



## ORIGINAL ARTICLE

# An assessment of growth ring identification in subtropical forests from northwestern Argentina



María Eugenia Ferrero<sup>a,\*</sup>, Ricardo Villalba<sup>a</sup>, Stella Maris Rivera<sup>b</sup>

<sup>a</sup> Grupo de Dendrocronología e Historia Ambiental, IANIGLA, CCT-CONICET-Mendoza, CC 330 (5500) Mendoza, Argentina

<sup>b</sup> CIMAD Centro de Investigación en Maderas. Facultad de Ciencias Agrarias y Forestales. UNLP, CC 31 (1900) La Plata, Argentina

## ARTICLE INFO

## Article history:

Received 27 September 2012

Accepted 29 January 2014

## Keywords:

Tree rings

Wood anatomy

Montane forests

Transitional forests

Chaco

Yungas

## ABSTRACT

Most subtropical forests in South America are located in regions with a marked seasonality in precipitation, which may induce the formation of annual bands in woody species. Due to the lack of precise information on tree-ring visibility, we evaluated the wood characteristics of 37 tree species in the subtropical Yungas and Chaco forests from northwestern (NW) Argentina. Anatomical features associated with the delimitation of growth bands were examined to establish the presence of tree rings. Different forest types reflect the precipitation gradients and wood anatomical features vary accordingly. Characteristics of wood structure are closely related to the dominant climatic patterns of each forest, revealing a common pattern of anatomical arrangements in terms of water transport and safety. In the Chaco and transitional forests, ring boundaries are related to marginal parenchyma whereas in montane forests growth ring boundary is mostly associated with the presence of thicker fibers at the end of the ring. The largest proportion of species with clearly marked growth rings occurs in the montane forest type of NW Argentina. Clear growth rings is a requisite for dendrochronological applications, hence the present work represents the first regional attempt to address the potential of subtropical species in South America to be used in dendrochronological studies.

© 2014 Elsevier GmbH. All rights reserved.

## Introduction

There have been numerous efforts to apply dendrochronological methods in tropical and subtropical regions worldwide. A fundamental requirement to conduct tree-ring studies is to identify clearly marked growth rings in the cross-section of woody species. In contrast to temperate and cold regions, the reduced temperature seasonality in subtropical and tropical regions hinders the formation of clearly distinctive growth rings. Relatively uniform temperatures throughout the year, without a marked cool season, facilitate the occurrence of an almost continuous cambial activity without a seasonal period of dormancy. However, in most tropical and subtropical regions there is a marked seasonality in precipitation with a pronounced dry season. Rainfall seasonality reinforces the weak seasonality in temperature resulting in an interval of cambial dormancy and the consequent formation of annual bands

in the wood. The combined seasonality in temperature and precipitation induces a cycle in tree physiology, frequently related to cambial inactivity during leaf abscission. In tropical forests of South America, several authors have documented for many species the occurrence of cambial inactivity during a period of two consecutive months with less than 50 mm of rainfall (Worbes, 1999; Brien and Zuidema, 2005). Indeed, recent studies have shown the dendrochronological potential of several species growing in tropical–subtropical regions of South America with marked rainfall seasonality (Grau et al., 2003; López and Villalba, 2011).

Ring width is the feature of woody species most commonly used to determine the variations in radial growth and environmental influences on tree growth (Fritts, 1976). According to Roig (2000), three different arrangements in the wood define ring boundaries: (1) differences in vessel diameter between early and latewood, (2) occurrence of flattened, thick fibers or tracheids in latewood, (3) presence of a marginal band of axial parenchyma.

The size and arrangement of vessels and other elements in the wood such as axial parenchyma or fibers are to some extent related to seasonal changes in water demand by trees (Carlquist, 1988). Broader vessels in the early wood conduct large amounts of water to supply evapotranspiration during the early budding and

\* Corresponding author at: Grupo de Dendrocronología e Historia Ambiental, IANIGLA, CCT-CONICET-Mendoza, Avenida Ruiz Leal s/n, Parque San Martín, CC 330 (5500) Mendoza, Argentina. Tel.: +54 261 5244207; fax: +54 261 5244201.

E-mail address: [mferrero@mendoza-conicet.gob.ar](mailto:mferrero@mendoza-conicet.gob.ar) (M.E. Ferrero).

blooming phases. Narrow vessels, generally located in the late-wood, are related to lower water requirements at the end of the growing season (Carlquist, 1988).

Parenchyma bands at the end of growth rings (“marginal parenchyma”) may contain starch, which can have two physiological functions: a store of photosynthates for rapid production of foliage or flowers; or a reserve from which sugars, by hydrolysis, could be transferred into vessels, altering their osmotic potential (Carlquist, 1988).

In addition, although fibers do not have sufficient conductive capabilities to form a subsidiary conductive system, they form a dense net around vessels which might reduce the risk of embolism (Carlquist, 1984, 1988).

The South American subtropics are covered with extensive semiarid forests or woodlands which provide a transitional canopy between tropical and temperate forests (Morello, 1967). Despite the large diversity of woody species and the enormous geographical differences in tree habitats engendered by the Andes in the subtropical forests of South America, few efforts have been conducted to identify species with visible growth rings to reconstruct the environmental history of such extensive regions. In addition, few or isolated dendrological descriptions of tropical–subtropical woody species are available (Worbes, 2002; Roig et al., 2005; López, 2011), and even fewer have put emphasis on tree-ring demarcation. In consequence, a dendrochronological survey of woody species from seasonal subtropical ecosystems will provide a valuable measure of the dendrochronological potential of the different subtropical environments in South America.

In the present work, we report the anatomical characteristics of woody species from subtropical forests in northwestern (NW) Argentina. We surveyed 37 trees to identify suitable species to be used in dendrochronology. The anatomical features related to annual band demarcation are described for each species.

## Materials and methods

### Study area: climate and vegetation

Subtropical forests in South America cover extensive regions with seasonal rainfall regimes (Murphy and Lugo, 1986). Vegetation is mostly deciduous, losing the leaves during the dry season. Although succulent and evergreen species occur in the driest forests, deciduousness increases as precipitation declines.

In this study, sample collection embraces two major subtropical forests from NW Argentina (22°–28° S): Chaco and Yungas formations (Fig. 1). The climate of the region is monsoonal with a large percentage (70–90%) of the precipitation concentrated in summer (November to March) and a marked dry winter season.

### Chaco

The “Gran Chaco” represents the vast Quaternary flatland of approx. 1,000,000 km<sup>2</sup> that extends over southeastern Bolivia, western Paraguay and NW Argentina. Vegetation forms heterogeneous patches of forests, savannahs and grasslands (Sarmiento, 1972). Across the east-to-southwest gradient, precipitation decreases from 1000 to 400 mm. Mean annual temperature ranges between 20 and 28 °C.

Although summers are extremely warm, few frost events occur in winter, leading the vegetation to be related to the dry and temperate formation of Monte and Andean Prepuna (Pennington et al., 2000). Chaco forests are dominated by *Schinopsis* tree species, associated with *Aspidosperma quebracho-blanco* D.F.K. Schltdt, and several species of *Bulnesia* and *Prosopis* (Sarmiento, 1972; Cabrera, 1976).

### Yungas

Yungas is a biome associated with the subtropical-tropical mountains in Argentina, Bolivia and Perú. In NW Argentina, Yungas occur as a narrow belt, 50–100 km wide, on the Andes slopes from the border with Bolivia to approx. 28° S. Three forest types occur along an elevation gradient, and vary accordingly to orographic precipitation regime that raises from the Chaco ecotone as elevation increases westwards. The *transitional forest* (“selva de transición”) extends from 400 m in the ecotone with the Chaco forest to ~700 m elevation. Summers are warm and humid. A marked water deficit is recorded during winter. Over 70% of the vegetation is deciduous. The *lower montane forest* (“selva montana”) occupies the lowest mountain slopes between 600 and 1700 m. Evergreen species are common with less than 20% being deciduous. Water seasonality is less marked than in the transition forest. Finally, the *upper montane forest* (“bosque montano”) from 1700 to 2500 m elevation represents the cooler and moister expression of the subtropical forests in NW Argentina. At higher elevations, the humid montane forests gradually change to mesic-dry mountain forests (Prepuna) and to grasslands and shrub steppe in the Puna (3000–3500 m).

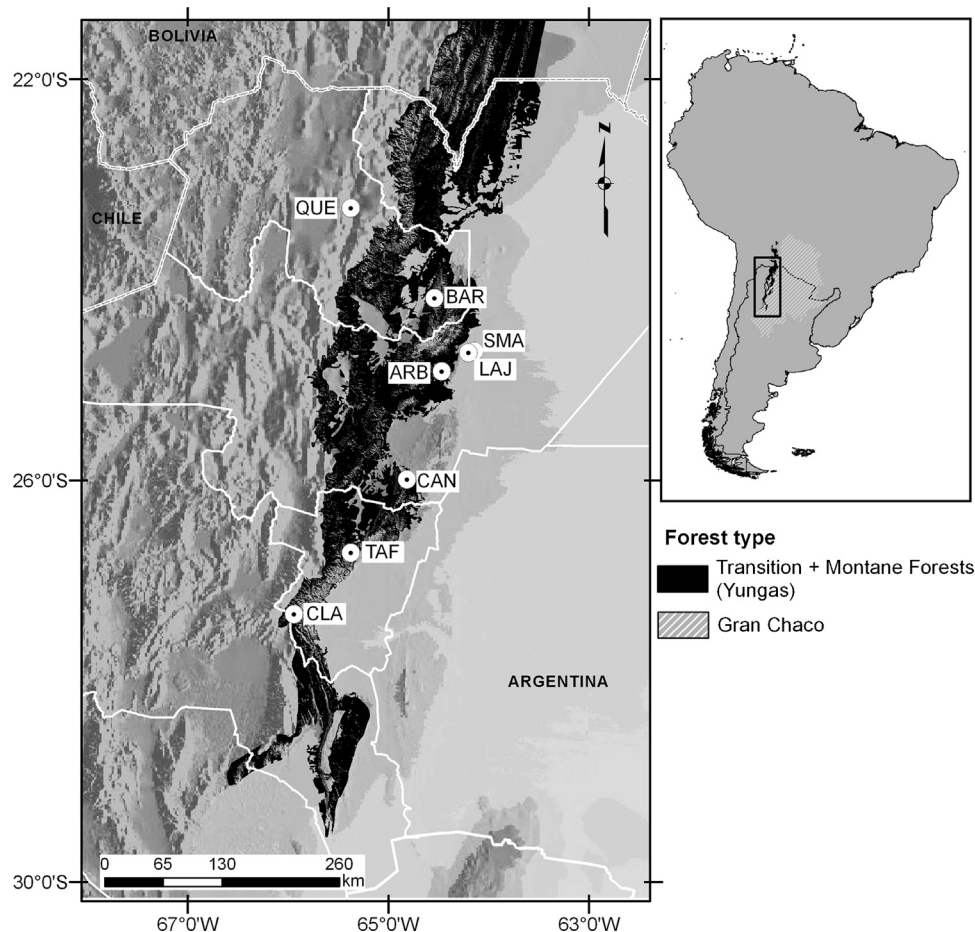
### Sample collection and processing

Stem cross-sections from transitional and montane forests in the Yungas and the flatlands in the Chaco forests were collected between 2004 and 2008 from the field and local sawmills in NW Argentina (Fig. 1). Samples were taken from the main bole in all cases, and more than one tree was sampled depending on the abundance or rarity of the species (Table 1). These samples were used to supplement previous collections undertaken during the 1980s by the Tree-Ring Laboratory from IANIGLA, in Mendoza, Argentina (CLA, TAF; see Fig. 1 for references). At the laboratory, cross-sections were polished following the standard dendrochronological methodology described in Stokes and Smiley (1968). Samples were examined under a magnifying lens. For each species we recorded (1) presence of tree rings, (2) arrangement of woody elements in early and latewood, and (3) arrangement of woody elements in relation to tree-ring boundaries. Other characteristics of the wood samples considered were the presence of false rings, wedging rings or growth anomalies which affect the circular uniformity of growth bands in a tree cross-section and consequently the ability to cross-date two or more radii from a single stem (match variations in ring width patterns between radii; Fritts, 1976).

Histological sections from the collected tree species were used to describe the arrangement of woody elements in relation to ring-boundary formation. Thin sections (30 µm thickness) were cut from small wood cubes with a sliding microtome, stained with safranin and mounted in Entellan. The arrangement of anatomical elements for each species was described following IAWA (1989) and Tortorelli (2009) terminology. Scientific names are according to the Argentinean Vascular Plants Catalog, Darwinion Botanic Institute ([www.darwin.edu.ar/Publicaciones/CatalogoVascII/CatalogoVascII.asp](http://www.darwin.edu.ar/Publicaciones/CatalogoVascII/CatalogoVascII.asp)). The histological wood collection is available at the Facultad de Ciencias Agrarias y Forestales, La Plata University, Argentina.

### Statistical analysis

In order to assign specific anatomical features in wood to the environmental conditions where a species develops, arrangements of the woody elements from each species were examined using Classification and Regression Trees (CART) analyses. CART models possess the advantage of combining in a single analysis continuous, ordinal, categorical and qualitative variables. Based on the



**Fig. 1.** Maps showing distribution of Chaco and Yungas forests. Locations of wood collections in NW Argentina are indicated: QUE, Quebraleña (MF/Prepuna); BAR, Sierras de Santa Bárbara (MF); SMA, San Martín (CH); LAJ, Lajitas (CH/TF); ARB, Arballito (TF); CAN, Sierras de la Candelaria (TF); TAF, Taficillo-San Javier (TF/MF); CLA, Cuesta del Clavillo (MF). Digital classification developed by S. Pacheco, Fundación ProYungas <http://www.proyungas.org.ar>. CH, Chaco; TF, transitional forest; MF, montane forest (lower + upper).

differences between groups, CART models separate the species consecutively into subgroups which are homogeneous in relation to the former assemblages (Breiman et al., 1984). This classification provides a tree-like clustering, with an associated dichotomy key, which identifies samples within each group (Urban, 2002). Anatomical variables in each species were analyzed using the CART-Split selection method (StatSoft Inc., 2001).

## Results

### Growth rings

Site locations for the collected species are shown in Fig. 1. Collections embrace 37 species from 20 families growing in diverse subtropical forest environments in NW Argentina. The anatomical features of some species, with emphasis on ring demarcation, are shown in Fig. 2. Of the total number of analyzed species, 15 showed clear growth bands. Within semiarid Chaco forests, three (*Lithraea ternifolia*, *Prosopis alba*, *Schinopsis lorentzii*) out of eight sampled species presented distinctive growth rings. Incomplete bands (wedge lenses) were recorded in *L. ternifolia*. *P. alba*, a dominant tree in Chaco forest formation, tends to form micro-ring packs (large number of very narrow, compressed rings). Individual rings in those packs are very difficult to identify and measure. Transition forests present five (*Ceiba insignis*, *Amburana cearensis*, *Enterolobium contortisiliquum*, *Pterogyne nitens*, *Fagara coco*) out of

19 sample species with marked growth bands. In this group of species only *C. insignis* showed wedge lenses. Most species pertaining to this formation tend to be fast-growing trees. Finally, eight species (*Alnus acuminata*, *Juglans australis*, *Cinnamomum porphyrium*, *Cedrela lilloi*, *Cedrela saltensis*, *Podocarpus parlatorei*, *Polylepis tomentella*, *Prunus tucumanensis*) in the montane forests show clearly distinctive bands. In the same formation, *Blepharocalyx salicifolius* and *Myrcianthes mato* exhibit bands and annual boundaries difficult to identify. *P. parlatorei*, the only conifer in the region, shows clear growth bands but a large proportion of wedging rings.

### Wood characteristics

Table 1 lists the studied species, their anatomic characteristics, as well as the forest formation to which they belong. In order to analyze the relationships between anatomical features and ring formation, the “forest type” variable was predicted as a function of growth ring presence (GR), ring boundary type (RB), porosity (POR), vessel grouping (VG) and paravascular parenchyma (PAR). Since most species are from the transitional forest (TF), the CART analysis started with a decision node *i* (root node) where all 37 species were assigned to this forest formation (Fig. 3, see the histogram box). The root node *i* splits into two nodes, *ii* and *iii*, separated according to the variable listed below the nodes; vessel grouping in this case. Eleven species within the cluster vessel grouping belong to the

**Table 1**

Tree species collected from subtropical forests formations in NW Argentina and growth ring characteristics.

| Family                  | Species                                                       | Forest type | Wood characters |    |    |     |    |     |
|-------------------------|---------------------------------------------------------------|-------------|-----------------|----|----|-----|----|-----|
|                         |                                                               |             | GR              | T  | RB | POR | VG | PAR |
| Anacardiaceae           | <i>Astronium urundeuva</i> <sup>a</sup>                       | TF          | (+)             | UM | F  | D   | C  | 2   |
|                         | <i>Lithraea ternifolia</i>                                    | CH          | +               | UM | F  | D   | S  | 2   |
|                         | <i>Schinopsis lorentzii</i> <sup>a</sup>                      | CH          | +               | I  | F  | SR  | S  | 2   |
| Apocynaceae             | <i>Aspidosperma quebracho-blanco</i> <sup>a</sup>             | CH          | (+)             | M  | F  | SR  | S  | 2   |
| Betulaceae              | <i>Alnus acuminata</i> <sup>a</sup>                           | MF          | +               | M  | F  | D   | D  | 2   |
| Bignoniaceae            | <i>Tabebuia nodosa</i>                                        | TF          | –               | UM | P  | D   | RM | 2   |
|                         | <i>Tecoma stans</i> var. <i>stans</i>                         | TF          | –               | UM | P  | SR  | RM | 1   |
| Bombacaceae             | <i>Ceiba insignis</i> <sup>a</sup>                            | TF          | +               | UM | P  | D   | S  | 0   |
| Fabaceae                | <i>Amburana cearensis</i> <sup>a</sup>                        | TF          | +               | UM | F  | D   | S  | 1   |
|                         | <i>Anadenanthera colubrina</i> var. <i>cebil</i> <sup>a</sup> | TF          | (+)             | UM | F  | D   | S  | 2   |
|                         | <i>Caesalpinia paraguayensis</i> <sup>a</sup>                 | CH          | (+)             | UM | –  | D   | S  | 1   |
|                         | <i>Enterolobium contortisiliquum</i> <sup>a</sup>             | TF          | +               | M  | P  | D   | S  | 1   |
|                         | <i>Erythrina crista-galli</i> <sup>a</sup>                    | TF          | –               | UM | P  | D   | S  | 1   |
|                         | <i>Myroxylon peruiferum</i>                                   | TF          | –               | UM | P  | D   | RM | 2   |
|                         | <i>Parapiptadenia excelsa</i>                                 | TF          | (+)             | UM | P  | SR  | RM | 1   |
|                         | <i>Prosopis alba</i> var. <i>panta</i>                        | CH          | (+)             | UM | P  | D   | S  | 1   |
|                         | <i>Prosopis kuntzei</i> <sup>a</sup>                          | CH          | (+)             | UM | P  | D   | S  | 1   |
|                         | <i>Prosopis nigra</i> var. <i>ragonesei</i>                   | CH          | (+)             | UM | P  | D   | S  | 1   |
|                         | <i>Pterogyne nitens</i>                                       | TF          | +               | I  | P  | D   | S  | 1   |
|                         | <i>Tipuana tipu</i> <sup>a</sup>                              | TF          | (+)             | UM | –  | D   | S  | 1   |
| Juglandaceae            | <i>Juglans australis</i> <sup>a</sup>                         | MF          | +               | M  | F  | R   | S  | 1   |
| Lauraceae               | <i>Cinnamomum porphyrium</i> <sup>a</sup>                     | MF          | +               | M  | F  | D   | RM | 0   |
| Meliaceae               | <i>Cedrela lilloi</i> <sup>a</sup>                            | MF          | +               | M  | P  | R   | S  | 0   |
|                         | <i>Cedrela saltensis</i> <sup>a</sup>                         | MF          | +               | M  | P  | R   | S  | 0   |
| Myrtaceae               | <i>Blepharocalyx salicifolius</i> <sup>a</sup>                | MF          | (+)             | UM | F  | D   | S  | 1   |
|                         | <i>Myrcianthes mato</i>                                       | MF          | (+)             | UM | F  | D   | S  | 1   |
| Nyctaginaceae           | <i>Pisonia zapallo</i>                                        | TF          | –               | UM | –  | D   | RM | 0   |
| Pinaceae: Podocarpaceae | <i>Podocarpus parlatorei</i> <sup>a</sup>                     | MF          | +               | UM | F  | –   | –  | –   |
| Rhamnaceae              | <i>Ziziphus mistol</i>                                        | TF          | –               | UM | F  | D   | S  | 1   |
| Rosaceae                | <i>Polylepis tomentella</i> <sup>a</sup>                      | MF          | +               | M  | F  | SR  | D  | 2   |
|                         | <i>Prunus tucumanensis</i> <sup>a</sup>                       | MF          | +               | M  | F  | D   | RM | 0   |
| Rubiaceae               | <i>Calycophyllum multiflorum</i>                              | TF          | (+)             | UM | –  | D   | RM | 2   |
| Rutaceae                | <i>Fagara coco</i>                                            | TF          | +               | UM | P  | D   | RM | 2   |
| Santalaceae             | <i>Acanthosyris falcata</i>                                   | TF          | –               | UM | F  | D   | D  | 1   |
| Sapotaceae              | <i>Sideroxylon obtusifolium</i>                               | TF          | –               | UM | –  | D   | D  | 1   |
| Ulmaceae                | <i>Phyllostylon rhamnoides</i>                                | TF          | –               | I  | –  | D   | RM | 2   |
| Zygophyllaceae          | <i>Bulnesia sarmientoi</i> <sup>a</sup>                       | CH          | –               | I  | P  | D   | D  | 1   |

Forest type = CH: Chaco forest, TF: transitional forest, MF: montane forests (lower + upper).

GR = Growth rings. + distinct, (+): distinct with difficulty, –: indistinct or absent.

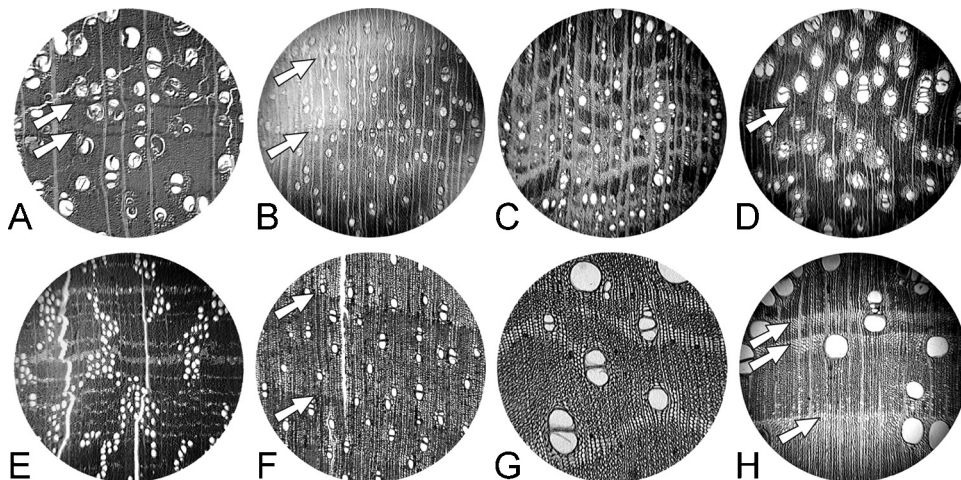
T = transition early/Late wood. M: marked, UM: unmarked, I: imprecise.

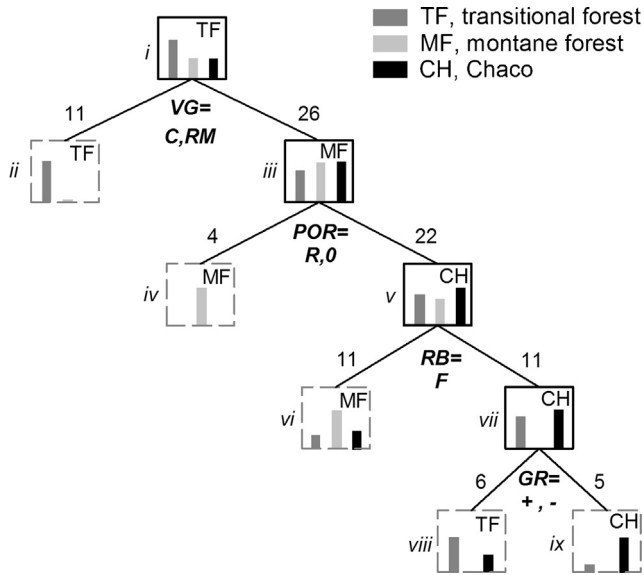
RB = Ring Boundary. F: flattened fibers, P: marginal parenchyma.

POR = Porosity. R: ring, SR: semi-ring, D: diffuse porous.

VG = vessel grouping. S: solitary, RM: radial multiple, C: clusters, D: diagonal aggregation, T: tangential aggregation (according to [Carlsquist, 1988](#)).

PAR = paravascular parenchyma. 1: abundant, 2: scarce, 0: no.

<sup>a</sup> Indicates two or more individuals sampled.**Fig. 2.** Wood cross-sections from subtropical species in NW Argentinean forests. (A) *Anadenanthera colubrina*, (B) *Schinopsis lorentzii*, (C) *Tabebuia nodosa*, (D) *Parapiptadenia excelsa*, (E) *Sideroxylon obtusifolium*, (F) *Fagara coco*, (G) *Tipuana tipu*, (H) *Cedrela lilloi*. Arrows indicate growth band boundaries. All pictures at 40× magnification.



**Fig. 3.** Classification tree for the “forest type” variable as a function of the anatomical characteristics of the 37 studied species. Full boxes are *decision nodes*; dashed boxes are *terminal nodes*. The variable used to separate the nodes is shown below the division (VG, vessel grouping; POR, porosity; RB, ring boundary; GR, growth rings; see Table 1 for variables description). Numbers indicate the species assigned to each node; node numbering is in Roman.

TF, whereas the remaining 26 species are tentatively classified as belonging to the montane forest (MF). According to the histograms, there are more species with radial grouping within the MF than in the Chaco forest (CH). Node *iii* splits the group according to wood porosity, grouping four species within ring porosity in the MF (node *iv*) and the remaining 22 species with diverse porosity types in the CH (node *v*). Based on growth ring boundaries, the nodes *vi* and *vii* separate MF from CH species, allocating 11 species with flattened-fiber boundaries to the MF and 11 species with marginal-parenchyma boundaries to the CH. Finally, tree species from TF and CH are classified by the presence (node *viii*) or absence (node *ix*) of tree rings.

## Discussion

### Tree rings in subtropical forests

There is a wide range of factors that determine the occurrence of growth rings in woody plants (Jacoby, 1989; Worbes, 2002). Seasonality in leaf production is a major driver of ring formation, however deciduous trees do not always show rings and, in turn, many evergreens have well marked rings (Carlquist, 1988). For instance, some tropical evergreen trees present clear and well-distinct annual tree rings (Worbes, 2002; Roig et al., 2005). Although leaf seasonality is a common characteristic in most subtropical trees from NW Argentina, a careful inspection of the anatomical features reveals that well-defined tree rings are not present in all species. Nevertheless, there are important relationships between wood traits and the different forest formations in subtropical NW Argentina.

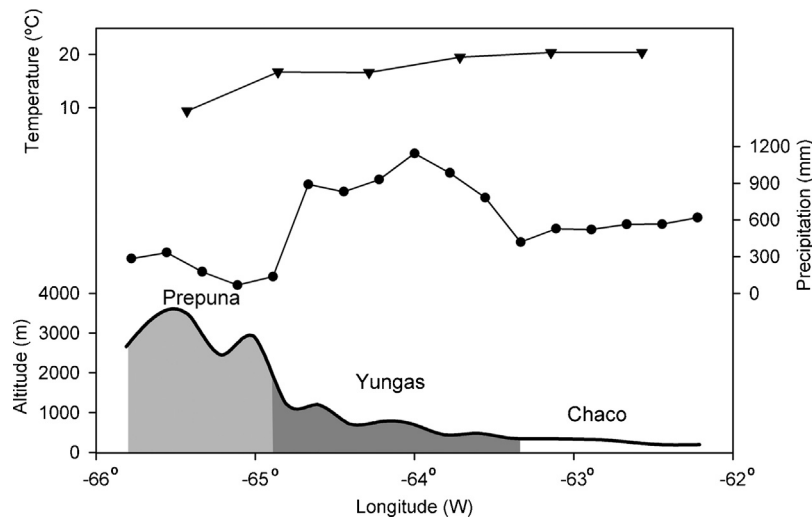
The arrangement of anatomical elements is a source of information about the environment and growth habitat of trees. In this sense, CART analysis was helpful in differentiating the wood characters more closely related to each type of forest. The classification tree based on anatomical features shows that trees from the transitional forest have vessels grouped in clusters; indeed, most species in the transition forest show vessel in groups, a characteristic

exclusive of this forest formation. From a climatic perspective, transitional forests are located between the dry Chaco and wet montane forests. High temperatures occur during a large part of the year and rainfall is concentrated in summer (November to March). Water deficit is more marked than in Yungas forests (Brown and Malizia, 2004). The abundance of vessels grouped in clusters allows trees to take advantage of the short period of abundant precipitation and reduces the risk of cavitation during the extended dry period over the year. On the other hand, although trees from the montane forest sometimes exhibit vessels arranged in ring porosity, trees in Chaco and montane forests generally present solitary vessels. Abundant and relatively large vessels at the beginning of the growth ring provide high conductive capacity. Moderate temperatures in the montane forest mitigate periods of water deficit, reduce cavitation of vessels and facilitate maintenance of active, functional vessels in the early wood during most of the growing season.

For trees in the category of “other porosity”, the woody elements related to growth-ring boundaries determined their incorporation in different groups. In the montane forest, ring boundaries are related to fibers with reduced lumen. In these species, reserves are stored in parenchyma bands surrounding or connected to conductive vessels. This anatomical trait is also recorded in deciduous species from southern Patagonian forests of Argentina and Chile (Tortorelli, 2009). In Chaco and transitional forest, tree-ring boundaries are mostly associated with the presence of marginal parenchyma. The hydrolysis of starch stored in the parenchyma may promote development of leaf and wood tissues even when moisture conditions at the beginning of the growing season do not facilitate tree growth (Carlquist, 1988). The marginal parenchyma also defines the boundaries of rings in other subtropical forests formations in South America. López (2011) who analyzed the wood of 11 trees in the dry Bolivian Chiquitanía forests found that tree rings are delimited by marginal parenchyma in 73% of the studied species. Along the same line, Roig et al. (2005) found that the marginal parenchyma is the most common feature associated with growth boundaries (72% of species) in trees from the Yucatán Peninsula, Mexico.

The occurrence of tree rings is not a distinctive feature of any subtropical forest formation in NW Argentina. Fifteen out of 37 studied species showed clear tree rings, nine of them in the montane forest. This relatively large concentration of species with marked annual bands occurring in the montane forest reflects the changes in temperature and precipitation introduced by the Andes topography (Fig. 4). Temperature decreases with elevation whereas rainfall varies in relation to elevation. From east to west, the flat landscape, in combination with high temperatures and low rainfalls, has promoted the development of wood characteristics reducing the unfavorable consequences of water stress. Westwards, the sub-Andean mountain ranges that intercept the humid air masses from northeasterly winds generate abundant orographic rainfalls which reach maximum values at middle altitudes in the montane forest belt.

In the Chaco plains, with mean yearly temperatures between 20 and 24 °C, rainfall decreases from 1200 mm in the eastern formation area to a minimum of 400 mm on the Andean foothills. This decrease in rainfall is accompanied by a lengthening of the winter dry season from 2 to 7 months. Even though most of the canopy species are deciduous (63%), the three dominant species (*S. lorentzii*, *A. quebracho-blanco* and *B. sarmientoi*) are brevi-deciduous or evergreen (Sarmiento, 1972). In the transitional forest (~600 m) where precipitation increases due to orographic effect, only 20% of the species lose their leaves during winter (dry season; Brown, 1995). Up to the montane environment, evapotranspiration is more reduced due to contribution of mists (Hunzinger, 1995), higher soil water capacity and lower temperatures. Winter tree dormancy is



**Fig. 4.** Altitudinal transect across subtropical forests in NW Argentina between 22° and 26° S latitude, showing changes in mean annual temperature (top), and total annual precipitation (middle) in relation to topography (bottom). Locations of weather stations within the latitudinal belt are indicated by inverted triangles (temperature) and dots (precipitation). Forest types are shown for the different altitudinal zones.

largely due to low temperatures and not to water deficit. During extreme weather events in winter, frosts and snowfalls occur in the upper montane forest (1500–2700 m). In consequence, more than 80% of the species are deciduous or semi-deciduous in this forest, reflecting the occurrence of relatively low temperatures and reduced precipitations in winter (Pacheco and Yapur, 2006).

In the context of the subtropical trees, it is interesting to note that delimitation of growth rings by fibers usually occurs in species that migrate on geological time scale from temperate to subtropical regions, such as *Alnus*, *Juglans* and *Prunus*, all of them currently located in the montane formation. In contrast, Neotropical trees show bands of marginal or vasicentric parenchyma as the most prominent feature for ring delimitation. This anatomical feature is recorded in many species from Chaco and transitional forests.

#### Dendrochronological potential of subtropical species

Fifteen tree species with distinctive growth bands were identified in the subtropical forest formation of NW Argentina. Five of these species, *A. acuminata*, *C. lilloi*, *J. australis*, *P. parlatorei*, and *S. lorentzii*, have been successfully used in previous dendrochronological studies (Boninsegna et al., 2009).

In the dry Chaco formation, two out of the nine sampled species show clearly distinct rings. As aforementioned, *L. ternifolia* presents wedging bands that greatly hinder cross-dating within and between trees. The species *P. alba* shows identifiable growth bands; nevertheless, this species tends to form micro-ring packs, making identification of individual rings in the pack extremely difficult. This anatomical feature has previously been related to fire in *Prosopis caldenia* (Dussart et al., 1997) and changes in water table depth in *Prosopis flexuosa* (Villagra et al., 2005). Additionally, most trees from the Chaco forest formation present dense and hard wood (>0.9 kg/dm<sup>3</sup>), which hampers the use of traditional increment borers for collecting wood cores. Extensive dendrochronological sampling of these species implies the collection of a large number of transverse sections. Opportunistic samplings of these species require the localization of areas under deforestation where cross-sections are collected from the stumps remaining in the field.

In the transitional forest, less than 30% of the species present well marked growth bands. In this group, *C. insignis* shows a large proportion of wedging rings hindering the use of this species for dendrochronological studies. Although showing distinctive annual rings, most cross-sections from *F. coco* indicate that this species has relatively short life spans, reducing its use to short-term dendrochronological applications.

Another important factor to consider in diverse subtropical forests is the relatively low abundance of individuals from a particular species. This is the case for *P. nitens* and *A. cearensis*, species with low population density due to past and current logging pressures, constrained multi-sampling and broad-scale studies.

Eight species (*A. acuminata*, *C. porphyrium*, *C. lilloi*, *C. saltensis*, *L. ternifolia*, *J. australis*, *P. parlatorei*, *P. tomentella*, *P. tucumanensis*, Table 1) from the montane forests showed clear growth bands. Moderately marked rings were recorded in *B. salicifolius* and *M. mato*. Although rings are clearly marked in *P. tucumanensis*, annual bands are not circularly uniform, a major obstacle for cross-dating samples, even from a single individual. Clearly marked rings were recorded in *C. saltensis* and *P. tomentella*. However, cross-dating of individual trees from these species is problematical due to lack of circular uniformity. Although the anomalous pattern of growth might be species-related, it could also reflect the larger influence of autogenic than environmental factors on the radial growth of both species. For *C. lilloi* in the Yungas, *C. odorata* in the Mato Grosso and *Polylepis tarapacana* in the Puna, good-quality chronologies have already been developed (Villalba et al., 1985; Dünisch et al., 2003; Argollo et al., 2004, respectively). Despite the presence of wedging rings in its wood, tree rings from *P. parlatorei* have successfully been used in studies of population dynamics (Carilla and Grau, 2010). Lastly, *C. porphyrium* fulfills all necessary conditions to be used in dendrochronological studies; further sampling of this species is needed in order to determine its dendrochronological potential.

The NW subtropical forests in Argentina are the most austral component of the seasonal tropical forests, a series of disjunctive vegetation patches along the tropical South America (Prado and Gibbs, 1993). The identification of ring boundaries in these subtropical forests opens up the possibility of extending our dendrochronological studies into low-latitude regions creating a tree-ring network of chronologies across the dry tropical forests in South America.

## Acknowledgments

This contribution is largely based on M.E. Ferrero PhD, supported by CONICET (National Council for Scientific and Technical Research of Argentina), ANPCyT-PICTR2002/123 and Inter-American Institute for Global Change Research (IAI) CRNII-2047 funds. Authors wish to thanks Rana Ledesma, Forestal Santa Bárbara SRL, A. Giménez (UNSE), J. Bernasconi, M. De Membiela, M. Morales and A. Ripalta for field and technical assistance, and N. Horak for English revision. We also appreciate editor and reviewers' comments that improved the manuscript.

## References

- Argollo, J., Solíz, C., Villalba, R., 2004. *Potencialidad dendrocronológica de Polylepis tarapacana en los Andes Centrales de Bolivia*. *Ecología en Bolivia* 39, 5–24.
- Boninsegna, J.A., Argollo, J., Aravena, J.C., Barichivich, J., Christie, D., Ferrero, M.E., Lara, A., Quesne, C.L., Luckman, B.H., Masiokas, M., Morales, M., Oliveira, J.M., Roig, F., Srur, A., Villalba, R., 2009. *Dendroclimatological reconstructions in South America: a review*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 281, 210–228.
- Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. *Classification and Regression Trees*. Wadsworth & Brooks/Cole Advanced Books & Software, Monterey, CA, 358 pp.
- Brienen, R.J.W., Zuidema, P.A., 2005. *Relating tree growth to rainfall in Bolivian rain forests: a test for six species using tree ring analysis*. *Oecologia* 146, 1–12.
- Brown, A.D., 1995. *Fenología y caída de hojarasca en las selvas montañas del Parque Nacional El Rey Argentina*. In: Brown, A.D., Grau, H.R. (Eds.), *Investigación, conservación y desarrollo en selvas subtropicales de montaña*. LIEY, Tucumán, pp. 93–114.
- Brown, A.D., Malizia, L.R., 2004. *Las selvas pedemontanas de las Yungas*. *Ciencia Hoy* 14, 53–63.
- Cabrera, A.L., 1976. *Regiones Fitogeográficas Argentinas Fascículo 1*. *Enciclopedia Argentina de Agricultura y Jardinería, Tomo II*. Editorial ACME s.a.c.i, Buenos Aires, 85 pp.
- Carilla, J., Grau, H.R., 2010. *150 years of tree establishment, land use and climate change in montane grasslands, Northwest Argentina*. *Biotropica* 42, 49–58.
- Carlquist, S., 1984. *Vessel grouping in dicotyledon wood: significance and relationship to imperforate tracheary elements*. *Aliso* 10, 505–525.
- Carlquist, S., 1988. *Comparative Wood Anatomy. Systematic, Ecological, and Evolutionary Aspects of Dicotyledon Wood*. Springer-Verlag, Berlin, pp. 436.
- Dünisch, O., Ribeiro Montóia, V., Bauch, J., 2003. *Dendroecological investigations on Swietenia macrophylla King and Cedrela odorata L. (Meliaceae) in the central Amazon*. *Trees* 17, 244–250.
- Dussart, E., Peinetti, R., Boninsegna, J.A., 1997. *Análisis del crecimiento de Prosopis caldenia Burkart en relación con parámetros ambientales y fuego*. XVIII Reunión Argentina de Ecología, Buenos Aires, pp. 21.
- Fritts, H.C., 1976. *Tree Rings and Climate*. Academic Press, London, 567 pp.
- Grau, H.R., Easdale, T.A., Paolini, L., 2003. *Subtropical dendroecology – dating disturbances and forest dynamics in northwestern Argentina montane ecosystems*. *Forest Ecology and Management* 177, 131–143.
- Hunzinger, H., 1995. *La precipitación horizontal: su importancia para el bosque y a nivel de cuencas en la Sierra de San Javier, Tucumán Argentina*. In: Brown, A.D., Grau, H.R. (Eds.), *Investigación, conservación y desarrollo en selvas subtropicales de montaña*. LIEY, Tucumán, pp. 53–58.
- IAWA, 1989. *List of microscopic features for hardwood identification*. *IAWA Bulletin n.s.* 10, 234–332.
- Jacoby, G.C., 1989. *Overview of tree-ring analysis in tropical regions*. *IAWA Bulletin n.s.* 10, 99–108.
- López, L., (Dissertation) 2011. *Historia de los cambios ambientales y la dinámica de los bosques nativos del Cerrado Boliviano: una apreciación dendrocronológica*. Universidad Nacional del Comahue.
- López, L., Villalba, R., 2011. *Climate influences on the radial growth of Centrolobium microchaete, a valuable timber species in the tropical dry forests of Bolivia*. *Biotropica* 43, 41–49.
- Morello, J., 1967. *Bases para el estudio fitoecológico de los grandes espacios (el Chaco argentino)*. *Ciencia e Investigación* 23, 252–267.
- Murphy, P.G., Lugo, A.E., 1986. *Ecology of tropical dry forest*. *Annual Review of Ecology and Systematics* 17, 67–88.
- Pacheco, S., Yapur, A., 2006. *Fenología de Cedrela en el Parque Nacional Calilegua Argentina*. In: Pacheco, S., Brown, A. (Eds.), *Ecología y producción de cedros (género Cedrela) de las Yungas australes*. Ediciones del Subtrópico, Fundación ProYungas, Tucumán, pp. 31–40.
- Pennington, R.T., Prado, D.E., Pendry, C.A., 2000. *Neotropical seasonally dry forests and quaternary vegetation changes*. *Journal of Biogeography* 27, 261–273.
- Prado, D.E., Gibbs, P.E., 1993. *Patterns of species distributions in the dry seasonal forests of South America*. *Annals of the Missouri Botanical Garden* 80, 902–924.
- Roig, F.A., 2000. *Dendrocronología en los bosques del Neotrópico: revisión y prospección futura*. In: Roig, F.A. (Ed.), *Dendrocronología en América Latina*. Ediunc, Mendoza, pp. 307–355.
- Roig, F.A., Osornio, J.J., Díaz, J.V., Luckman, B., Tiessen, H., Medina, A., Noellemeier, E.J., 2005. *Anatomy of growth rings at the Yucatán Peninsula*. *Dendrochronologia* 22, 187–193.
- Sarmiento, G., 1972. *Ecological and floristic convergences between seasonal plant formations of tropical and subtropical South America*. *Journal of Ecology* 60, 367–410.
- StatSoft, Inc., 2001. *STATISTICA (Data Analysis Software System), Version 6*. [www.statsoft.com](http://www.statsoft.com)
- Stokes, M.A., Smiley, T.L., 1968. *An Introduction to Tree-Ring Dating*. The University of Chicago Press, Chicago, 73 pp.
- Tortorelli, L.A., 2009. *Maderas y Bosques Argentinos, Tomos I y II*. Orientación Gráfica Editora SRL, Buenos Aires.
- Urban, D.L., 2002. *Classification and regression trees*. In: McCune, R., Grace, J.B. (Eds.), *Analysis of Ecological Communities*. MjM Software Design, Oregon, pp. 222–232.
- Villagra, P.E., Villalba, R., Boninsegna, J.A., 2005. *Structure and growth rate of Prosopis flexuosa woodlands in two contrasting environments of the central Monte desert*. *Journal of Arid Environments* 60, 187–199.
- Villalba, R., Boninsegna, J.A., Holmes, R.L., 1985. *Cedrela angustifolia and Juglans australis: two new tropical species useful in dendrochronology*. *Tree-Ring Bulletin* 45, 25–35.
- Worbes, M., 1999. *Annual growth rings, rainfall-dependent growth and long-term growth patterns of tropical trees from the Caparo Forest Reserve in Venezuela*. *Journal of Ecology* 87, 391–403.
- Worbes, M., 2002. *One hundred years of tree-ring research in the tropics – a brief history and an outlook to future challenges*. *Dendrochronologia* 20, 217–231.