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ORIGINAL ARTICLE

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

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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.

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; Brienen 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

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blooming phases. Narrow vessels, generally located in the latewood, 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^2 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. Schldt, 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). 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