MATCHING DENDROCHRONOLOGICAL DATES WITH THE SOUTHERN HEMISPHERE ^{14}C BOMB CURVE TO CONFIRM ANNUAL TREE RINGS IN *PSEUDOLMEDIA RIGIDA* FROM BOLIVIA

Laia Andreu-Hayles[1,2,†] • Guaciara M Santos[3,†] • David A Herrera-Ramírez[4] •
Javier Martin-Fernández[1] • Daniel Ruiz-Carrascal[5,6] • Tatiana E Boza-Espinoza[7] •
Alfredo F Fuentes[8,9] • Peter M Jørgensen[9]

ABSTRACT. This study used high-precision radiocarbon bomb-pulse dating of selected wood rings to provide an independent validation of the tree growth periodicity of *Pseudolmedia rigida* (Klotzsch & H. Karst.) Cuatrec. from the Moraceae family, collected in the Madidi National Park in Bolivia. ^{14}C content was measured by accelerator mass spectrometry (AMS) in 10 samples from a single tree covering over 70 yr from 1939 to 2011. These preliminary calendar dates were determined by dendrochronological techniques and were also used to select the samples for ^{14}C AMS. In order to validate these preliminary dates using the established Southern Hemisphere (SH) ^{14}C atmospheric concentration data set, the targeted rings were selected to be formed during periods before and after the ^{14}C bomb spike nuclear tests (i.e. 1950s–1960s). The excellent agreement of the dendrochronological dates and the ^{14}C signatures in tree rings associated with the same dates provided by the bomb-pulse ^{14}C atmospheric values for the SH (SHCal zone 1–2) confirms the annual periodicity of the observed growth layers, and thus the high potential of this species for tree-ring analysis. The lack of discrepancies between both data sets also suggests that there are no significant latitudinal differences between the ^{14}C SHCal zone 1–2 curve and the ^{14}C values obtained from the selected tree rings at this geographic location (14°33′S, 68°49′W) in South America. The annual resolution of *P. rigida* tree rings opens the possibility of broader applications of dendrochronological analysis for ecological and paleoclimatic studies in the Bolivian tropics, as well as the possibility of using wood samples from some tree species from this region to improve the quality of the bomb-pulse ^{14}C SHCal curve at this latitude.

INTRODUCTION

The tropical Andes are considered a biodiversity hotspot (Myers et al. 2000), highly vulnerable to ongoing climate change, as well as an important provider of goods and services. The Madidi National Park in northwestern Bolivia, where our study site is located, is among the most diverse protected areas on Earth. It comprises unique high-altitude environments and continuous forests along an elevation gradient from above 4000 to below 1000 m asl. With more than 2000 tree species and a distinct seasonality dominated by marked wet/dry seasons, this site offers highly suitable conditions to explore dendrochronological potential in the fragile Andean region.

Tree rings are very useful sources of past environmental conditions that can provide information on forest growth and the relationships between trees and climate. They can also extend and/or fill in the gaps in climate records beyond instrumental periods in areas where climate data are scarce, incomplete, and even nonexistent (Fritts 1976). Tree-ring research also provides relevant data, such as growth rates and tree lifespans, used in growth modeling that might be applied to sustainable management of timber production (Schöngart 2008). However, before tree-ring records can be used as proxy data for ecological or climatological research, tree growth periodicity must be determined. After more than a century of tree-ring research in the tropics, few studies have succeeded in providing reliable, useful paleorecords, mainly due to difficulties in detecting the factor triggering growth periodicity, presence of wedging rings, and crossdating problems, among others (e.g. Worbes 2002).

1. Tree-Ring Laboratory, Lamont-Doherty Earth Observatory of Columbia University, Palisades, NY, USA.
2. Institut Català de Ciències del Clima (IC3), Barcelona, Catalonia, Spain.
3. Department of Earth System Science, University of California, Irvine, CA, USA. Corresponding author. Email: gdossant@uci.edu.
4. Universidad Nacional de Colombia Sede Medellín, Colombia.
5. Escuela de Ingenieria de Antioquia, Colombia.
6. International Research Institute for Climate and Society, Columbia University, Palisades, NY, USA.
7. Universidad Nacional de San Antonio Abad del Cusco, Cusco, Perú.
8. Herbario Nacional de Bolivia, La Paz, Boliva.
9. Missouri Botanical Garden, St. Louis, MO, USA.
† Co-first author: contributed equally to this work.

In environments where trees have a well-defined annual growing season, dendrochronological techniques can assign absolute calendar dates to every single growth layer or tree ring (Stokes and Smiley 1968; Fritts 1976). This is the main reason tree rings have been extensively used in temperate climates, while the tropics remain relatively unexplored due to the difficulty of identifying consistent, well-defined wood layers (tree rings) corresponding to annual growing periods (Bräuning 2011). Major progress in tropical dendrochronology in recent decades has shown that some tropical trees produce annual bands due to cambial dormancy driven by unfavorable environmental conditions during a season of the year (Rozendaal and Zuidema 2010). However, this may not be the case for all tropical species. The application of ^{14}C bomb-pulse dating of selected tree rings can provide an independent validation of dendrochronological dates for tropical tree species (e.g. Biondi and Fessenden 1999; Hua et al. 1999), which can be particularly useful when the species phenology is unknown.

The aboveground nuclear weapon tests performed during the 1950s and 1960s produced large amounts of nuclear fallout, including excess ^{14}C. Since the partial Nuclear Test Ban in 1963, the excess of atmospheric ^{14}C has decreased almost exponentially due to oceanic and terrestrial uptake, fossil-fuel dilution, and atmospheric mixing. Therefore, the effect of CO_2 fixation on the excess ^{14}C, especially from new plant growth tissue, can be used as a time-specific signal. Direct ^{14}C measurements of atmospheric CO_2 for the bomb-pulse period have typical uncertainties from 1 yr to several years depending on the calendar year (i.e. the bomb-pulse timeframe) (Hua and Barbetti 2004). Determination of age accuracy can be improved by plotting multiple ^{14}C data (y axis) associated with preliminary dendrochronology calendar dates (x axis) together with atmospheric ^{14}C curves. The simultaneous matching between several ^{14}C data and the ^{14}C calibration curves highly reduces the uncertainty associated with ^{14}C dating. This circumvents the pitfall that a single ^{14}C value can be associated with different calendar dates. This approach has assisted in validating annual patterns of tree species, as well as to detect problems associated with dendrochronological techniques or inadequacies of ^{14}C wood sample processing (e.g. Biondi and Fessenden 1999; Hua et al. 1999; Fichtler et al. 2003; Menezes et al. 2003; Westbrook et al. 2006; Biondi et al. 2007; Wils et al. 2009; Soliz-Gamboa et al. 2011).

The ^{14}C bomb-pulse data sets are subdivided in zones considering the effects of atmospheric circulation and the Intertropical Convergence Zone (ITCZ; e.g. Hua and Barbetti 2004), as well as variations due to different latitudinal sources and sinks in the ocean and/or in land (Krakauer et al. 2006). Temporal changes in atmospheric ^{14}C concentrations due to anthropogenic disturbance produced by nuclear testing, even during the pre-bomb period, have been documented in both hemispheres (Hogg et al. 2013; Hua et al. 2013; Reimer et al. 2013).

In the Southern Hemisphere (SH), the spatial distribution of bomb-pulse ^{14}C atmospheric curves (SHCal, Hogg et al. 2013) closely follow the division established for the Northern Hemisphere (NH), with the main difference being that SHCal zones 1 and 2 are considered a single zone (SHCal zone 1–2). The seasonal movement of the ITCZ, and the quick diffusion of the atmospheric ^{14}C excess during its transport over the Equator and SH zone 3, allowed ^{14}C concentrations to level out and become almost uniform over the entire zone (see Figure 2 in Hua et al. 2013). The zonal subdivision in the SH, especially at the ascending part of the bomb-pulse curve, is also based on good agreement between tree-ring data sets from Muna Island, Indonesia (5°S, 122°E; 1950–1972) and the Doi Inthanon, Thailand (19°N, 99°E; 1950–1972; see Figure 1 in Hua et al. 2013). The excess of atmospheric ^{14}C finally reached a global equilibrium in the late 1960s, and became evenly distributed in all locations (including the NH zones), as atmospheric ^{14}C signatures overlapped with each other within ±1σ from 1973 onward. Nevertheless, for the short period between 1950 to 1972 only

two data sets are available at lower latitudes in SH zones 1–2 and 3: (a) the atmospheric samples from Suva, Fiji (18°S, 178°E; 1958–1972) and (b) the tree rings from Muna Island, Indonesia (5°S, 122°E; 1950–1972), respectively (Hua et al. 2013 and references therein). Unfortunately, there are no ^{14}C records currently available in South America for the entire timespan of the bomb period. In this context, finding suitable long-living tropical tree species to be used for improving the bomb-pulse ^{14}C atmospheric record for the SHCal is an important issue that deserves attention.

Tree species with dendroclimatic potential in the tropical Andes have been recently reviewed (Boninsegna et al. 2009; Bräuning 2009; Villalba et al. 2011). Particularly in Bolivia, several species have already proved to be of value for dendrochronological analyses: *Polylepis tarapacana* Phil. in the Altiplano (17–22°S; 3800–4800 m asl; Solíz et al. 2009); *Polylepis pepei* B.B. Simpson, *P. subsericans* J.F. Macbri, and *P. rugulosa* Bitter at high elevations (13–16°S; 4000–4500 m asl; Jomelli et al. 2012); *Centrolobium microchaete* (Mart. ex Benth.) H.C. Lima in the lower dry forest (15–16°S; 200–420 m asl; Lopez and Villalba 2011); and *Cedrela odorata* L., *Amburana cearensis* (Allemão) A.C. Sm., *Cedrelinga cateniformis* (Ducke) Ducke, and *Tachigali vasquezii* Pipoly in rainforests (10–11°S; ~100 m asl; Brienen and Zuidema 2005, 2006). Our study site is located in the Madidi National Park in the Bolivian tropical Andes, where a sample from *Pseudolmedia rigida* (Klotzsch & H. Karst.) Cuatrec from the Moraceae family was collected. Although the high dendrochronological potential of *P. rigida* was reported in Peru based on anatomical tree-ring structures (Beltrán-Gutiérrez and Valencia-Ramos 2013), the periodicity of its tree rings has never been reported. The main goals of this study are thus (1) to assess if tree rings observed in the *P. rigida* studied sample are annual by means of classical dendrochronological techniques and ^{14}C measurements, and (2) to evaluate if there are latitudinal discrepancies between ^{14}C values obtained in this geographical site and the existing bomb-pulse SHCal ^{14}C curves. To fulfill these purposes, 10 tree rings were processed for high-precision ^{14}C accelerator mass spectrometry (AMS) measurements. We selected tree rings within a ~70-yr range, from 1939 to 2011, with calendar dates provided by dendrochronological techniques.

MATERIALS AND METHODS

Site and Tree Species Features

The location of our study site (14°33′S, 68°49′W) over the Global Multi-Resolution Topography (GMRT) synthesis (Ryan et al. 2009) is shown in Figure 1. The studied sample, a half of a disk from the stem (cross-section) of an individual of *P. rigida*, is shown in Figure 2. The sample was extracted from a tree that had fallen earlier in 2012 and was collected in October at 1015 m asl in the Madidi National Park in Bolivia. A sterile voucher of basal re-sprouts from the fallen tree was collected and deposited at the National Herbarium of Bolivia (T. E. Boza E. - 2900; http://tropicos. org/Specimen/100743077). It matches well the fertile specimens of *P. rigida* identified by C. Berg (a Moraceae specialist), which were previously collected in the same area. The sampled tree was growing on mountainous hillsides with well-drained soils in a basimontane seasonal humid forest, according to bioclimatic belts defined by Rivas-Martinez et al. (2011), which in the Madidi National Park are found at altitudes ranging from 1000 to 1800 m asl. The nearest weather station is located at 1415 m asl in the town of Apolo, 41 km from the collection site in the same bioclimatic belt. The mean annual temperature is 20.5°C, while average annual precipitation is 1558 mm (Navarro and Maldonado 2002) distributed during the wet season (September to May), which is followed by a short dry season (June to August). These forests are semideciduous, with dense canopies at 12–20 m above the ground, several understory levels, and abundant woody lianas. The floristic composition of this forest is a mix of species of wide distribution in neotropical humid forests such as *Apuleia leiocarpa* (Vogel) J.F. Macbr., *Garcinia gardneriana* (Planch. & Triana) Zappi, *Pouteria bilocu-*

laris (H.J.P. Winkl.) Baehni, and *Trichilia pleeana* (A. Juss.) C. DC. Also, there are some species typical of dry forests of the Pleistocenic arch, such as *Hymenaea courbaril* L. and *Amburana cearensis*. The presence of *P. rigida*, usually frequent and sometimes abundant, is a good indicator of the occurrence of this type of vegetation (A. F. Fuentes, personal communication). These forests are currently threatened by human activities due to their accessible topographic situations and the occurrence of rich soils suitable for agriculture.
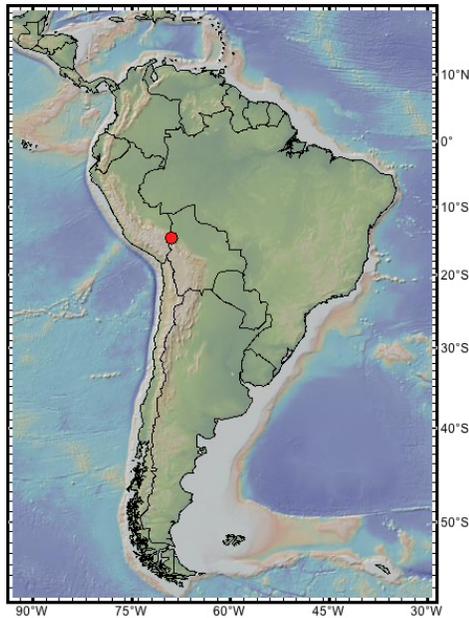

Figure 1   Location (dot) where the analyzed sample was collected in the Madidi National Park, Bolivia. This map was generated using GeoMapApp (URL: http://www.geomapapp.org).

Distributed mainly across the northwestern corner of South America, extending to Costa Rica and Panamá, *P. rigida* is a relatively common tropical tree species growing between 0 and 2000 m asl in Bolivia, northwestern Brazil, Peru, Ecuador, Colombia, and Venezuela. *P. rigida* is a strictly dioecious medium to tall tree; leaves are simple, entire, small to medium sized; flowers small in heads, whitish; fruits are small and covered by a red fleshy perianth (Berg 1972; Cardona-Peña et al. 2005). In the Madidi region, *P. rigida* can be mistakenly identified as *P. laevigata* Trécul, a species found in more humid and less seasonal areas. Both species can easily be differentiated in their sterile state by the presence on the lower leaf surface of small oblongoid, ellipsoid, or ovoid-capitate pluricellular trichomes on *P. rigida* vs. globose-capitate on *P. laevigata* (Berg 2001).

Dendrochronological Methods

The stem disk was processed at the Tree-Ring Laboratory of the Lamont-Doherty Earth Observatory using standard dendrochronological methods (Stokes and Smiley 1968; Fritts 1976). The sample was air-dried and sanded progressively with finer grit sand papers until the cells were perfectly visible under a microscope and four radii were analyzed (Figure 2A). This species has a diffuse-porous wood without a distinct earlywood/latewood pattern. The boundaries between annual growth layers are defined by marginal parenchyma, whereas vasicentric parenchyma surrounds the pores (Figure 2B–C). Pore density is low (about 3 pores/mm^2), composed by a combination of single and multiple (2–3) pores of large size (>200 μm).

Figure 2 Panel (A) shows the cross-section of *Pseudolmedia rigida* with white lines indicating the four radii that were crossdated using dendrochronological techniques. Panel (B) shows details of anatomical features of a wedging ring (year 1993) that becomes a locally absent ring (LAR) in some parts of the stem disk. Note that the parenchyma delimiting the boundary is continuous and ends touching the previous ring boundary. This indicates that growth during that year was not produced along all the cambium. LAR can also be called "missing" rings or "pinching" rings. Panel (C) shows details of anatomical features of false rings (FR): years 1969 and 1968 in radius C (above) and year 1978 in radius B (below). Note how the parenchyma delimiting the boundary of the ring is discontinuous and disappeared without meeting the previous ring boundary.

Visual crossdating techniques (Yamaguchi 1991) were used to match the growth patterns among the four studied radii. This method ensures the correct chronosequence of the tree rings at every single radius. Figure 3 illustrates the rings identified in each radius, as well as locally absent rings (LAR) and/or false rings (FR). All the radii had both LAR and FR. LAR were detected when a wedging ring was observed in a different portion of the cross-section (Figure 2B), whereas FR were detected when the parenchyma delimiting the ring boundary was not continuous along the circumference of the stem (Figure 2C). The comparison among the radii with the described crossdating technique was crucial for avoiding erroneous preliminary calendar dates of each single ring when LAR and/or FR were present. Once the radii were crossdated, the width of every single ring for each radius was measured to a precision of 0.01 mm using WinDendro version 2012c (Regent Instruments, Canada) after scanning the samples at 2400 dpi with a flatbed scanner (Epson Expression 10000XL). The resulting data underwent a quality dating control with the program COFECHA (Holmes 1983). The raw tree-ring series for each radius are shown in Figure 4.

Ten individual tree rings were selected to represent years before and after the ^{14}C bomb peak based on the preliminary calendar dates provided by the dendrochronological techniques. If the preliminary dates are correct, the resulting tree-ring ^{14}C measurements should match with the
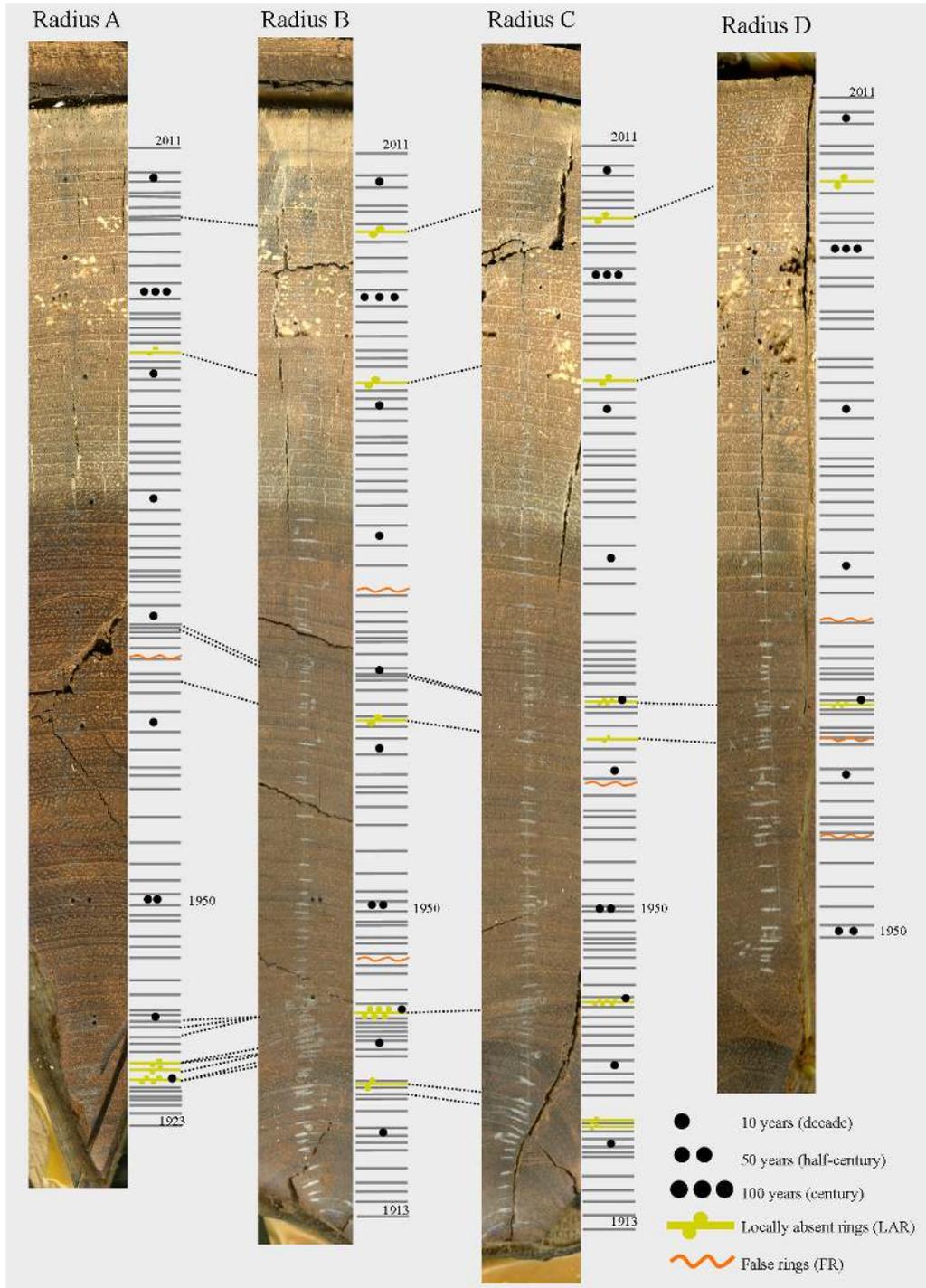
Figure 3 Crossdating sketch: Four radii were analyzed using visual crossdating techniques. Note that all the radii have locally absent rings (LAR) and false rings (FR). The correct calendar year associated with each single ring was obtained just by comparison of tree-ring growth patterns and wood anatomical features among all radii.

averaged point in time when atmospheric ^{14}C signatures were fixed into the *P. rigida* woody tissues. Consequently, tree-ring ^{14}C data should closely follow the expected atmospheric ^{14}C values, such as (a) a ^{14}C/C dilution response to burning of fossil fuel since the Industrial Revolution (the Suess effect; McCormac et al. 1998) before the onset of bomb ^{14}C in the mid-1950s, (b) its rapid increase during the bomb-peak period, and (c) its continuous decrease from the post-bomb era up to recent time. About 10–20 mg of wood material from the selected rings was collected between the radii A and B (Figure 2). The individual rings were carefully sampled by separating the individual growth layer bands (entire annual tree ring) manually using a scalpel under a microscope. The wood material from each ring was stored in individual laboratory-grade polypropylene plastic microvials and labeled for shipment to the laboratory for ^{14}C analyses. The calendar dates as sample identifiers was the only information provided to the ^{14}C laboratory in relation to the dendrochronological proceedings.

Radiocarbon Analysis

^{14}C analyses were performed at the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Facility of University of California, Irvine (KCCAMS/UCI). The wood samples were subjected to an extraction method to isolate one of its most immobile fractions (e.g. holocellulose) prior to ^{14}C AMS analyses. Since the amount of C within wood materials is estimated to be ~45% by dry weight and the procedure has a recovering rate ranging from 15 to 44% (depending on wood characteristics and preservation), about 15 mg or less of whole wood were necessary for our analyses. Therefore, wood material from individual tree rings was processed, allowing us to obtain the highest calendar age resolution provided by the bomb-pulse ^{14}C dating method.

Wood aliquots were initially subjected to an acid-base-acid (ABA) pretreatment (Santos and Ormsby 2013) followed by a bleaching step (1N HCl and 1M NaClO$_2$ at 70°C in a fume hood for approximately 6 hr) to isolate holocellulose (Southon and Magana 2010). After bleaching, the holocellulose residues were rinsed with pure water until pH neutral, dried, and then stored. Approximately 2 mg of extracted holocellulose residue were oxidized to CO_2 via the evacuated sealed-tube combustion technique (Santos et al. 2004). The evolved CO_2 was cryogenically cleaned and reduced to graphite in the presence of H$_2$ at 550°C with prereduced Fe powder as catalyst (Santos et al. 2004, 2007). Graphite samples were pressed into aluminum target holders for ^{14}C analyses. These analyses were performed using a modified compact AMS system (NEC 0.5MV 1.5SDH-1), which uses a fast beam switcher for sequential injection of ^{12}C, ^{13}C, and ^{14}C (Beverly et al. 2010). The ^{14}C/^{12}C isotopic ratio of each sample was (a) corrected for isotopic fractionation using the on-line δ^{13}C AMS values of the respective graphite samples analyzed; (b) background-corrected by means of Queets-A (^{14}C-free) wood samples, subjected to the standard holocellulose extraction as mentioned above; and (c) normalized to the ^{14}C activity of OX-I by measuring an independent set of six OX-I graphite targets (our primary standard), following the established protocol of Santos et al. (2007).

Besides the 10 individual tree rings, another two targets each of reference materials from the Fourth International Radiocarbon Intercomparison (FIRI) exercise and the International Atomic Energy Agency (IAEA) were also measured. Aliquots of subfossil FIRI-H wood (Scott et al. 2004) were subjected to holocellulose extraction, when IAEA C3 cellulose (Le Clercq et al. 1998) were used to evaluate combustion/graphitization procedures and spectrometer tuning accuracy and precision. Measurement uncertainties were based on statistical errors calculated using the number of counts measured from each target, and background corrections. An external error was calculated from the reproducibility of individual analyses from the primary and secondary standards (OX-I, FIRI-H, and IAEA C3) and yielded accuracy and precision better than 0.25%. Measured ^{14}C abundances are given using the fraction modern carbon (FmC) notation (Stuiver and Polach 1977).

RESULTS AND DISCUSSION

Importance of Dendrochronological Visual Crossdating

Standard dendrochonological procedures involve visual crossdating among samples from different individuals by assessing synchrony in tree growth patterns, the common growth variability among trees from the same stand in a forest (Stokes and Smiley 1968). For trees located in temperate climates with well-defined growing and dormancy seasons, this method successfully ensures the assignment of an absolute calendar year to every single tree ring. However, in tropical environments with a less marked seasonality, the common growth pattern shared among trees in a stand may indicate that changes in the same environmental factor are limiting radial growth in the studied trees, but it cannot alone be considered as evidence of annual growth layers. This less distinct seasonality, with an absence of a dormancy (non-growing) period, does not allow us to rule out that more than one annual change in the limiting environmental factor may occur.

Figure 3 illustrates how visual crossdating was done for the four radii analyzed in the *P. rigida* cross-section (Figure 2A). None of the four radii analyzed in the cross-section show all the rings for the studied period because LAR (Figure 2B) and/or FR (Figure 2C) were present in all of them. In this study, the application of visual crossdating techniques within radii of the same tree individual was crucial in order to obtain the correct chronosequence in the radius from which wood material was extracted to perform the ^{14}C measurements in the selected predated rings. The detection of visible rings in at least one of the radii assists in identifying LAR, whereas discontinuous parenchyma in the tree-ring boundaries indicates FR. Without the comparison among the four radii, the establishment of the correct preliminary dates for the wood material to be analyzed would have not been possible. Our study corroborated that the presence of wedging rings, very common in the tropics, required the analysis of cross-sections (Worbes 2002). The two cores recommended in standard procedures to account for internal variability within individual trees (Cook and Kairiukstis 1990) would not have been sufficient to detect all the LAR in the studied sample and would have provided erroneous dates for the observed tree rings.

The internal crossdating within the same individual resulted in a very effective way of ensuring that all the growth layers were counted in the correct calendar order and was supported by the ^{14}C results (Figure 5). The application of standard dendrochronological procedures involving the processing of samples from multiple trees was not possible in our case because just one sample from this species was available.

Comparing ^{14}C Data from Preliminary Crossdated Tree Rings with SH ^{14}C Atmospheric Curves

Our high-precision ^{14}C AMS data from the selected dendrochronologically dated tree-ring samples of *P. rigida* (Table 1, Figure 5) show a slight depletion of the atmospheric ^{14}C signal associated with the Suess effect (i.e. 1939, 1947, 1955—the pre-^{14}C bomb spike), an increase in response to the detonation of nuclear weapons (i.e. 1961 and 1965), followed by a decrease in the years associated with the post ^{14}C bomb period (1970, 1978, 1988, 2001, 2011) due to the subsequent uptake by other large C sinks (such as oceans and the biosphere).

Figure 5 also shows the *P. rigida* FmC ^{14}C tree-ring data validated against SHCal zone 1–2 and SHCal zone 3 from 1950 to 2011 (Hua et al. 2013). A good agreement was found between our ^{14}C data and both ^{14}C SHCal data sets, but the match was better with the zone 1–2 record than zone 3. Both SHCal data sets were used because the Madidi National Park falls in the putative boundary between these zonal regions in South America. Because the spatial extent of the bomb-pulse SH ^{14}C records currently available is limited (i.e. none in the Western Hemisphere at this geographic loca-

tion, especially between 1950 and 1972), it cannot be guaranteed that the zonal boundary between zone 1–2 and zone 3 was in fact accurately delimited (see Figure 2 in Hua et al. 2013).
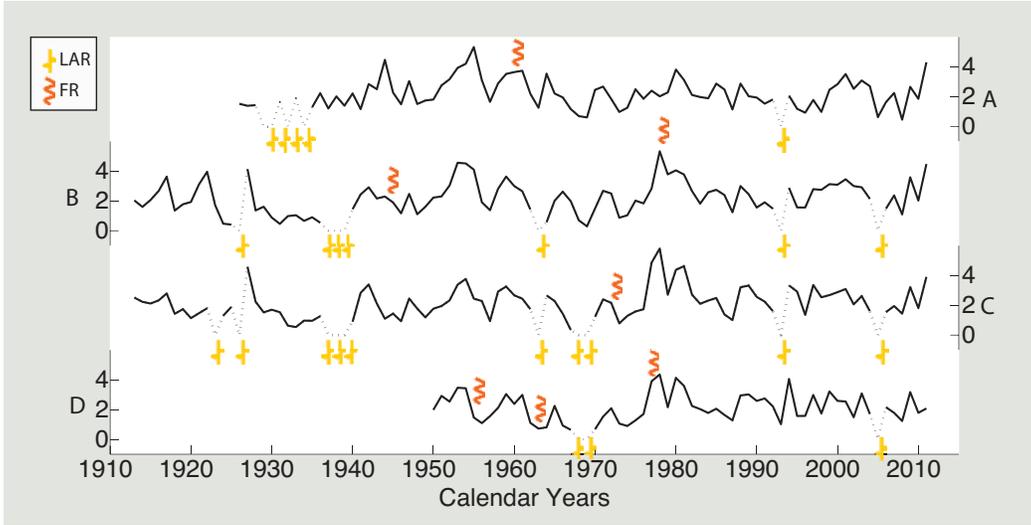

Figure 4 Raw tree-ring width data (mm) for each radius. Note that all radii measured in the studied sample of *Pseudolmedia rigida* have locally absent rings (LAR) and false rings (FR).
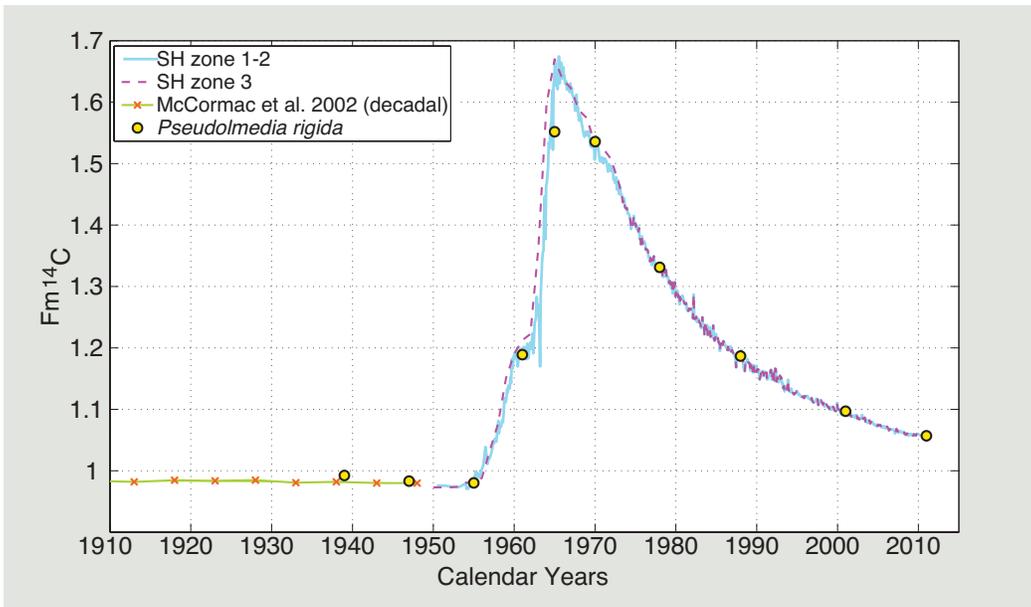

Figure 5 The fraction modern carbon (FmC) values of the analyzed sample of *Pseudolmedia rigida* collected in Bolivia and the atmospheric record compilations for SHCal zone 1–2 (solid line) and zone 3 (dashed line) from 1950 to 2011 (Hua et al. 2013). The decadal Tasmanian wood ¹⁴C data from 1903 to 1948 of McCormac et al. (2002) are also shown, corresponding to the period of 0–55 cal BP of the pre-bomb data from the SHCal13 calibration curve (as mentioned in Hogg et al. 2013). Here, the uncertainties of our ¹⁴C data are not shown because they are smaller than the size of the symbols (Table 1 shows the ±1σ measurement errors). Note that the *x* axis covers the same time period as the *x* axis in Figure 4.

Table 1 ¹⁴C data for *Pseudolmedia rigida* (14°33′S; 68°49′W), Bolivia. All ¹⁴C results are shown as FmC signatures. The individual statistical error bars of the ¹⁴C data were calculated based on counting statistics and scatter in multiple measurements on each sample, along with propagated uncertainties from normalization to a primary modern standard (OX-I), background subtraction based on processed blank (¹⁴C-free wood), and isotopic fractionation corrections provided by the on-line δ^{13}C AMS values, following instrumental analysis described in Santos et al. (2007).

Year AD	UCIAMS#	Fm¹⁴C	
		Mean	±1σ
1939	129018	0.9923	0.0021
1947	129017	0.9831	0.0021
1955	129016	0.9803	0.0022
1961	129015	1.1890	0.0025
1965	139545	1.5518	0.0026
1970	139546	1.5357	0.0030
1978	129014	1.3313	0.0028
1988	129013	1.1868	0.0025
2001	129012	1.0969	0.0023
2011	129011	1.0568	0.0022

Tropical tree-ring/¹⁴C-dated ages based on measurements done in a single ring or multiple rings uniquely belonging to the attenuated ¹⁴C concentration of the post-¹⁴C bomb period (e.g. from 2000 onward, increasing the uncertainty of ¹⁴C calibrated ages of the wood tissue—Dezzeo et al. 2003; Giraldo Jimenez and del Valle Arango 2011; Moreno Valoyes 2013) cannot always ensure conclusive results in relation to absolute calendar dates. In contrast, our work involved an accurate assessment of the calendar year of the rings analyzed followed by high-precision ¹⁴C bomb-pulse dating of individual selected wood rings. The analysis of tree rings belonging to the pre- and post-bomb period is an effective way of guaranteeing the correct, precise, and absolute dating of the studied tree-ring samples. With this approach, which has been also used in previous investigations already cited (e.g. Biondi and Fessenden 1999), discrepancies between the calendar year assigned to the tree rings by visual crossdating and the ¹⁴C SHCal curve can be precisely determined or refuted. Our results show that systematic growth layer bands of *P. rigida* are indeed annual rings, as no offsets between our ¹⁴C and traditional crossdating dates were detected (Figure 5). The remarkably good agreement between the tree-ring/¹⁴C data and the SH zone 1–2 compilation data set assures the potential of this species for dendrochronological analysis.

Relevance of the Finding

Our results provide evidence of tree rings with annual resolution from a tropical tree species, *P. rigida*, confirming its high dendrochronological potential previously reported by Beltrán-Gutiérrez and Valencia-Ramos (2013). With more than 2000 tree species, the Madidi National Park offers many possibilities for ecological, paleoclimatic, and geomorphological studies among others, supported by tree-ring analyses. At a larger spatial scale, our findings also support the high potential for developing dendrochronology in the tropical Andes. The generation of tree-ring chronologies in this region of the world may provide critical information for understanding the response of these fragile ecosystems to ongoing climate change, as well as paleoclimate records for estimating past climate conditions. The latter is particularly critical since the lack of good coverage of climate data in this region of the world is challenging the understanding of the tropical climate system and the reliability of future model projections (Herzog et al. 2011: Chapter 7).

Moreover, the development of tree-ring chronologies with annual resolution in the South American tropical areas may also be extremely useful for improving the bomb-pulse ^{14}C SH timescale calibration curves. Currently, SHCal is mainly based on measurements from material collected in higher latitudes (below 18°S) and from the Eastern Hemisphere, where most of SH landmasses are found. Nevertheless, the SH data set is still lacking records, especially from the early bomb period. The incorporation of new species from the tropical zone exposed to the ITCZ will highly increase the quality of the SHCal curves. Highly precise ^{14}C measurements on annual samples from species located along a latitudinal gradient in the tropical Andes may have a unique value to validate the current boundaries between the SHCal curve zone 1–2 and zone 3, which could also have changed through time.

CONCLUSIONS AND FUTURE DIRECTIONS

The use of tree-ring/^{14}C crossdating is a known valuable tool for the validation of annual growth patterns of species in tropical environments. In the present study, a preselected set of 10 individual tree rings from 1939 to 2011 was separated from *P. rigida*, a tropical tree with suggested high dendrochronological potential but unknown tree-ring periodicity. The samples were subjected to hollocellulose extraction and measured by high-precision ^{14}C AMS (≤0.3%). The ^{14}C bomb-pulse results confirm the existence of annual rings in this tropical tree. Therefore, these results allow for the possibility of developing a tree-ring width chronology of *P. rigida*, and suggest that many other species can also produce annual rings in this region. This is relevant for the following reasons: (1) as proxy data for paleoclimatological investigations for this tropical region; (2) to reveal forest growth dynamics, response to seasonal patterns, and possible impacts due to further climate changes and anthropogenic activities; and (3) to provide insight for future management practices and preservation of endangered species and areas.

The present data can be incorporated into the bomb-pulse SHCal ^{14}C data sets to better define the boundary of SHCal zone 1–2 and zone 3 for this geographical location, and therefore improve the quality of the SHCal ^{14}C curves. In addition, future ^{14}C measurements of *P. rigida*, a relatively common species with a broad distribution in northern South America, can further help to assess those boundaries.

^{14}C measurements before and after the ^{14}C bomb peak are highly advisable to validate the calendar dates provided by dendrochronological techniques in tree-ring samples coming from the tropics. Future research involving extensive fieldwork campaigns in the tropical Andes may very likely detect more suitable tree species for dendrochonological analyses. With the appropriate investment of time and resources towards developing a dense tree-ring chronology network along the tropical Andes, high-quality paleoclimatic data (potentially with annual resolution) can be achieved to fill the current gap of paleorecords in the tropical zones in South America.

ACKNOWLEDGMENTS

REFERENCES

Beltrán-Gutiérrez L, Valencia-Ramos G. 2013. Anatomía de los anillos de crecimiento de 80 especies arbóreas potenciales para estudios dendrocronológicos en la Selva Central, Perú. *Revista de Biología Tropical/International Journal of Tropical Biology* 61:1025–37.

Berg CC. 1972. *Olmedieae, Brosimeae (Moraceae)*. Flora Neotropica Monograph 7. New York: Hafner Publishing.

Berg CC. 2001. *Moreae, Artocarpeae, and Dorstenia (Moraceae) with Introductions to the Family and Ficus and with Additions and Corrections to Flora Neotropica Monograph 7*. Flora Neotropica Monograph 83. New York: Hafner Publishing.

Beverly RK, Beaumont W, Tauz D, Ormsby KM, von Reden KF, Santos GM, Southon JR. 2010. The Keck Carbon Cycle AMS Laboratory, University of California, Irvine: status report. *Radiocarbon* 52(2):301–9.

Biondi F, Fessenden JE. 1999. Radiocarbon analysis of *Pinus lagunae* tree rings: implications for tropical dendrochronology. *Radiocarbon* 41(3):241–9.

Biondi F, Strachan SD, Mensing S, Piovesan G. 2007. Radiocarbon analysis confirms the annual nature of sagebrush growth rings. *Radiocarbon* 49(3):1231–40.

Boninsegna JA, Argollo J, Aravena JC, Barichivich J, Christie D, Ferrero ME, Lara A, Le Quesne C, Luckman BH, Masiokas M, Morales M, Oliveira JM, Roig F, Srur A, Villalba R. 2009. Dendroclimatological reconstructions in South America: a review. *Palaeogeography, Palaeoclimatology, Palaeoecology* 281(3–4):210–28.

Bräuning A. 2009. Climate variability of the tropical Andes since the late Pleistocene. *Advances in Geosciences* 22:13–25.

Bräuning A. 2011. Editorial note for the special issue on 'Tropical Dendroecology.' *Trees* 25(1):1–2.

Brienen R, Zuidema P. 2005. Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis. *Oecologia* 146(1):1–12.

Brienen RJW, Zuidema PA. 2006. Lifetime growth patterns and ages of Bolivian rain forest trees obtained by tree ring analysis. *Journal of Ecology* 94(2):481–93.

Cardona-Peña V, Fuetes A, Cayola L. 2005. Las moráceas de la región de Madidi, Bolivia. *Ecología en Bolivia* 40:212–64.

Cook ER, Kairiukstis L. 1990. *Methods of Dendrochronology in Applications in the Environmental Sciences*. Dordrecht: Kluwer. 394 p.

Dezzeo N, Worbes M, Ishii I, Herrera R. 2003. Annual tree rings revealed by radiocarbon dating in seasonally flooded forest of the Mapire River, a tributary of the lower Orinoco River, Venezuela. *Plant Ecology* 168(1):165–75.

Fichtler E, Clark DA, Worbes M. 2003. Age and long-term growth of trees in an old-growth tropical rain forest, based on analyses of tree rings and ^{14}C. *Biotropica* 35(3):306–17.

Fritts H. 1976. *Tree Rings and Climate*. New York: Academic Press. 433 p.

Giraldo Jimenez JA, del Valle Arango JI. 2011. A growth study of *Prioria copaifera* (Caesalpinaceae) using dendrochronological techniques. *Revista de Biologia Tropical* 59(4):1813–31.

Herzog S, Martinez R, Jørgensen P, Tiessen H. 2011. *Climate Change and Biodiversity in the Tropical Andes*. São José dos Campos, Brazil and Paris, France: Inter-American Institute of Global Change Research (IAI) and Scientific Committee on Problems of the Environment (SCOPE). 348 p.

Hogg A, Hua Q, Blackwell P, Buck C, Guilderson T, Heaton T, Niu M, Palmer J, Reimer P, Reimer R, Turney C, Zimmerman S. 2013. SHCal13 Southern Hemisphere calibration, 0–50,000 cal yr BP. *Radiocarbon* 55(4):1889–903.

Holmes RL. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43:68–78.

Hua Q, Barbetti M. 2004. Review of tropospheric bomb ^{14}C data for carbon cycle modeling and age calibration purposes. *Radiocarbon* 46(3):1273–98.

Hua Q, Barbetti M, Worbes M, Head J, Levchenko VA. 1999. Review of radiocarbon data from atmospheric and tree ring samples for the period 1945–1997 AD. *IAWA Journal* 20(3):261–83.

Hua Q, Barbetti M, Rakowski AZ. 2013. Atmospheric radiocarbon for the period 1950–2010. *Radiocarbon* 55(4):2059–72.

Jomelli V, Pavlova I, Guin O, Soliz-Gamboa C, Contreras A, Toivonen JM, Zetterberg P. 2012. Analysis of the dendroclimatic potential of *Polylepis pepei*, *P. subsericans* and *P. rugulosa* in the tropical Andes (Peru-Bolivia). *Tree-Ring Research* 68(2):91–103.

Krakauer NY, Randerson JT, Primeau FW, Gruber N, Menemenlis D. 2006. Carbon isotope evidence for the latitudinal distribution and wind speed dependence of the air-sea gas transfer velocity. *Tellus B* 58(5):390–417.

Le Clercq M, van der Plicht J, Gröning M. 1998. New ^{14}C reference materials with activities of 15 and 50 pMC. *Radiocarbon* 40(1):295–7.

Lopez L, Villalba R. 2011. Climate influences on the radial growth of *Centrolobium microchaete*, a valuable timber species from the tropical dry forests in Bolivia. *Biotropica* 43(1):41–9.

McCormac FG, Hogg AG, Higham TFG, Lynch-Stieglitz J, Broecker WS, Baillie MGL, Palmer J, Xiong L, Pilcher JR, Brown D, Hoper ST. 1998. Temporal variation in the interhemispheric ^{14}C offset. *Geophysical Research Letters* 25(9):1321–4.

McCormac FG, Reimer PJ, Hogg AG, Higham TFG, Baillie ML, Palmer JG, Stuiver M. 2002. Calibration of the radiocarbon time scale for the Southern Hemisphere: AD 1850–950. *Radiocarbon* 44(3):641–51.

Menezes M, Berger U, Worbes M. 2003. Annual growth ring and long term growth patterns of mangrove trees from the Bragança Peninsula, North Brazil.

Wetlands Ecology and Management 11(4):233–42.

Moreno Valoyes M. 2013. Influencia del clima local y del ENSO en el crecimiento de abarco (*Cariniana pyriformis*), Chocó, Colombia [Maestría thesis]. Medellín: Universidad Nacional de Colombia.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403(6772):853–8.

Navarro G, Maldonado M. 2002. *Geografía Ecológica de Bolivia: Vegetación y Ambientes Acuáticos*. Cochabamba, Bolivia: Centro de Ecología Simón I. Patiño-Departamento de Difusión. 719 p.

Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Bronk Ramsey C, Buck CE, Cheng H, Edwards RL, Friedrich M, Grootes PM, Guilderson TP, Haflidason H, Hajdas I, Hatté C, Heaton TJ, Hoffmann DL, Hogg AG, Hughen KA, Kaiser KF, Kromer B, Manning SW, Niu M, Reimer RW, Richards DA, Scott EM, Southon JR, Staff RA, Turney CSM, van der Plicht J. 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon* 55(4):1869–87.

Rivas-Martínez S, Rivas-Sáenz S, Penas A. 2011. Worldwide bioclimatic classification system. *Global Geobotany* 1:1–634.

Rozendaal D, Zuidema P. 2010. Dendroecology in the tropics: a review. *Trees* 25(1):3–16.

Ryan WBF, Carbotte SM, Coplan JO, O'Hara S, Melkonian A, Arko R, Weissel RA, Ferrini V, Goodwillie A, Nitsche F, Bonczkowski J, Zemsky R. 2009. Global Multi-Resolution Topography synthesis. *Geochemistry, Geophysics, Geosystems* 10(3):Q03014, doi:10.1029/2008GC002332.

Santos GM, Ormsby K. 2013. Behavioral variability in ABA chemical pretreatment close to the ^{14}C age limit. *Radiocarbon* 55(2):534–44.

Santos GM, Southon JR, Druffel-Rodriguez KC, Griffin S, Mazon M. 2004. Magnesium perchlorate as an alternative water trap in AMS graphite sample preparation: a report on sample preparation at KCCAMS at the University of California, Irvine. *Radiocarbon* 46(1):165–73.

Santos GM, Moore RB, Southon JR, Griffin S, Hinger E, Zhang D. 2007. AMS ^{14}C sample preparation at the KCCAMS/UCI Facility: status report and performance of small samples. *Radiocarbon* 49(2):255–70.

Schöngart J. 2008. Growth-oriented logging (GOL): a new concept towards sustainable forest management in Central Amazonian várzea floodplains. *Forest Ecology and Management* 256(1–2):46–58.

Scott EM, Boaretto E, Bryant C, Cook GT, Gulliksen S, Harkness DD, Heinemeier J, McGee E, Naysmith P, Possnert G, van der Plicht H, Van Strydonck M. 2004. Future needs and requirements for AMS ^{14}C standards and reference materials. *Nuclear Instruments and Methods in Physics Research B* 223–224:382–7.

Solíz C, Villalba R, Argollo J, Morales MS, Christie DA, Moya J, Pacajes J. 2009. Spatio-temporal variations in *Polylepis tarapacana* radial growth across the Bolivian Altiplano during the 20th century. *Palaeogeography, Palaeoclimatology, Palaeoecology* 281(3–4):296–308.

Soliz-Gamboa C, Rozendaal DMA, Ceccantini G, Angyalossy V, van der Borg K, Zuidema PA. 2011. Evaluating the annual nature of juvenile rings in Bolivian tropical rainforest trees. *Trees* 25(1):17–27.

Southon JR, Magana AL. 2010. A comparison of cellulose extraction and ABA pretreatment methods for AMS ^{14}C dating of ancient wood. *Radiocarbon* 52(3):1371–9.

Stokes M, Smiley T. 1968. *An Introduction to Tree-Ring Dating*. Chicago: University of Chicago Press. 73 p.

Stuiver M, Polach HA. 1977. Discussion: reporting of ^{14}C data. *Radiocarbon* 19(3):355–63.

Villalba R, Luckman B, Boninsegna J, D'Arrigo R, Lara A, Villanueva-Diaz J, Masiokas M, Argollo J, Soliz C, LeQuesne C, Stahle D, Roig F, Aravena J, Hughes M, Wiles G, Jacoby G, Hartsough P, Wilson RS, Watson E, Cook E, Cerano-Paredes J, Therrell M, Cleaveland M, Morales M, Graham N, Moya J, Pacajes J, Massacchesi G, Biondi F, Urrutia R, Pastur G. 2011. Dendroclimatology from regional to continental scales: understanding regional processes to reconstruct large-scale climatic variations across the Western Americas. In: Hughes MK, Swetnam TW, Diaz HF, editors. *Dendroclimatology*. Dordrecht: Springer Netherlands. p 175–227.

Westbrook JA, Guilderson TP, Colinvaux PA. 2006. Annual growth rings in a sample of *Hymenaea courbaril*. *IAWA Journal* 27(2):193–7.

Wils TH, Robertson I, Eshetu Z, Sass-Klaassen UG, Koprowski M. 2009. Periodicity of growth rings in *Juniperus procera* from Ethiopia inferred from crossdating and radiocarbon dating. *Dendrochronologia* 27(1):45–58.

Worbes M. 2002. One hundred years of tree-ring research in the tropics—a brief history and an outlook to future challenges. *Dendrochronologia* 20(1–2):217–31.

Yamaguchi DK. 1991. A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research* 21:414–6.