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Evaluating the annual nature of juvenile rings in Bolivian tropical rainforest trees

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Abstract Knowledge on juvenile tree growth is crucial to understand how trees reach the canopy in tropical forests. However, long-term data on juvenile tree growth are usually unavailable. Annual tree rings provide growth information for the entire life of trees and their analysis has become more popular in tropical forest regions over the past decades. Nonetheless, tree ring studies mainly deal with adult rings as the annual character of juvenile rings has been questioned. We evaluated whether juvenile tree rings can be used for three Bolivian rainforest species. First, we characterized the rings of juvenile and adult trees anatomically. We then evaluated the annual nature of tree rings by a combination of three indirect methods: evaluation of synchronous growth patterns in the tree- ring series, ^{14}C bomb peak dating and correlations with rainfall. Our results indicate that rings of juvenile and adult trees are defined by similar ring-boundary elements. We built juvenile tree-ring chronologies and verified the ring age of several samples using ^{14}C bomb peak dating. We found that ring width was correlated with rainfall in all species, but in different ways. In all, the chronology, rainfall correlations and ^{14}C dating suggest that rings in our study species are formed annually.

Keywords Juvenile tree-rings · Adult tree-rings · Tropical forest · Dendrochronology · ^{14}C bomb peak dating · Rainfall correlations

Introduction

The juvenile stage is crucial in the life cycle of tropical forest trees. In this phase, trees grow from the dark forest understory to the forest canopy, a process that lasts several decades to a century (Lieberman and Lieberman 1987; Martínez-Ramos and Alvarez-Buylla 1998; Worbes and Junk 1999; Vieira et al. 2005). Knowing which factors govern juvenile growth is important to understand how trees successfully reach the canopy (Brienen and Zuidema 2006a) and for designing forest management systems (Brienen and Zuidema 2006b). Notwithstanding the importance of information on juvenile tree growth, long-term data are hardly available, as most permanent research plots exist for less than 20 years (Peacock et al. 2007). Tree-ring analysis offers the possibility to reconstruct the full growth history of a tree, including its juvenile phase, and thus provides the essential information to evaluate juvenile growth strategies (Worbes 1999, 2002; Brienen et al. 2006; Rozendaal et al. 2010).

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Over the past decade, the number of ring analysis studies of tropical trees has increased (Worbes 2002; Brienen and Zuidema 2005; Schongart et al. 2006). In tropical forests with a distinct dry season, clear tree rings can be recognized anatomically, and these are often annual (Worbes 1999; Alves and Angyalossy-Alfonso 2000). Most tree-ring studies have considered only adult rings, discarding the innermost juvenile rings of adult trees, or the recently produced rings of extant juvenile trees. Juvenile rings were not used as their annual nature is often questioned (Dünisch et al. 2003; Brienen and Zuidema 2005). Three reasons to doubt the annual character of juvenile rings have been suggested: (1) diameter growth of juvenile trees may be limited by light availability rather than seasonally low water availability, as is the case for adult trees (Sass et al. 1995). During periods of deep shade, cambial dormancy may be induced in these trees, resulting in rings that are unrelated to seasonality (Fritts 1976; Carlquist 2001). (2) The anatomical ring definition of juvenile trees may differ from that of adult trees of the same species (Fukazawa 1984; Worbes 1999; Carlquist 2001). Also, juvenile rings of slow-growing individuals often exhibit a high frequency of wedging rings (Sass et al. 1995). (3) The high number of rings counted on some juvenile trees makes their annual nature suspicious if one takes into account that most tropical forests are rather dynamic (Baker et al. 2005).

Thus, in order to apply ring analysis to evaluate growth patterns of juvenile tropical trees, clarity should be obtained about the recognition and the annual character of juvenile rings. In natural forest stands, directly checking the annual nature of rings by ring counting in trees of known age (Worbes 1995) is usually impossible. There are several alternatives to evaluate periodicity in juvenile growth in an indirect way. First, a commonly used and successful method is to search for synchronous growth patterns across trees-ring series, and use these to develop a chronology. The chronology describes the common fluctuations of standardized ring width values of a group of trees (Stahle 1999; Worbes 1999; Brienen and Zuidema 2005; Schongart et al. 2006). Finding such common growth fluctuations over time is an indication that rings are likely to be formed annually. Another method is to correlate the tree-ring chronology with instrumental climate data (rainfall, temperature). Significant correlations with climatic variables provide very strong support that rings are formed annually (Worbes 1999; Brienen and Zuidema 2005; Schongart et al. 2006). If a chronology cannot be built, or correlations with climatic variables are not found, there is still a third way to evaluate the periodicity of ring formations by using the ^{14}C bomb peak dating (Worbes and Junk 1989; Vieira et al. 2005). The nuclear experiments of the late 1950s and 1960s raised the levels of ^{14}C in the atmosphere (Hua and Barbetti 2004). These atmospheric ^{14}C values were compiled by several researchers and, nowadays, a calibrated curve of the excess of ^{14}C [p.mil] (D^{14}C) allows a confident dating based on the isotope ^{14}C levels after 1955 (Hua and Barbetti 2004). This method is especially useful for dating rings of juvenile trees of which the inner rings were formed after 1955.

In this study, we aimed to evaluate the annual nature of juvenile tree-rings for three Bolivian rainforest species. To this purpose, we first, described the juvenile ring structures anatomically and compared these with adult rings. We then used a combination of methods (evaluation of synchronous growth patterns in the tree-ring series, ^{14}C bomb peak dating and correlations with rainfall) to evaluate the annual character of juvenile rings. We end by discussing the suitability of these methods.

Study area and species

The study area is located in the northern part of Bolivia, Department of Pando. The climate in the region is seasonal, with a distinct dry season from May to September with precipitation below 100 mm per month. The mean total precipitation is 1,690 mm and the mean temperature is 27°C (Riberalta, 11°00′S 66°07′ W, averages for 1943–2007 and 1951–2004, respectively). The study was carried out at the logging concession “Los Indios” (10°26′S, 65°33′W) located at 86 km from the town of Riberalta. The forest at the study site is semi-deciduous forest with a dense canopy at 30–35 m and some emergent trees up to 45 m. The understory is composed of trees of 15–25 m and a shrub level of variable density of 1–6 m height (Navarro and Maldonado 2006).

We studied three canopy tree species *Clarisia racemosa* Ruiz & Pavón (Moraceae), *Peltogyne* cf. *heterophylla* M.F.Silva (Fabaceae) and *Cedrelinga catenaeformis* Ducke (Fabaceae), (further referred to by genus name). The study species differ in shade tolerance but none of them is a pioneer (sensu Swaine and Whitmore 1988) (see Table 1 for more details). Two of the species have been used for adult tree-ring research in the past (Brienen and Zuidema, 2005, 2006a, b; Brienen et al. 2006), but definitions for juvenile rings have not been established.

Data collection

From April to July 2007 we collected 45–48 stem disc samples per species from trees of 1- to 35-cm-diameter at breast height (dbh) (Table 1). Using a chainsaw, the samples of *Clarisia* were collected at 50 cm height and *Peltogyne* and *Cedrelinga* were collected at 1 m. Additionally, we collected three wood pieces of 20 cm^2 per species, from

Table 1 Characteristic of the studied species

Species	Family	Ecological group	Leaf fall behaviour		Collected samples	
			Juvenile	Adult	No.	dbh range[d]
Clarisia racemosa Ruiz and Pavón	Moraceae	Shade tolerant[a]	Evergreen[c]	Evergreen[a]	45	1–30
Peltogyne cf. *heterophylla* M.F. Silva	Fabaceae	Shade tolerant[b]	Evergreen[c]	Brevi-deciduous[b]	48	1–30
Cedrelinga catenaeformis Ducke	Fabaceae	Long-lived pioneer[a]	Evergreen[c]	Brevi-deciduous[a]	46	1–35

[a] (Mostacedo et al. 2003)

[b] (Pinard et al. 1999)

[c] Personal observations

[d] dbh measured in centimetres at 1.30 m height

large felled trees, which were used for characterization of adult rings. All samples were air-dried and polished using grits up to 1,000. In order to improve the quality of the grinding, *Clarisia* and *Peltogyne* were polished in a constant flow of water.

We then selected a subsample of five stem discs per species, based on ring visibility and estimated dates of the rings between 2 and 10 cm dbh in the period 1959–1980, this, to improve the accuracy of the ^{14}C dating method. Each disc was cut cross-sectionally in order to obtain two disc copies. On each copy the same main radius of 2 cm-width was marked. As main radius we selected the longer radius or the radius that had best visibility of the rings. One of the copies was used to take sections for anatomical tree-ring characterization while the other was prepared for tree-ring analysis and ^{14}C dating.

Anatomical tree-ring characterization

Pieces of wood of 2 cm^3 from the juvenile discs were obtained in a radial sequence from bark to pith. At the same time, a piece of 2 cm^3 was obtained from each adult tree. The wood pieces of *Clarisia* and *Peltogyne* were softened by boiling in water for more than 120 h while *Cedrelinga* was boiled for approximately 20 h. Then, we obtained transversal sections, of 20- to 40-µm-thickness, with a sliding microtome. After dehydrating we stained the sections using safranin 1% and astra blue 1% (Gerlach 1984). The sections were then fixed on permanent slides for microscopy observations. We also examined the polished samples using a stereomicroscope. The anatomical characteristics that define the ring boundaries were photographed under the stereomicroscope and microscope.

Tree-ring series and synchronous growth

The tree-rings were identified on all 45–48 samples of juvenile trees using a 40× magnification stereomicroscope. To detect ring structures, we used anatomical markers of ring boundaries, characterized from the transversal sections. We pinpoint the rings in the main radius and in at least two other radii per tree. The samples were dated following the Schulman convention (1956) by which the calendar year assigned to the ring correspond to the year in which growth begins. We visually cross-dated the radii within the trees following every tenth ring along the disc, correcting, in this way, for locally absent and false rings. Rings widths were measured along the radii at 0.01 mm precision using a LinTab 5 measurement device and TSAPWin software.

The quality of the cross-dating within and between trees was verified using the software COFECHA (Holmes 1983). A mean stand chronology per species was developed using cross-dated trees that showed a synchronous growth pattern. Each tree-ring series was first detrended using the Hugershoff growth curve provided by ARSTAN, this in order to remove the size-dependent growth variation. Then each tree was standardized and then averaged with the others (Cook 1985; Cook and Kairiukstis 1990). Standardization was performed using the windows version of ARSTAN (Cook and Kairiukstis 1990; Cook and Holmes 1996). ARSTAN generates standard chronologies by combining standardized tree-ring series with bi-weight robust estimation (Cook and Holmes 1996). We used a 20-year window with an overlap of 10 years between adjacent windows to determine the mean correlation coefficients (Rbar; Briffa 1995).

^{14}C dating

^{14}C bomb peak dating was applied to five samples per species. We collected samples of at least 50 mg of wood from three tree-rings supposedly formed in the period 1969–1981. The samples were taken between 2 and 5 cm from the pith. An extra sample was collected from four trees (two for *Clarisia* and two for *Peltogyne*) in the period 1957–1959 closer to the pith in order to verify the annual character of the earlier rings. The $D^{14}C$ [p.mil] determination was done in the holocellulose portion of the samples, at the Van de Graaff Laboratory at Utrecht University, according to their protocol for Accelerator Mass Spectrometry analysis (van der Borg et al. 1987).

We determined the date for the obtained positive $D^{14}C$ values using the program CALIbomb (http://intcal.qub.ac.uk/CALIBomb) with the data set compiled for the southern hemisphere (SH1) (Hua and Barbetti 2004). For each sample, we summed all probabilities of the possible ages up to $\approx 95\%$ (2-sigma errors; $P < 0.05$) and assigned the most likely date based on all samples belonging to one tree.

Rainfall correlations

We evaluated the presence of correlation between the standard chronologies and the rainfall data using the monthly precipitation record for Riberalta for 1943–2000. Significant correlations of the chronology with rainfall were checked for the current growing season (Sep–Apr, $T-0$), 1 year ($T-1$) and 2 years before ($T-2$) the year of ring formation. In this study, annual precipitation was considered as the sum of the monthly precipitation from September to August. The record for Riberalta was provided by SENAMHI (Servicio Nacional de Meteorologia e Hidrologia, Bolivia). For *Cedrelinga* we used a shorter period (1957–2006), as juvenile trees were rather young. We calculated Pearson correlations in SPSS v.16.0

Results

Anatomical tree-ring characterization

All three species presented diffuse porous rings at both adult and juvenile stages (Figs. 1, 2, 3). We did not find indications that ring structures differ across life stages for our study species. However, there were differences in the visibility of the ring-boundaries between juvenile and adult trees.

In *Clarisia*, juvenile growth ring boundaries were not clearly distinguishable. There is a band (two to four cells wide) of marginal parenchyma cells (Fig. 1), normally followed by a fibrous zone (Fig. 1a, b, d). In the juvenile phase, the marginal parenchyma can be both at the end or the beginning of the fibrous zone. Confluent parenchyma forming bands can obscure the ring-boundary identification when it overlaps with the marginal parenchyma in both juvenile and adult trees. In adult trees, however, rings are identified with less difficulty, as the marginal parenchyma is not very often overlapping with confluent parenchyma forming bands (Fig. 1b, d).

Peltogyne presented clear ring boundaries (Fig. 2). Marginal parenchyma and small-diameter vessels can be used as ring boundary markers. Also, the degree of confluence of vasicentric and aliform parenchyma is important to distinguish the boundaries (Fig. 2b, d). In juvenile wood, the tree-ring identification presents some difficulties due to the existence of deposits in the vessels and axial parenchyma, which produces a general darkening of the wood (Fig. 2b). These darker regions are caused by fibrous zones, regions where there are smaller amounts of parenchyma and vessels (Fig. 2b). In addition, rings closer to pith can be discontinuous and wedging rings are common (Fig. 2c). We therefore advise that boundary structures that are visible in at least 25% of the discs are considered as ring boundaries. We found resin/mucilage canals in juvenile and adult trees, but these are not strictly associated with ring limits (Fig. 2d).

The ring boundaries of *Cedrelinga* trees are not easily distinguishable in both juvenile and adult stages (Fig. 3). Fibre cells of the late wood become thick-walled and radially flattened (Fig. 3c, d). These boundary markers are not always evident as seen in Fig. 3b, and may become more dubious in periods of slow growth in adult trees. False rings are common, formed by discontinuous thick-walled and radially flattened fibre cells (Fig. 3c, d). Thus, without adequate training ring identification in the adult and juvenile stage may be cumbersome.

Tree-ring series

Results from COFECHA indicated high inter-series correlation within trees for all the species (Table 2). A group of trees with synchronous growth pattern was identified for each species, leading to a successful chronology development (Fig. 4; Table 2). The chronology for *Clarisia* included 29% of the all sampled trees, and this was 27% for *Peltogyne* and 26% for *Cedrelinga*. All chronologies included at least two of the five trees used for ^{14}C dating. In the case of *Cedrelinga*, we used the ^{14}C dating to correct ring definitions in three samples before building the chronology. The Rbar of the chronologies was 0.25, 0.27 and 0.21 for *Clarisia*, *Peltogyne* and *Cedrelinga*, respectively, which verifies the presence of synchrony. The trees used to build the chronologies had variable diameter and age (Fig. 5).

^{14}C dating

^{14}C bomb peak dating was conducted in order to verify the annual nature of the juvenile tree-rings. Figure 6 shows the relation of sampled ring date obtained from ring counts and that determined by ^{14}C dating. The ring dates were verified (with a 95% confidence level) for two discs (trees) of

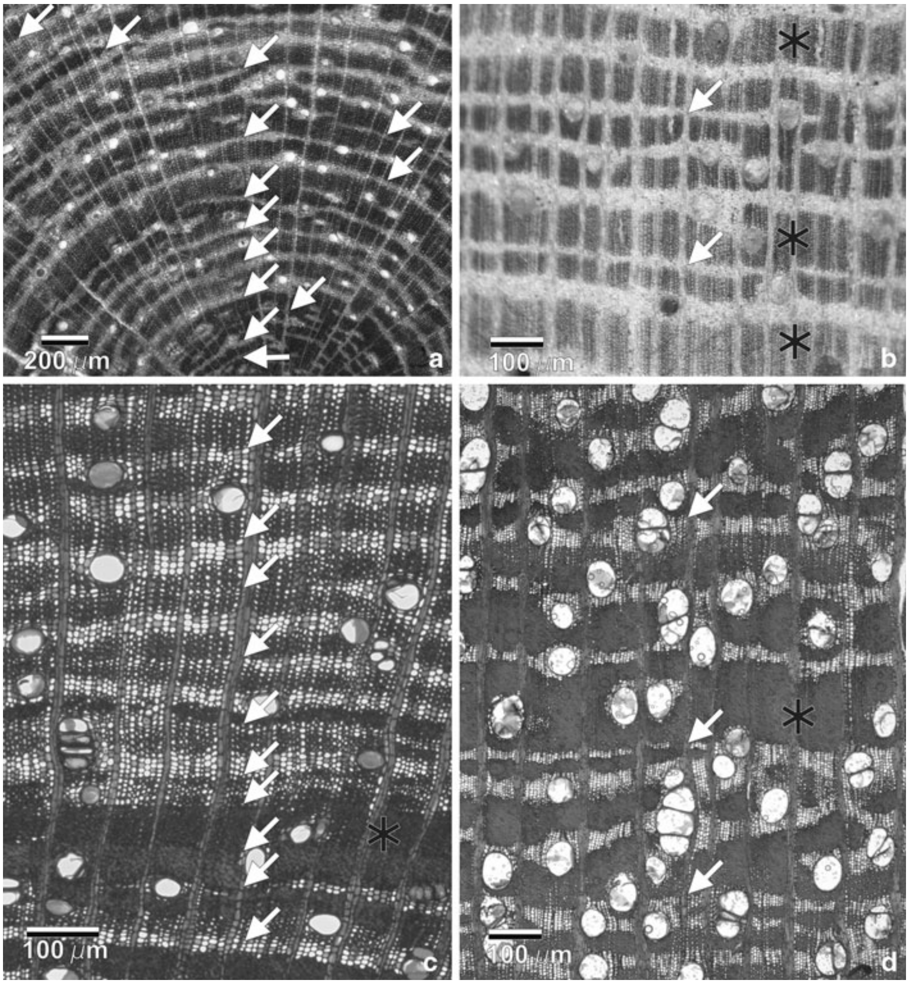

Fig. 1 *Clarisia racemosa*. Transversal sections. **a**, **c** Juvenile tree, **b**, **d** Adult tree. Growth ring markers characterized by a band of marginal parenchyma (*arrows*). Fibrous zones indicated by *asterisks* (*)

Clarisia and three discs of *Peltogyne*, with an error of ±1 year. These trees had been already included in the chronologies.

For those rings for which the ring date did not match the ^{14}C date, we calculated the difference in years and compared these for each disc. In the supplementary information (S1) we provide a list of ring age, ^{14}C age and their difference for all sampled rings. If the difference in dating was constant across samples from one disc, the error in the ring counting occurred in the wood that was formed at a later date (thus, in direction to the bark). Still, in this case, the occurrence of consistent differences in age indicates that during the period covered by the sampled rings (between oldest and youngest rings) rings were formed annually. We found that this was the case for most of the discs and species (Fig. 6, S1). The maximum difference in dating was 9 years for *Clarisia*, 17 years for *Peltogyne* and >40 years for *Cedrelinga*. Large dating errors in ring analysis are probably associated with long periods of growth suppression, in which the growth in diameter is reduced such that ring recognition is not possible.

In the case of *Cedrelinga*, none of the ring dates was confirmed by ^{14}C dating (Fig. 6), but the consistent dating differences across samples within discs suggest annual ring formation. Based on the ^{14}C dating, ring boundary definition was improved, and tree-ring identification on three of the discs was corrected: in these samples, we initially identified false rings or we missed rings in the more recent wood. These corrected samples were used as a base to build the chronology. A fourth sample could not be corrected given the difficulty of ring recognition. The fifth sample had a D^{14}C value much younger than expected (S1), which made it impossible to obtain a precise dating (data not shown in Fig. 6).

Rainfall correlations

Following verification of the annual character of the juvenile tree-rings, we proceeded with correlating chronologies with rainfall records. The correlation functions exhibited a different pattern among species. The chronology for *Clarisia* showed a significant negative correlation

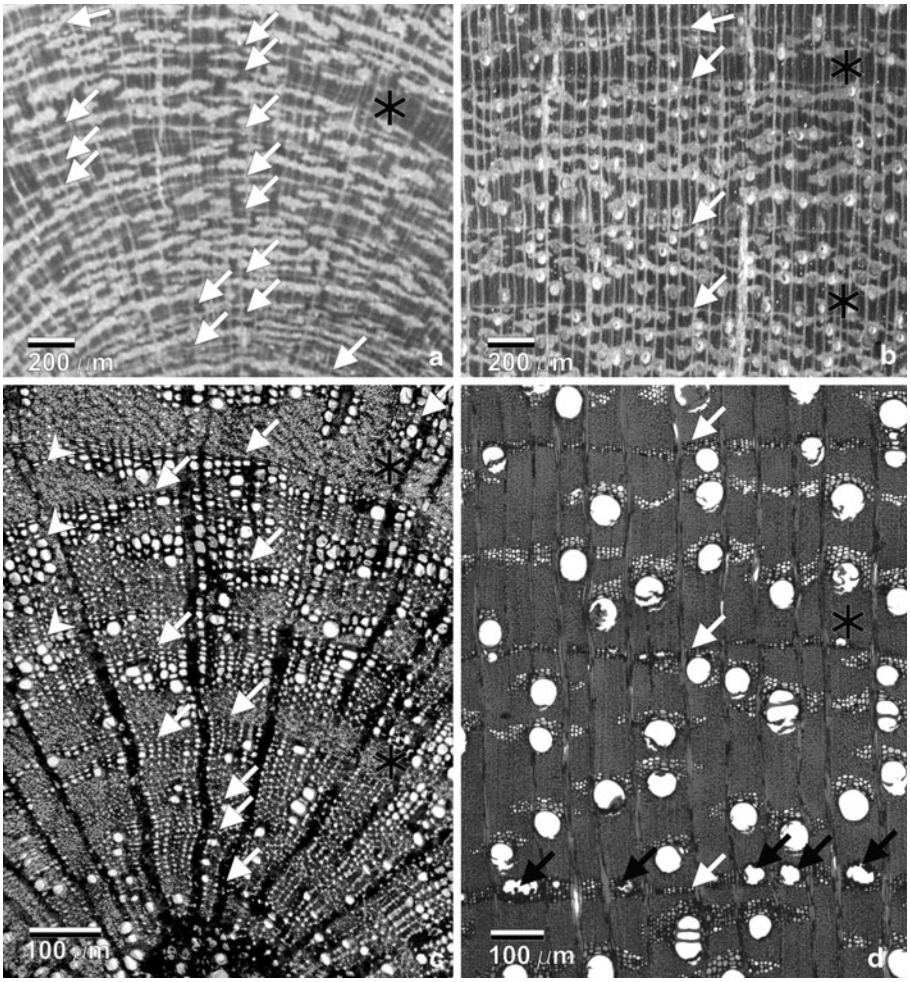

Fig. 2 *Peltogyne* cf. *heterophylla*. Transversal sections. **a**, **c** Juvenile tree, **b**, **d** Adult tree. Marginal parenchyma and small-diameter vessels can be used as ring boundary markers (**a**–**d** *white arrows*). Fibrous zones indicated by *asterisks* (*). *Rings* closer to pith can be discontinuous and *wedging rings* are common (**c** *arrow heads*). Resin/mucilage canals in juvenile and adult trees (**d** *black arrows*)

with precipitation in December, January and February of the current growing season. This negative correlation was also significant when we accounted for the total rainfall in the growing season (September–April) and the annual total precipitation (September–August, Fig. 7). The correlation for *Peltogyne* was positive ($P < 0.05$) with rainfall 1 year prior to the year of ring formation. Also, a general positive relation of ring width with rainfall during the previous year was found, but this was significant only for total dry-season rainfall and total annual rainfall (Fig. 7).

Surprisingly, the chronology of *Cedrelinga* showed a negative overall response to precipitation (Fig. 7). Wider rings in this species appeared to be associated with low wet-season rainfall during the current growing season or low total annual rainfall 2 years before ring formation (Fig. 7).

Discussion

Our results suggest that juvenile tree-rings of three Bolivian rainforest species are produced annually. In all cases, the annual character of the ring formation was verified by checking for synchronous growth patterns, ^{14}C bomb peak dating and correlations of ring width with rainfall.

Due to the ecological differences between the juvenile and adult trees of the studied species (Table 1), we expected variations in the anatomical ring characterization as suggested by some authors (Fukazawa 1984; Carlquist 2001). However, these differences were not distinct at ring-boundary level. Probably, other variables such as vessel distribution, vessel number, vessel area (Heliñska-Raczkowska and Fabisiak 1999; Domec and Gartner 2003; Christensen-Dalsgaard et al. 2007) or measures of the axial parenchyma (Climent et al. 1998) can provide more information on variation in anatomy between juveniles and adults trees.

The ^{14}C dating proved to be a useful tool to verify the annual nature of the rings of *Clarisia* and *Peltogyne*. In the case of *Cedrelinga*, which presented more difficulties in the boundary definition, the use of ^{14}C allowed the correction of misidentified ring boundaries. Later, using the corrected samples as a basis, we built a chronology for this species. As the combination of methods has provided clarity on the

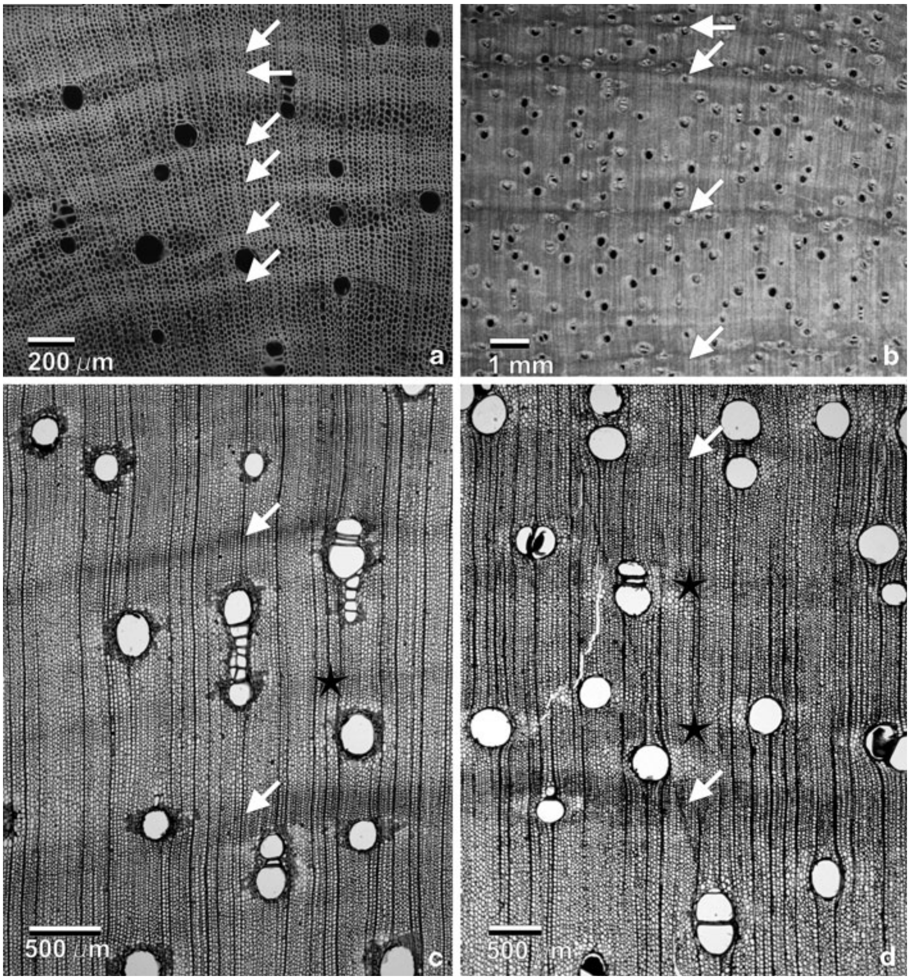

Fig. 3 *Cedrelinga catenaeformis*. Transversal sections. **a**, **c** Juvenile tree, **b**, **d** Adult tree. Growth ring markers characterized by thick-walled and radially flattened latewood fibres. **a**, **b** General aspect of the growth ring markers (*arrows*), **c**, **d** details of the thick-walled latewood fibres of the growth rings (*arrows*). False rings indicated by *stars*

Table 2 Statistics of the tree-ring chronologies

Species	Chronology time span	Number of trees (radii)	Tree-ring index		Mean sensitivity*	Serial correlation*	Autoregresion order			Rbar	
			Mean	SD			T−1	T−2	T−3	Mean	SD
Clarisia	1837–2006	14 (41)	0.94	0.35	0.47	0.36	0.40	0.11	–	0.25	0.24
Peltogyne	1840–2006	13 (39)	0.97	0.42	0.68	0.38	0.35	0.31	−0.24	0.27	0.29
Cedrelinga	1957–2006	12 (38)	1.00	0.28	0.47	0.37	0.23	–	–	0.21	0.04

All data presented, by exception of those marked with asterisk (*) were extracted from the output of the program ARS41d_XP

* Data from COFECHA

annual character of ring formation in our study, we recommend conducting ^{14}C dating in early phases of tree-ring studies for species in which ring recognition is not straightforward or with a high frequency of wedging or false rings. As ^{14}C dating provides several probable year intervals (Hua and Barbetti 2004; Vieira et al. 2005), we advice to enhance the reliability of this method by taking at least three samples per tree.

The comparison of dates obtained by ring boundary analysis and those obtained by ^{14}C bomb peak dating may provide quantitative information about the accuracy of dating. A mean probability of ring misidentification for each species can be calculated, using the period of time under analysis and the number of misidentified rings. For *Clarisia* the mean probability to misidentify a ring was 9.9 ± 9%, i.e. there was a chance to add one false ring or to miss one true ring for every ten rings. For *Peltogyne* the mean misidentification probability was 12.9 ± 17.1%, so there is a chance to misidentify one ring for every ten rings. The highest difference in the dating was of 40 rings for a *Cedrelinga* tree; this sample was especially difficult. If we leave this sample out, the mean probability to misidentify a

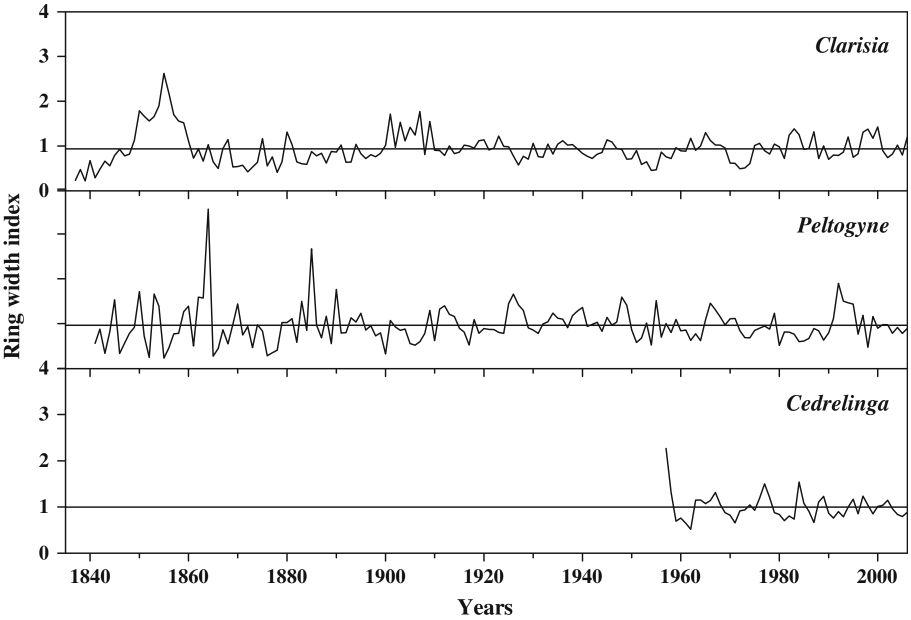

Fig. 4 Standard chronologies for juvenile trees of three Bolivian rainforest species. Note that the high temporal variation in the first years of *Cedrelinga* and *Peltogyne* chronologies was due to low sample size

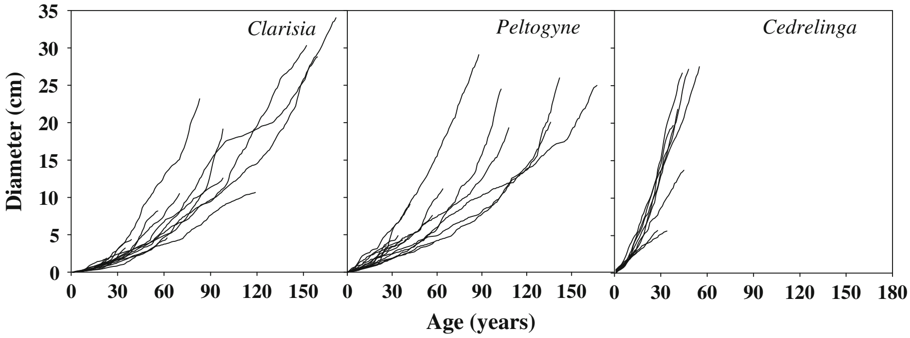

Fig. 5 Age versus diameter relations for juvenile trees of three Bolivian rainforest species. Only those samples used to build the chronologies are shown

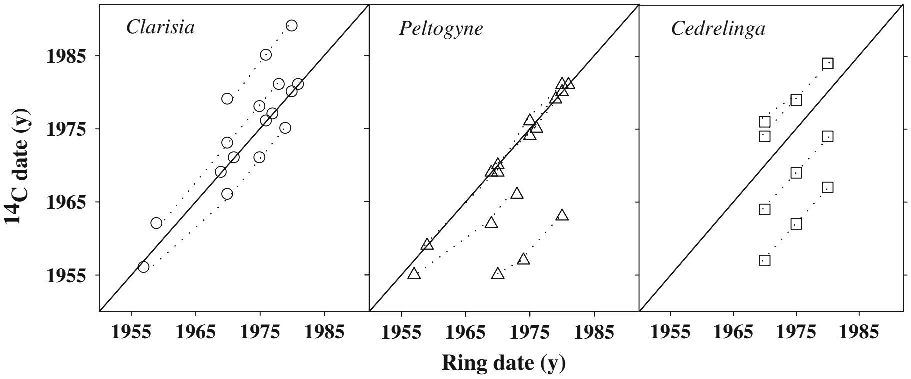

Fig. 6 Relation between dates obtained from ring counts and from ^{14}C analysis for three Bolivian rainforest species. Points at the solid $y = x$ line are exact matches of ring and ^{14}C dates. *Dotted lines* link points belonging to the same tree

ring for *Cedrelinga* was 19.6 ± 10.7% and thus two out of every ten rings. These errors in the dating can be corrected by crossdating among samples. However, due to the difficulty of the ring boundary recognition, some errors could be persistent and prevent the addition of more samples in the chronologies.

We were able to develop juvenile tree-ring chronologies for all the species of this study, using trees of variable age and diameter (Fig. 5). The low percentages of samples included in each chronology probably reflect the lack of strong common signal due to temporal variation in microsite conditions and perhaps, persistent dating problems. Despite these problems we show that trough tree-ring analysis we may obtain long-term data of juvenile growth in the tropics. Long-term juvenile data are valuable for the evaluation of important ecological hypotheses related to

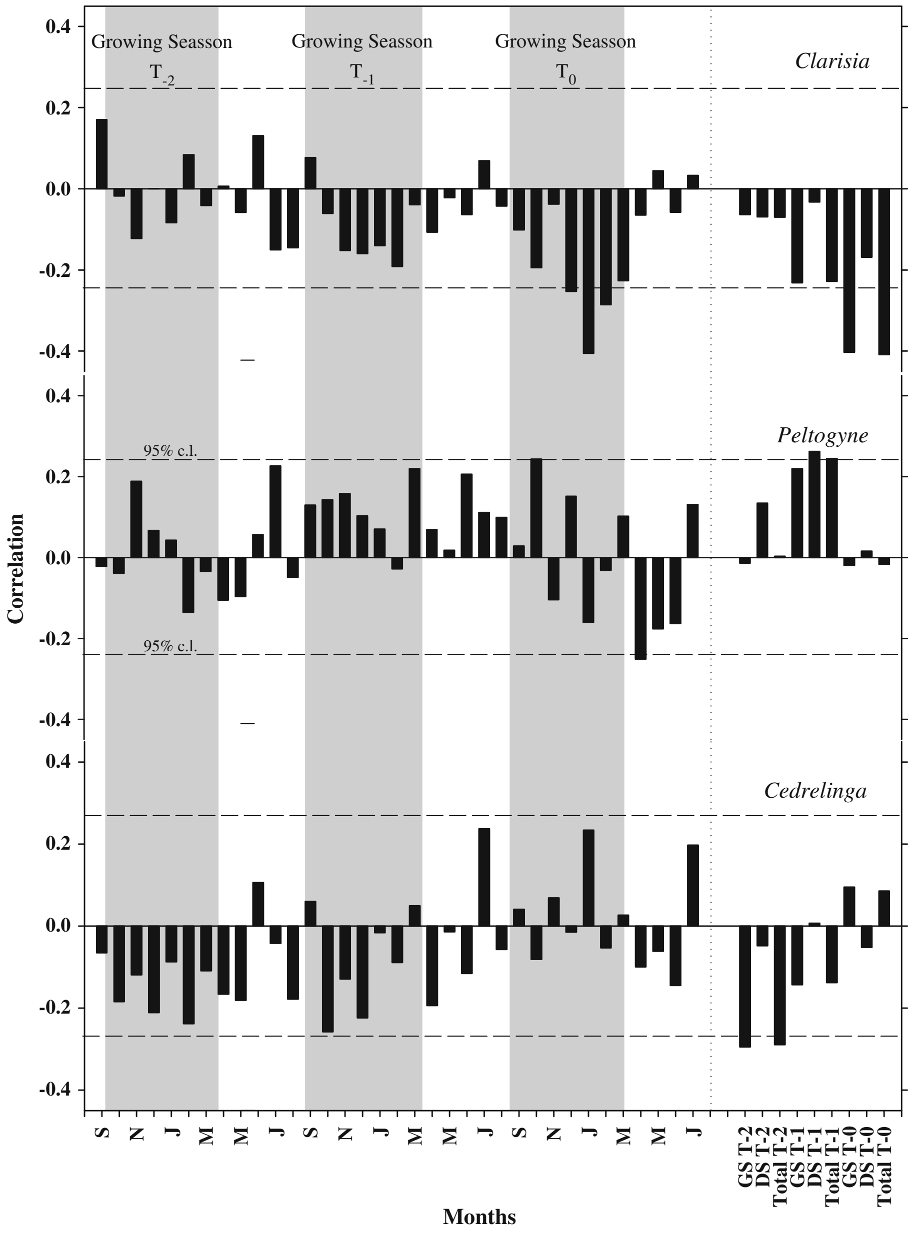

Fig. 7 Correlations of standard chronologies with the average monthly rainfall for juvenile trees of three Bolivian rainforest species. Rainfall of 35 consecutive months was used, as well as total rainfall during the growing season (*GS*), dry season (*DS*) and total annual precipitation for current growing year ($T-0$), previous year ($T-1$) and the year before that ($T-2$). Correlation coefficients are significant ($P < 0.05$) if >0.24 for *Clarisia* and *Peltogyne* and >0.27 for *Cedrelinga* (*stippled horizontal lines*)

growth and survival of juvenile trees in the tropics (Rozendaal et al. 2010).

The ages of our juvenile trees ranged from 30 to 160, 40 to 160 and 30 to 60 years for *Clarisia*, *Peltogyne* and *Cedrelinga*, respectively. The ages we report, for *Clarisia* and *Peltogyne* are in concordance with those reported by Vieira et al. (2005) and Brienen and Zuidema (2006b) for shade-tolerant individuals <30 cm dbh. These studies showed that trees growing in the understory can have low growth rates over their entire life. In contrast, light-dependent trees present faster growth rates (Clark and Clark 1996; Vieira et al. 2005; Chambers et al. 1998; Brienen and Zuidema 2006b; Brienen et al. 2010) comparable to those reported for *Cedrelinga* in this study.

The majority of the tropical zones experience a dry season, or reduced precipitation for several months. Such seasonality is believed to produce clear rings by the induction of cambial dormancy (Worbes 1995, 2002; Carlquist 2001; Schongart et al. 2006). As a consequence, the ring width is expected to respond to rainfall (Carlquist 2001). Our three tree species presented different responses to rainfall, both in sign and in time (Fig. 7). *Clarisia* presented a negative correlation with the rainfall of the growing season. *Peltogyne* showed a positive correlation with the rainfall of the season prior to the ring formation, in contrast with the absence of correlations reported for the adult trees (Brienen and Zuidema 2005). Finally, *Cedrelinga* presented a negative correlation with the rainfall

2 years before the growing season, which contrasts with reported positive correlation of the adult trees with the rainfall of the growing season (Brienen and Zuidema 2005). Complex reactions of juvenile trees to rainfall are likely if one takes into account that juveniles are evergreen trees and are growing in the low-light conditions of the forest understory (Worbes 1999). In addition, field and laboratory observations suggest different use of resources of our study species. *Clarisia* integrates silica in its structure, which may give it advantages against herbivores, as it increases wood toughness. Being a long-lived pioneer, *Cedrelinga* seems to invest mainly in height growth, at the expense of mechanical stability; for instance, we often observed juvenile trees of this species growing noticeably inclined. Finally, *Peltogyne* accumulates starch which could be mobilized to allow growth during periods of low resource availability. Worbes (1999) already discussed the occurrence and relevance of starch accumulation in tropical tree rings. In all, it is clear that such specific-species morphological and life-history attributes importantly determine responses to rainfall.

Our results show that rainfall may also be limiting growth in juvenile trees. The positive correlations between ring width and rainfall (*Peltogyne*), are comparable with other studies, (Stahle 1999; Worbes 1999; Brienen and Zuidema 2005; Schongart et al. 2006; Therrell et al. 2006; Solíz et al. 2009). Interestingly, negative correlations with rainfall were also observed (*Cedrelinga* and *Clarisia*). A negative correlation is difficult to interpret, but may be caused by the positive correlation of rainfall with cloudiness (Clark and Clark 1994; Lovejoy and Schertzer 2006), which results in lower solar radiation loads during high-rainfall years. For light-limited juvenile trees in the forest understory, this may lead to negative growth-rainfall correlations.

Correlations between growth and rainfall 1 year prior to that of ring formation are not commonly found for tree species, but have been reported before for some tropical trees (Dünisch et al. 2003; Brienen and Zuidema 2005). For a tropical dry montane climate, Solíz et al. (2009) proposed that the sum of several years may be even a better predictor of growth. However, with our current knowledge on the factors determining diameter growth of the study species and on historical forest dynamics, the climate-growth relations that we report here will remain difficult to explain.

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