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Review

Distilling allometric and environmental information from time series of conduit size: the standardization issue and its relationship to tree hydraulic architecture

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Trees are among the best natural archives of past environmental information. Xylem anatomy preserves information related to tree allometry and ecophysiological performance, which is not available from the more customary ring-width or wood-density proxy parameters. Recent technological advances make tree-ring anatomy very attractive because time frames of many centuries can now be covered. This calls for the proper treatment of time series of xylem anatomical attributes. In this article, we synthesize current knowledge on the biophysical and physiological mechanisms influencing the short- to long-term variation in the most widely used wood-anatomical feature, namely conduit size. We also clarify the strong mechanistic link between conduit-lumen size, tree hydraulic architecture and height growth. Among the key consequences of these biophysical constraints is the pervasive, increasing trend of conduit size during ontogeny. Such knowledge is required to process time series of anatomical parameters correctly in order to obtain the information of interest. An appropriate standardization procedure is fundamental when analysing long tree-ring-related chronologies. When dealing with wood-anatomical parameters, this is even more critical. Only an interdisciplinary approach involving ecophysiology, wood anatomy and dendrochronology will help to distill the valuable information about tree height growth and past environmental variability correctly.

Keywords: cell chronology, dendrochronology, signal versus noise, tree-ring anatomy, wood anatomy, xylem hydraulic response.

Introduction

Trees are impressive life forms. Being sessile and long-living organisms that occur across a vast range of contrasting environments and under a variety of disturbance regimes, they must be able to cope with many different internal and external changes (Hinckley et al. 2011). During ontogenetic development, the size of a tree increases by many orders of magnitude, which is paralleled by a constant adjustment of tree structure to maintain the capacity to procure and transport resources from the environment and to grow and reproduce despite the variability of biotic and abiotic factors. Nevertheless, all trees develop with the same basic anatomical and physiological design (Enquist 2003). In regions where detectable and reliable annual rings

are formed, the fluctuations of environmental conditions may leave a permanent imprint on several measurable ring properties usually related to its width, structure and chemical composition (Hughes 2011). This coexistence of multiple properties potentially contains distinct and complementary information associated with biomass accumulation and environmental variability and explains why tree rings are among the most widespread, precise and accurate natural archives (Bradley 1999, Swetnam et al. 1999).

Among the different tree-ring properties, wood-anatomical features represent an emerging set of parameters (Fonti et al. 2010). Conduit dimension, commonly expressed as cross-sectional lumen diameter or area, retains a special significance

within the anatomical tree-ring features because of its direct link to the tree hydraulic architecture. Thanks to this, lumen area could bridge some gaps between radial and axial growth patterns and other tree responses related to environmental variability, allometric constraints during ontogenesis and physiological regulation. The increasing number of papers published in recent years (for a thorough review, see [Fonti et al. 2010](#)) confirms the promising potential of this approach ([Drew et al. 2013](#), [Fonti et al. 2013](#), [Liang et al. 2013](#)). However, a main obstacle to the interpretation of the different types of information in conduit-lumen patterns is the insufficient understanding of the role of changing conduit dimension during ontogeny. This is especially true because trees are mostly unselective and, in a way, biased recorders. They are unselective in that many environmental inputs that affect tree growth can leave an identical signature within the tree-ring sequences and biased because, being living organisms, this tracing is never a pure physical process but is filtered and modulated by individual physiological responses ([Carrer 2011](#), [Meinzer et al. 2011](#)). Working with tree-ring features such as conduit dimension therefore means having to deal with this ambiguity between internal and external (specific and unspecific) signals ([Cook 1990](#)).

Classical tree-ring research follows specific sampling criteria designed to identify sites, species and trees ([Fritts 1976](#), [Cook and Kairiukstis 1990](#)), followed by a specific processing of the ring-width series called standardization ([Cook et al. 1990](#)). Standardization is of such outstanding importance in tree-ring research that [Fritts \(1976\)](#) defined it as 'such a basic procedure in dendrochronology that it is considered by some to be a principle'. The intent of standardization is manifold: (i) to remove non-stationary processes related to the mostly size-related (and to a lesser extent age-related) trend or disturbance pulses (in the case of ring width, the generally decreasing trend with age is due substantially to the geometric constraint of adding an annual wood layer over an expanding surface represented by the stem cross-section); (ii) to stabilize the variance of tree-ring series, which are commonly heteroscedastic; and (iii) to homogenize the growth rate among samples (despite living in the same location, some trees grow faster and others slower; therefore, it is better to assign the same weight to all samples before they enter the mean growth curve; [Cook et al. 1990](#), [Helama et al. 2004](#), [Biondi and Qeadan 2008](#)). Throughout more than one century of tree-ring research, an endless number of different standardization methods have been proposed, and the discussion about the optimal procedure is still very active within the broad dendrochronological community ([Melvin and Briffa 2008](#), [Nicault et al. 2010](#), [Briffa and Melvin 2011](#)).

In time series of wood-anatomical ring properties, such as conduit-lumen area, defining the appropriate standardization approach for the specific information of interest is particularly critical because knowledge from several research fields, including tree physiology, dendrochronology and wood

anatomy, is required. In the following, focusing on time series of conduit-lumen area, we first give some relevant background about long-term trends that usually govern this parameter. We detail different aspects of how to extract environmental and ontogenetic information from these data by using an appropriate standardization technique and illustrate this with examples. To conclude, we offer some guidelines and perspectives for potential applications of the different kinds of information recorded in time series of conduit-lumen area.

The hydraulic constraints on conduit size during ontogenesis

One of the main functions of xylem tissue is the delivery of water throughout the plant from the rootlets up to the stomata ([Zimmerman 1983](#)). To sustain optimal tree functioning, the hydraulic system must be efficient and plastic in order to cope with internal and external (i.e., environmental) variability. The major source of internal variability is tree growth itself; during ontogenesis, there is usually a significant increase in the path length that water must cover. According to the classic Hagen–Poiseuille formula, resistance through an ideal tube scales with the fourth power of its diameter and linearly with length ([Tyree and Ewers 1991](#), [West et al. 1999](#)); therefore, if all xylem conduits were of the same diameter from the apex to the base, the hydrodynamic resistance would increase linearly as the tree grows in height. This could lead to catastrophic consequences for plant physiology, either inducing water deficits due to insufficient supply ([Ryan and Yoder 1997](#)) or necessitating osmotic adjustments to lower the leaf water potential and sustain transpiration and leaf hydration under increasingly high xylem tensions. This would trigger the risk of hydraulic failure by cavitation, a primary cause of productivity loss and plant mortality ([Choat et al. 2012](#)). However, by widening the diameter of xylem conduits from the stem apex downwards, trees are able to minimize the adverse effect of height growth on pathway length resistance. In other words, downwards widening of xylem conduits provides an effective mechanism to supply the distal leaves with water irrespective of the absolute root-to-leaf distance ([Becker et al. 2000](#), [Enquist 2002](#)).

In recent years, a number of investigations have reported substantial conduit widening for vascular plants independent from any species and organism size. The theoretical degree of widening towards which all plants should 'universally' converge is still debated (see [West et al. 1999](#), [Savage et al. 2010](#)), yet empirical data available in the literature, reporting the pattern of axial variation of xylem conduit dimension against the distance from the stem apex, suggest a convergence towards a power trajectory ($y = aL^b$, with y being the conduit dimension, a the allometric constant and L the distance from the stem apex) with a scaling exponent (b) varying slightly around 0.2 ([Sperry et al. 2012](#), [von Allmen et al. 2012](#), [Anfodillo et al. 2013](#), [Olson and Rosell 2013](#),

Olson et al. 2014) throughout ontogeny (Weitz et al. 2006). However, slight deviations from this general trend can be found in the presence of significant mechanical constraints, where conduits are usually narrower (e.g., around the root collar or branch junctions; Zimmerman 1983, Tyree and Alexander 1993), or in tall trees, where xylem conduits seldom increase in size for the first few metres from the ground (Mencuccini et al. 2007). Nonetheless, these local deviations do not confute the overall validity of the trees' general strategy of conduit widening.

The physiological mechanism behind this distinct pattern of axial widening of xylem conduits still has to be identified precisely. However, hormonal signalling related to auxin production and transport and the duration of cell expansion during xylogenesis seem to play a key role in controlling the xylogenetic process (Aloni 2013) and the final conduit size (Anfodillo et al. 2012), respectively.

The fact that the change in conduit dimension with cambial age (i.e., from the pith outwards) reflects the adjustment of the pathway length resistance to height growth (Anfodillo et al. 2006) implies that it is not ageing per se (Petit et al. 2008) but rather the increase in tree height with ontogeny that is the underlying driver of this pattern. In other words, the conduit-lumen diameter in a tree increases with cambial age at rates dependent on the rates of stem elongation. For instance, assuming the hypothetical case of a constant annual height

growth from seedling to maturity, conduit diameter would likewise increase with cambial age according to a pattern very similar to that of the axial widening (Figure 1).

Ideally, trees approach their maximal height soon after maturity (Husch et al. 2003), and the imprint of this achievement on anatomical characteristics can be identified in the levelling off of the time series of conduit-lumen area (Anfodillo et al. 2006), also known as Sanio's first law (Sanio 1872). This trend, visible in most of the cell chronologies after the cambial age of around 100 years and clearly evident in the longest ones (Figures 2 and 3), does not represent the only signal retained in the conduit-dimension series, yet it represents one of the most significant and unambiguous ones (Figure 1). Thus, identification of environmental signatures requires, as for tree-ring width series, a disentanglement from such a long-term growth pattern.

Pervasive features in time series of conduit dimension: dealing with standardization

Until now, most investigations on conduit dimension have focused on short- (few years; Rossi et al. 2008, Gricar et al. 2011) to medium-term (few decades) time scales (Fonti et al. 2007, Olano et al. 2012). In these cases, standardization is not that critical, either because the time period considered is too short or because most of the researchers adopted the

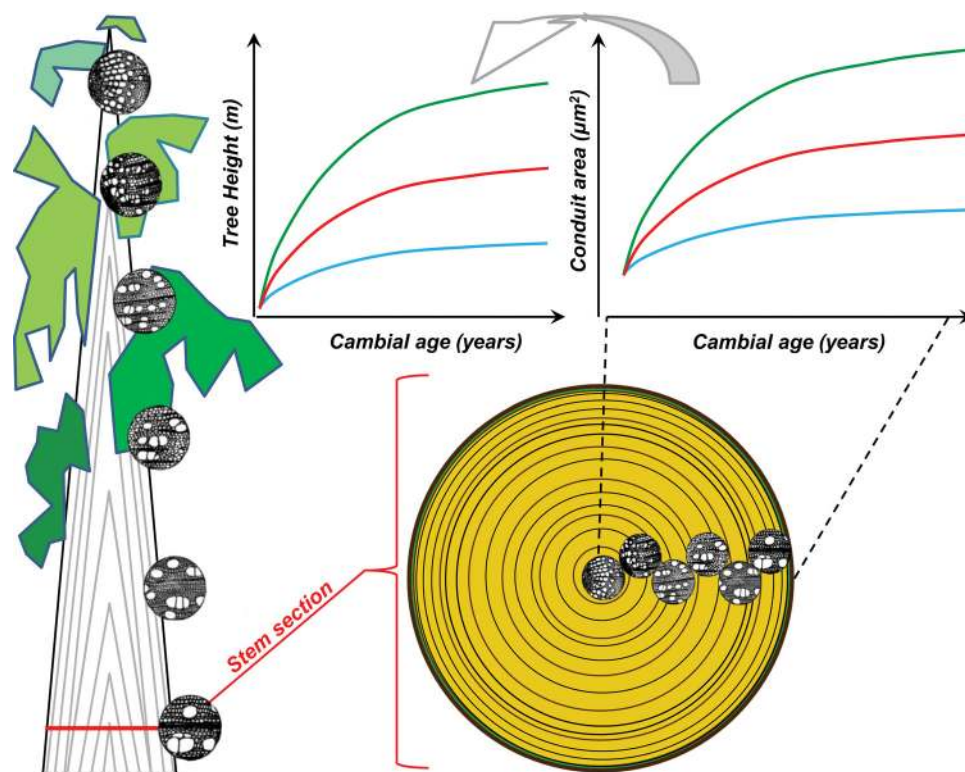


Figure 1. The typical theoretical age-related trend in tree height and the corresponding change in conduit dimension represented in the two upper plots for three trees with different growth rates. This correspondence can be detected by following the conduit dimension either along the stem within the same annual ring or across a section from the pith outwards.

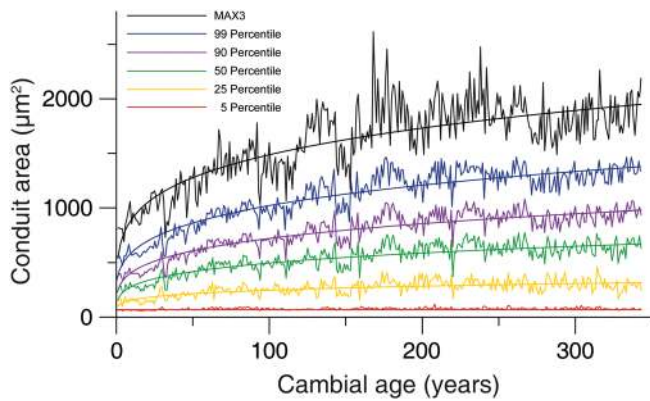


Figure 2. Time series of conduit-lumen area extracted from a *Picea abies* sample (PIAB3 in Table S2 available as Supplementary Data at *Tree Physiology* Online) using different percentiles and the average size of the three widest conduits (MAX3). The monotonic power-related increasing trend is always visible except when considering the fifth percentile. See Figure 3 caption and Tables S1 and S2 available as Supplementary Data at *Tree Physiology* Online for further information on the sample, data collection and regression statistics.

classical dendrochronological approach of sampling the oldest and biggest trees, thus avoiding the early years/decades with the common significant increase in conduit dimension. However, the recent progress in digital image-analysis systems now allows series of wood-anatomical features to be extended to time scales similar to those of other tree-ring parameters (von Arx and Carrer 2014). Consequently, to make proper use of the potential, three pervasive features should be considered when building conduit-size chronologies in order to improve the extraction of the signal of interest and the selection of the most appropriate method to standardize the series:

- (i) The increasing trend. The typical monotonic increasing trend of conduit size becomes apparent from Figures 1 and 2. This trend is appreciable whichever statistics we choose to express the yearly value of conduit dimension. It only disappears when choosing the fifth percentile, i.e., selecting only the smallest conduits per year. Indeed, the minimal conduit

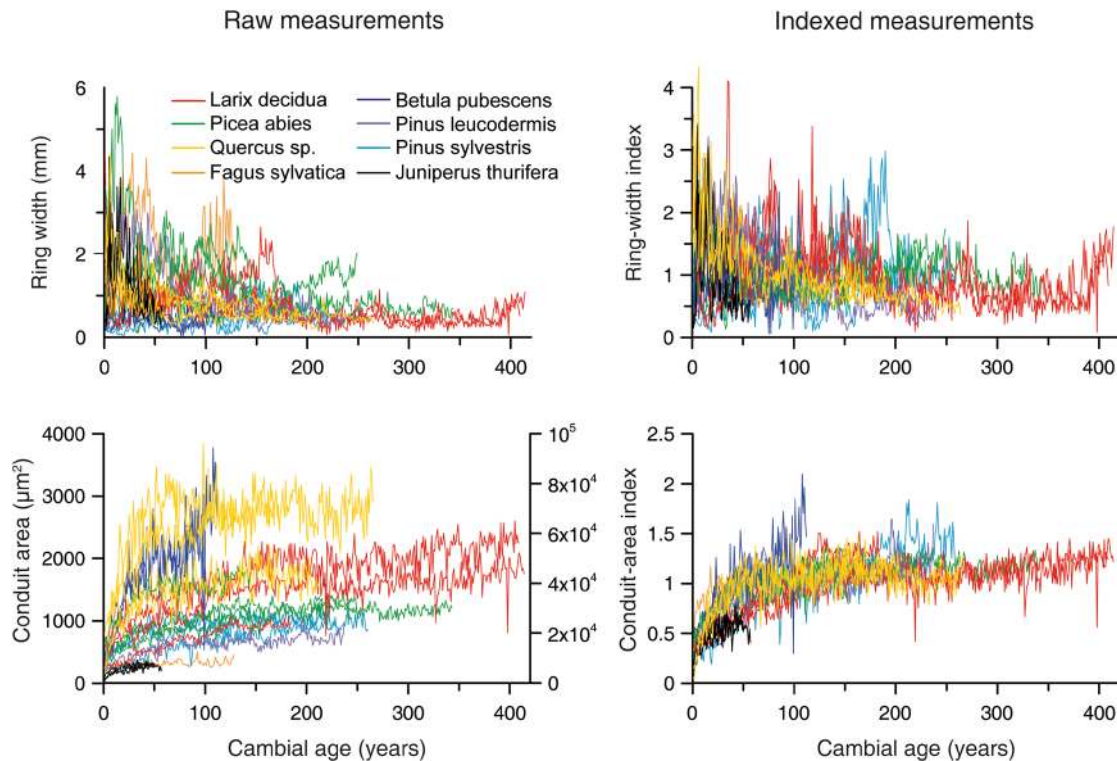


Figure 3. Comparison of time series of ring width and 90th percentile conduit-lumen area among different species. For an easier comparison, raw series (left panels) have been rescaled, dividing each yearly value by the corresponding mean series value. Note the high variability in the tree-ring sequences compared with the convergence in the long-term pattern of conduit area. The right axis for the raw series of conduit area refers to the *Quercus* sp. and *Fagus* samples. Samples are from different species (*P. abies*, *Larix decidua*, *Pinus sylvestris*, *Pinus leucodermis*, *Juniperus thurifera*, *Betula pubescens*, *Fagus sylvatica* and *Quercus* sp.) and different regions (high and low elevation in the Alps and Siberia), with different wood anatomy (ring-porous, diffuse-porous and coniferous), evergreen vs deciduous and grown in different historic times (relic oak sample vs dead or living trees). We selected one core per species, paying attention to include or be very close to the pith in order to catch most of the early-life dimensional change in conduit-lumen area. We were consistent in processing, measuring and analysing the material; all samples were prepared following the standard protocol for wood microscopical analysis (Fonti and Garcia-Gonzalez 2008, Gärtner and Schweingruber 2013), and digital images were automatically processed and analysed using the image analysis tool ROXAS v1.6 (Fonti et al. 2009, Wegner et al. 2013, von Arx and Carrer 2014). We measured almost all the conduits visible in each image with only minor editing. The number of conduits per ring was 12–25,285, with an average value (mean \pm SD) of 149 ± 338 for the angiosperms and 2087 ± 2242 for the conifers. More information on the samples can be found in Table S2 available as Supplementary Data at *Tree Physiology* Online.

size can be considered a threshold value rather stable in time and defined by both biophysical and methodological limits; a xylem conduit cannot be indefinitely small, and our capacity to detect small conduits is bound to sample preparation, magnification, image resolution and other technical issues. On the contrary, the increasing trend is stronger for the largest conduits. This is because they contribute the most to overall water transport and thus are under the strongest control to maintain constant the pathway length resistance as the tree grows taller.

- (ii) The consistency of the trend. Figure 3 depicts the parallel measurements of ring width and conduit lumen from the same cores. Despite all the differences among samples, the overall long-term trend in conduit size is very similar and significantly more consistent than that of ring width (Figure S1 available as Supplementary Data at *Tree Physiology* Online). It simply represents the yearly imprint of height growth on the anatomical features of the xylem. Dendrochronological and tree-ring anatomical investigations should consider this trend as the common major component of long-term variability in conduit dimension. Unless the research topic focuses on height growth, this trend represents a component similar to the one related to stem diameter and ring width and should often be removed, or at least considered, to reveal the other information retained in the tree-ring series (Cook 1990).
- (iii) The smaller decadal variability in conduit size compared with ring width. Abrupt growth changes in tree-ring width sequences, i.e., transient pulses of growth releases or suppressions, are a common feature in most samples coming from the interior of closed-canopy forests or from sites previously affected by any forest disturbance (Schweingruber et al. 1986). Conduit-lumen area is less prone to these abrupt changes (Figure 3, Figure S1 available as Supplementary Data at *Tree Physiology* Online). A tree can significantly change its stem-diameter growth rate and may even stop growing for a few consecutive years, but it always has to ensure the delivery of water to the top of the crown, because it is very unlikely that it could undergo dramatic changes in its height and therefore in its conduit dimension.

As in tree-ring research, there is probably no single strict rule to adopt for the standardization of conduit-dimension chronologies because this depends on the specific scientific question under investigation. However, any valid standardization approach should be in agreement with the hydraulic constraints on conduit size during ontogenesis and the aforementioned related pervasive features. Stochastic methods (e.g., smoothing spline, Gaussian filters) are very flexible and may therefore always be appropriate as long as they are tuned to keep the information of interest in relationship to the characteristics of the series. Among the deterministic methods, power functions are

particularly appropriate because they have a sound biophysical basis (i.e., related to the axial widening of xylem conduits and average stem elongation during ontogeny), whereas the negative exponential models used for ring-width series are clearly inappropriate. Lastly, methods such as the regional curve standardization (Briffa and Melvin 2011) should perform like the power functions in view of the consistent height-related trend.

Outlook on some practical applications

Time series of lumen size (cross-sectional diameter or area) of xylem conduits encode information about the relationship with tree height development, which does not necessarily correspond to ring-width growth patterns. The universal and consistent increasing trend of time series of conduit size until tree maturity, typically expressed by a power function, implies that any deviation will reflect positive or negative pulses of height growth. Adequate consideration of this fact allows time series of lumen size to be used optimally for some interesting applications.

First, on a sub-annual basis, while photoperiod seems to control the rate of cell production (Rossi et al. 2006) and the final conduit size undergoes a form of apical control owing to the duration of enlargement (Anfodillo et al. 2012), the overall process of conduit formation lasts not much longer than a couple of weeks for the earlywood tracheids of a mature conifer (Rossi et al. 2013). This fact, when combined with the precise position of each conduit within the ring, potentially allows a phenological-based tuning of the time windows for the climate–growth association up to the sub-monthly or fortnightly level. This would permit, for example, the extraction of detailed climate information not only related to the mean monthly or seasonal modes but also on the role of extreme events (e.g., heatwaves, mechanical damage related to wind storms, frost events during the growing season) that often occur on much shorter time scales but can leave profound legacies (e.g., wind damage, reduction of living biomass, loss of branches) at the ecosystem level (Babst et al. 2012).

Second, on an annual basis, adding an anatomical measure, such as conduit size, can help to improve handling of the well-known age-related issues that frequently afflict the information extracted with the classical set of tree-ring parameters (Briffa and Melvin 2011). More specifically, tree-ring-based climate reconstructions might benefit from the introduction of conduit-size chronologies; the latter quantify the ‘void’ in the wood, which is therefore somehow the opposite of the well-established density measurements. Nevertheless, the biologically related trends in conduit size are fully independent of those of the other tree-ring parameters. Comparing time–frequency domains among different parameters could thus help in distinguishing the climatic signature from the other components.

Finally, on a multi-annual level, conduit-size chronologies, together with ring width, density and basal-area increment,

could allow a much more accurate estimate of the wood production and of long-term changes in carbon sequestration. Recent studies proved that it is possible to combine biometric and eddy-covariance quantifications of carbon allocation to different storage pools with classical tree-ring parameters (Babst et al. 2014). This new link with conduit size adds a better estimation of height growth and will probably contribute to a better quantification of terrestrial carbon uptake, reducing the uncertainties linked to the carbon cycle–climate feedback mechanisms (Pan et al. 2011). The intriguing perspective is that, focusing on the most likely power-function-related axial pattern of conduit dimensions from trees of various age and epochs, it will be possible to make a quantitative comparison of present and past tree height growth. Parameterization of future vegetation models could be greatly improved by introducing long-term dynamic information related to height development (Keith et al. 2010, McMahan et al. 2010, Meinzer et al. 2011, Stephenson et al. 2014).

Concluding remarks

The recent technological advances in image analysis applied to the field of wood anatomy open up a fascinating perspective for dendroecological studies that cover time frames as long as the more established ring-width or wood-density chronologies. This creates the need to achieve a better understanding of the biophysical and physiological mechanisms influencing the short- to long-term variation in wood-anatomical features. Only then will a sound standardization of long time series be possible, and only then can the maximal potential of tree-ring anatomy be exploited fully. In this article, we provide such a background to one of the most promising anatomical features, conduit-lumen area. Knowledge of the mechanistic relationships between lumen dimension, tree hydraulic architecture and height growth will permit the information recorded at the anatomical level to be extracted. Applying an appropriate standardization technique and being able to understand the long-term trends in conduit-lumen area will probably allow long chronologies to be related to intra-annual climate fluctuations, as well as the extraction of valuable information about tree height growth.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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