaceae lianas likely reflects their high sensitivity to water deficit and cambial arrest (Pace et al., 2015; Pace and Angyalossy, 2013), with the cambium being active in the Bignoniaceae liana *Tynanthus cognatus* (Cham.) Miers for only about two months (Lima et al., 2010). Leguminosae also is a promising group for dendrochronology with several lianas with distinct annual growth rings (Brandes et al., 2011, 2015), and something further reinforced by the present study. Malpighiaceae, although with a large number of species with distinct growth rings, are not recommended here, because their growth rings are not as easily seen (check Fig. 3B) as in the previous two families and they tend to get less and less clear while some cambial variants of the group, such as fissured stems, develop (Cabanillas et al., 2017). Two main temperate species have been used in dendrochronological studies, *Hedera helix* L. (Araliaceae) and *Vitis vinifera* L. (Vitaceae) (Castagneri et al., 2013; Davis and Evert, 1970; de Micco et al., 2018; Esau, 1948; Garfi and Ficarrotta, 2003; Heuzé et al., 2009; Maxwell et al., 2016; Nola, 1997; Roig-Puscama et al., 2021; Schnitzler and Heuzé, 2006; Tyminski, 2013; Verheyden et al., 2006), but species from other families are equally good candidates for dendrochronological research.

4.3. Growth ring anatomical markers

The main anatomical markers detected in the present study were thick-walled and/or radially flattened latewood fibre and marginal parenchyma, especially common in tropical species. Semi-ring-porous and ring-porous wood occur mainly in temperate species (Silva et al., 2021;
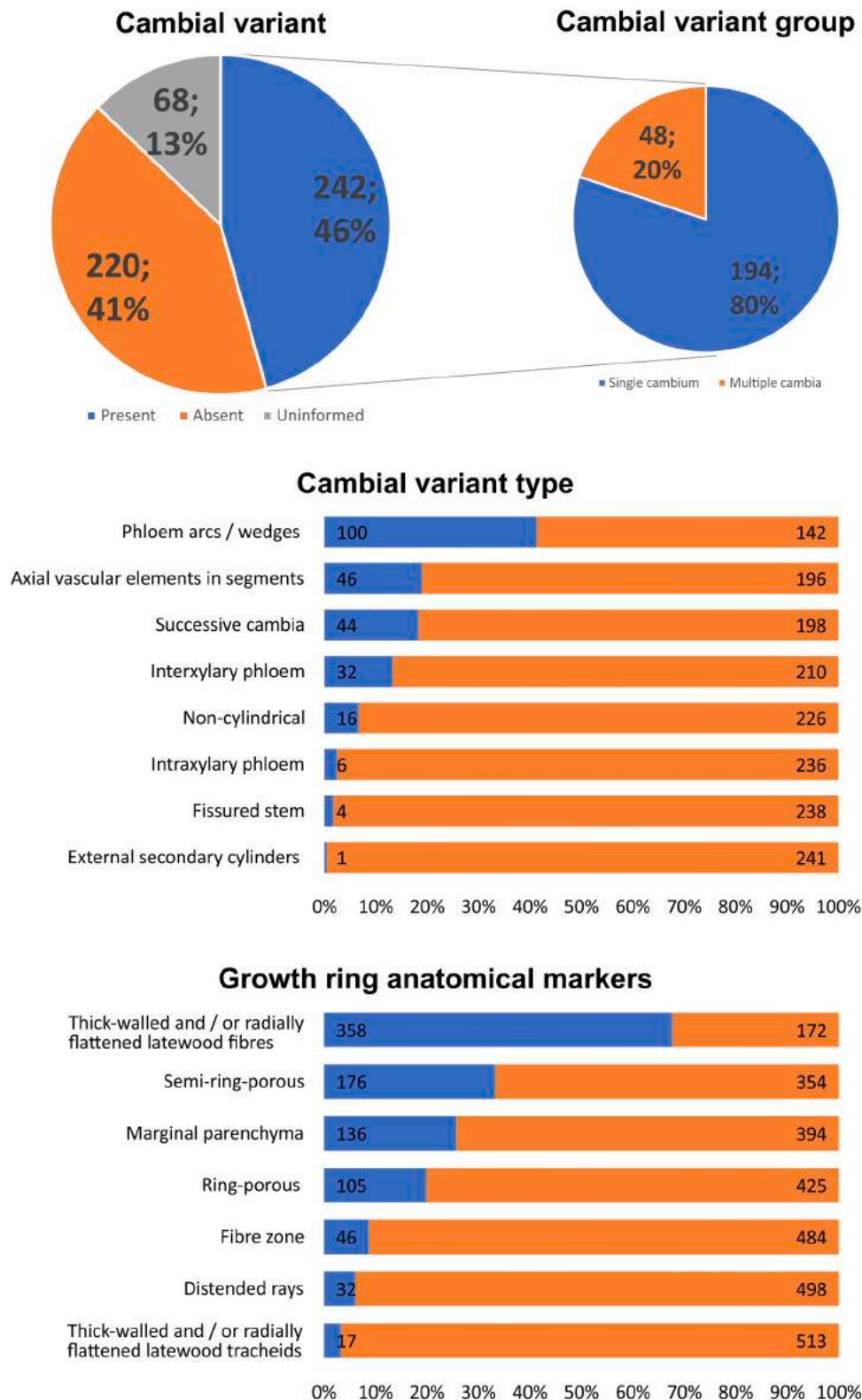
Cambial variant

Cambial variant group

Cambial variant type

Growth ring anatomical markers

Fig. 4. Proportion of lianas with distinct growth ring and cambial variants product of a single cambium or multiple cambia. We detailed the proportion of species with distinct growth rings by cambial variant type and by anatomical growth ring markers. Data source: Table S1. In bar graphs, blue = feature present, orange = feature absent. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Wheeler et al., 2007), but are also found in several tropical lianas, especially in species of Bignoniaceae and Leguminosae, perhaps reflecting a higher sensitivity to seasonal climatic cues than trees.

The anatomical markers of growth rings evolved many times in several lineages of the seed plants, being homoplastic, and reflecting environmental conditions (Schweingruber, 2007; Silva et al., 2021). Favourable and unfavourable conditions for growth can produce thick-walled and/or radially flattened latewood fibres as product of
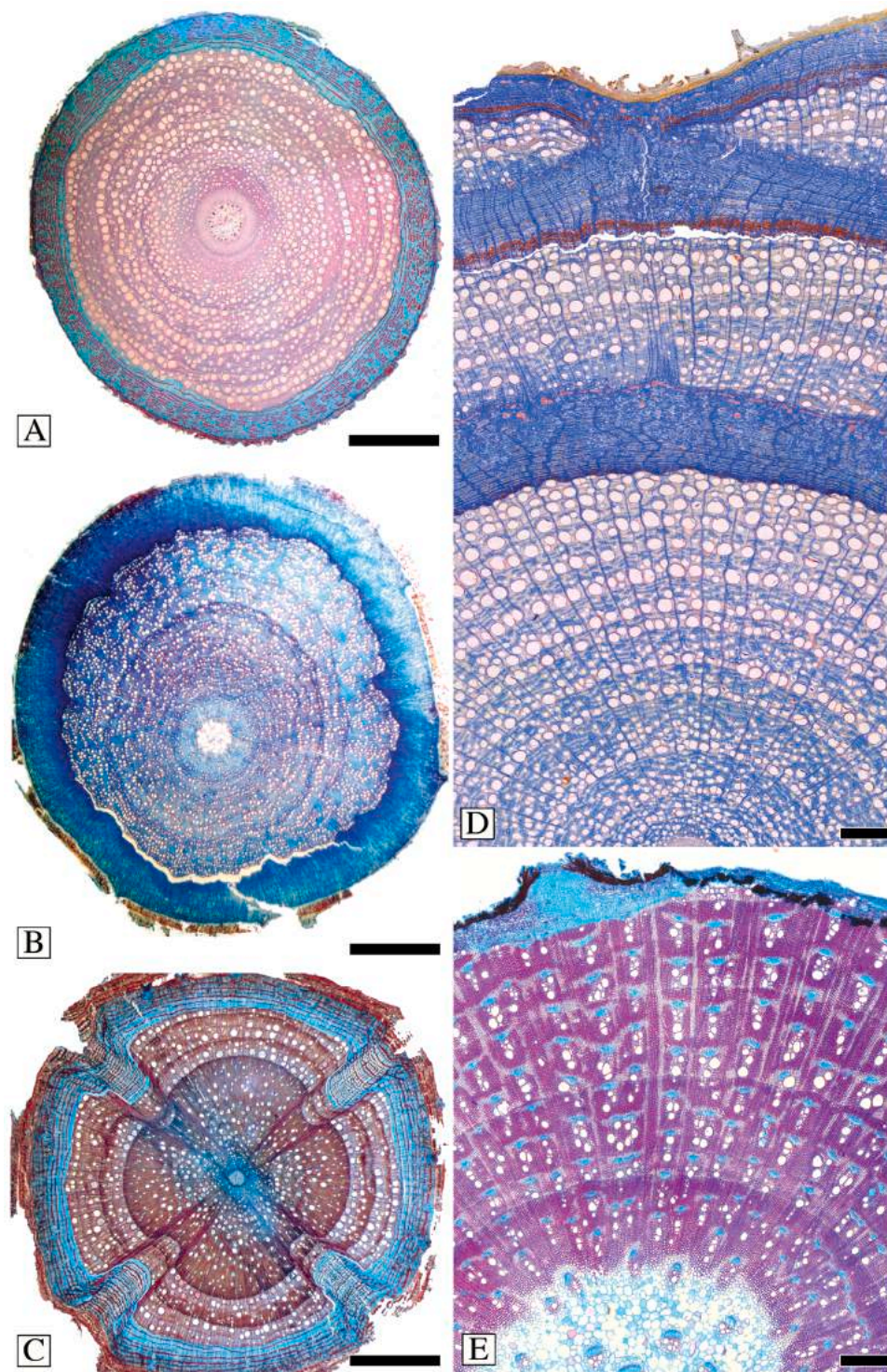
Fig. 5. Growth rings in lianas. A. *Dalbergia frutescens* (Leguminosae), well-delimited growth rings, marked by semi-ring porosity, marginal parenchyma and radially flattened fibres. B. *Heladena multiflora* (Malpighiaceae), growth rings ranging from delimited to almost indistinct, wood diffuse porous, growth rings delimited by radially narrow fibres and marginal parenchyma. C. *Fridericia chica* (Bignoniaceae), stem furrowed with four equidistant phloem wedges. Well-delimited growth rings, marked by semi-ring porosity, marginal parenchyma and radially flattened fibres. D. *Wisteria sinensis* (Leguminosae), stem with successive cambia. Three increments are evident here, and all of them with well-delimited growth rings, marked by ring porosity and radially flattened fibres. E. *Pisoniella glabrata* (Nyctaginaceae), stem with interxylary phloem and medullary bundles. Well-delimited growth rings, marked by radially flattened fibres and a line of axial marginal parenchyma. Scale bars: A, C = 0.8 mm; B = 0.4 mm; D = 2 mm; E = 0.4 mm. Fig. A by courtesy of A. Lima, D by courtesy of the Botanical Society of America, Onyenedum and Pace (2021), E by courtesy of Israel Cunha Neto.

changes in the plant physiology and consequent cambial products. This feature increases mechanical support and would be associate to the occurrence of wide vessel elements in ring-porous wood (Silva et al., 2021). Semi-ring-porous and ring-porous woods are thought to support efficient water conduction during the wet season or summer and safety in the dry season or winter (Silva et al., 2021). Marginal parenchyma would be associated to the storage of non-structural carbohydrates and is frequent in tropical species, especially in tropical dry forests and deciduous species (Silva et al., 2021). These growth ring anatomical markers mentioned above were frequent in lianas, which would be

associated to the abundance of lianas in seasonal dry forests (DeWalt et al., 2015), where they experience seasonal favourable and unfavourable conditions. These features also are highly homoplastic, arose and were lost in several lineages of plants, as the liana habit (Gentry, 1992; Isnard and Feild, 2015; Silva et al., 2021).

4.4. Annual growth rings and seasonal cambial activity in lianas

In many lianas, especially from temperate regions, annual growth rings have been proven by cross-dating and correlation with climatic
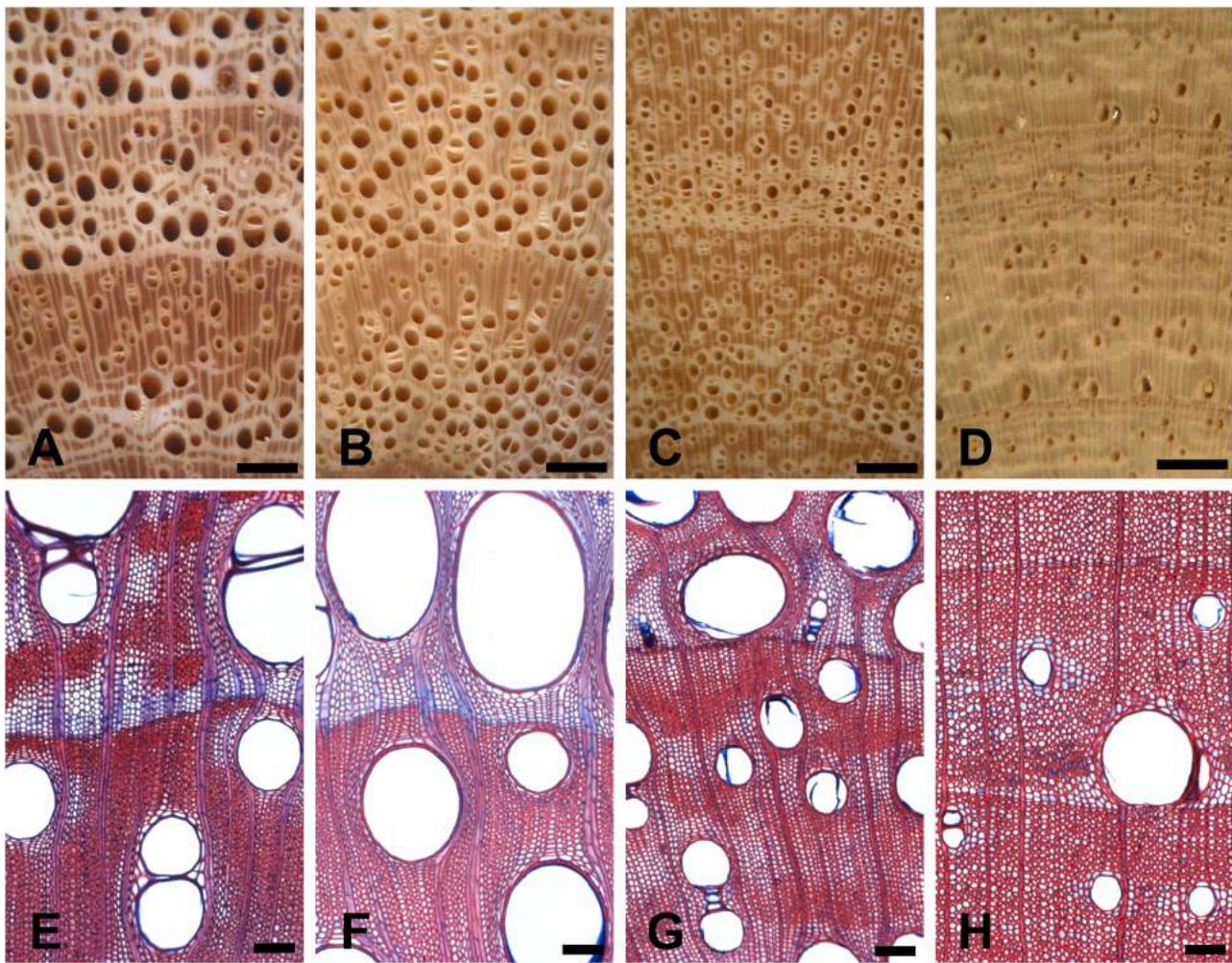
Fig. 6. The main growth ring markers in four leguminous lianas under stereomicroscopy (A–D) and bright field microscopy (E–H). *Piptadenia micracantha* Benth. (A, E), *Piptadenia adiantoides* (Spreng.) J.F.Macbr. (B, F), *Acacia tenuifolia* (L.) Willd. (C, G), and *Dalbergia frutescens* (Vell.) Britton (D, H). These species present growth ring boundaries delimited by thick-walled and radially flattened latewood fibres (E–H), semi-ring-porosity (A–D), marginal parenchyma (A–H), and fibrous zone (A–D). Scale bars: A–D = 1 mm; E–H = 0.1 mm.

and environmental variables (de Micco et al., 2018; Garfi and Ficarrotta, 2003; Heuzé et al., 2009; Maxwell et al., 2016; Nola, 1997; Tyminski, 2013). In tropical lianas, more methods have been applied to test the annual nature of the growth rings, such as vascular cambium activity, cambial wounding, cross-dating and relationship with climatic factors, demonstrating an annual growth, with active cambium during the wet season and inactive cambium during the dry season (Angyalossy et al., 2015; Brandes et al., 2011, 2015; León-Gómez and Monroy-Ata, 2005; Lima et al., 2010). Some studies suggest that lianas can keep growing during the dry seasons, even if at a lower rate than that of the wet season, conferring an adaptive advantage over the trees and explaining the abundance in the seasonal forests (León-Gómez and Monroy-Ata, 2005; Schnitzer, 2005). Based on these findings and considering the low number of papers that have demonstrated the seasonal cambial activity and annual growth rings (~ 13), as well as the low number of species evaluated (~ 17), we recommend testing the cambial activity periodicity and growth ring formation in lianas to advance dendrochronological applications, mainly in species with cambial variants since it is so underexplored (Angyalossy et al., 2015). Several methods can be used to this as cambial wounding, cambial activity, cross-dating, radiocarbon, and x-ray densitometry (Brandes et al., 2011, 2015; Callado et al., 2013; Lima et al., 2010; Linares et al., 2017; Stahle, 1999; Worbes, 1995).

4.5. Challenges and research priorities

Most of the lianas with distinct growth rings reported in this study have cambial variants, mainly produced by a single cambium. When the stem is regular, the growth ring analysis can be performed by conventional dendrochronological methods (Speer, 2010). But, when there are cambial variants, the development of new methodologies might be necessary to overcome their variant type of growth. For example, in species with phloem arcs/wedges or non-cylindrical stem (flattened, lobed and quadrangular) it will be necessary to evaluate the differences between growth rings in arcs, wedges, and lobes. Less xylem is produced under the phloem wedges by the variant cambia and is side-by-side to a xylem produced previously (check Fig. 5C). In Bignoniaceae, it has been shown that cambial activity in the arcs starts near the phloem wedges, then progressing towards the centre of the arcs, often producing wedging rings in stem's central portions (Lima et al., 2010). The cambial variant produced by a single cylindric cambium, as axial vascular elements in segments or diffuse interxylary phloem, likely can also be analysed by conventional dendrochronological methods, with attention to the large rays or phloem strands. But lianas with concentric interxylary phloem, as have been shown recently in Nyctaginaceae (Cunha Neto et al., 2021), must be analysed in light of the cambial activity to elucidate the process of growth rings and phloem islands formation. Some legume species with lobed, quadrangular stems and phloem

arcs/wedges, although presenting distinct growth rings, were disregarded from further dendrochronological studies because of the oscillation in boundaries distinction and difficulties in analyses (Brandes et al., 2011). However, even with considerable structural variability in wood triggered by evolutive, mechanical and ecophysiological processes, if suitable methods are applied, invaluable information can be recovered from growth rings (Büntgen et al., 2014; Schweingruber and Poschlod, 2005; Schweingruber, 2007).

Some lianas with distinct growth rings have multiple cambia (e.g., *Wisteria sinensis*, Leguminosae; Nejapa et al., 2021; Fig. 5D). In this case, it will be necessary to study successive cambia formation process and activity to evaluate ways to get temporal information. What may be the 10th growth ring in the central cylinder can be the second of the next growth increment produced by the successive cambium (check Fig. 5D). In addition, successive cambia are sometimes confused with growth rings. Although there is evidence that successive cambia can be formed annually and keep active for one growing season (Rajput, 2016), they are different features. Successive cambia would bring valuable temporal information if periodicity and the process of formation be verified.

Wedging rings (discontinuous rings) have been reported in lianas (Brandes et al., 2011; Lima et al., 2010). However, they are not exclusive of them and may be also present in trees (Fritts, 1976; Speer, 2010). More studies are critical to evaluate how frequent is this feature, which may impair the synchronisation of series, mainly if using samples collected with an increment borer. Moreover, lianas display complex 3D architectures and therefore standard procedures for liana collections must carefully consider the research objectives. Some of these challenges include lianas that branch close to the ground with a very irregular main stem, twining lianas, lianas that loop to the ground and root before ascending into the canopy, lianas that loop to the ground and root, but the loops have branches ascending to the canopy, and lianas with adventitious roots (Gerwing et al., 2006). In that case, using complete or partial sections of liana stems would be recommended.

Mechanical properties of liana stems change with age. The wood stiffness is affected by the stem form, cellular composition and commonly decreases due to the mechanical demands of the host/support relationship (Rowe et al., 2004). Moreover, in many species, a self-supporting period is detected until a support is found, leading to a wood anatomy shift after reaching the support (Isnard and Silk, 2009; Rowe and Speck, 2015). The attachment mechanisms also can affect lianas' growth by anatomical, hydraulic conductivity and cambium transcriptional profile changes (Lima, 2020). Dendrochronological studies can help to understand the structural changes in lianas over time and the environmental factors associated with growth form plasticity (Rowe and Speck, 2015).

Lianas, with their inherent complexity, also are challenging in quantitative ecology. Populations age structure, basal area increment, biomass accumulation and carbon sequestration are some examples of fundamental data to understand forest structure and dynamics, but hard to obtain. Recent progresses have been observed in biomass calculation by allometric equations for tropical lianas (Addo-Fordjour and Rahmad, 2013; Gehring et al., 2004; Miao et al., 2016; Schnitzer et al., 2006) and in the understanding liana-carbon relationship (di Porcia e Brugnera et al., 2019; Manzanedo et al., 2018; van der Heijden et al., 2015), populations age structure (Schnitzler and Heuzé, 2006), and other parameter associated to the lianas on forest structure (DeWalt et al., 2015; Schnitzer et al., 2015; Vargas et al., 2021). But knowledge gaps yet remain, especially in age and long-term growth dynamics. Methods to determine growth rates and the age of individuals are necessary. Lianas have a plastic growth, changing its rates abruptly over their lifetime, preventing estimates of age by size (Ladwig and Meiners, 2015). Their growth rings can provide age and growth assessments and help to infer forest structure and dynamics, the process of lianas colonisation and liana-host interactions (Castagneri et al., 2013; Godoy-Veiga et al., 2018; Nola, 1997; Venegas-González et al., 2020).

Another intriguing question remains in the mechanistic explanation

of liana global abundance. Lianas are more abundant in seasonal dry forests, where they are paradoxically more susceptible to cavitation because of their efficient but vulnerable conducting system. Deeper roots in lianas have been presented as the main explanatory mechanism to solve this paradox, allowing lianas to access deep water sources and growth in the dry seasons (Schnitzer, 2005). But this mechanistic explanation lacks empirical evidence, and some findings did not corroborate this hypothesis (Amorim et al., 2018; Angyalossy et al., 2015; Brandes et al., 2015, 2011; Carvalho et al., 2016; Lima et al., 2010). New hypotheses have been proposed relating this abundance pattern to drought resilience and to different water uptake, distribution, and storage mechanisms (Amorim et al., 2018). Moreover, the increase in liana abundance has been associated with the increase in atmospheric carbon, elevating lianas growth and favouring their competitiveness (Granados and Körner, 2002; Schnitzer, 2005). As a feature of the secondary vascular tissue, growth rings can provide temporal evidence about hydraulic and growth changes and can help test hypotheses, as that lianas growth during the dry season and that recent increase in atmospheric carbon favoured the lianas' growth.

Although lianas have been ignored for a long time, advances were achieved in the last decades with a rising number of publications, helping to elucidate the biology, evolution, and ecology of lianas (Isnard and Silk, 2009; Schnitzer et al., 2015; Vargas et al., 2021). Multiscale and multidisciplinary research approaches are fundamental for achieving further advances (Onyenedum and Pace, 2021; Isnard and Silk, 2009) and challenges arise as climbing plants present so many ecological, functional and structural peculiarities. These features affect growth rings formation, climate response, ecological sensitivity and, consequently, bring difficulties to cross-date and extract associated data. Evaluate the periodicity of growth ring formation, time-series synchronisation, consistency in growth trends, climate-growth and environment-growth relationship are research priorities that can help us understand the mechanisms associated with lianas' distribution, diversity and responses to climate changes.

5. Conclusions

We could verify that the growth ring in lianas is a common feature and occur in lianas from both tropical and temperate regions, being described in at least 74 families. They are present in lianas with and without cambial variants, with one or multiple cambia in the stems. The most common growth ring markers were thick-walled and/or radially flattened latewood fibres, semi-ring-porous, marginal parenchyma and ring-porous. Since there is a need to develop reliable methods to measure liana growth and age, we hope that the lianas list presented here can leverage further analyses, evaluating the periodicity of growth ring formation, and advancing in the dendroecological application.

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.

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2021.125920.

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