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Technical note

Spatiotemporal alignment of radial tracheid diameter profiles of submontane Norway spruce

Dominik Florian Stangler[a,*], Martin Mann[a,b], Hans-Peter Kahle[a], Elena Rosskopf[a], Siegfried Fink[c], Heinrich Spiecker[a]

[a] Institute of Forest Sciences, Chair of Forest Growth and Dendroecology, Albert-Ludwigs-University Freiburg, Tennenbacherstr. 4, 79106 Freiburg, Germany
[b] Department of Computer Science, Bioinformatics Group, Albert-Ludwigs-University Freiburg, Georges-Köhler-Allee 106, 79110 Freiburg, Germany
[c] Institute of Forest Sciences, Chair of Forest Botany, Albert-Ludwigs-University Freiburg, Bertoldstr. 17, 79085 Freiburg, Germany

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ABSTRACT

Studying intra-annual wood formation dynamics provides valuable information on how tree growth and forests are affected by environmental changes and climatic extreme events. This study has the aim to evaluate and to quantify synergetic potentials emerging from a combination of current state of the art techniques used to monitor intra-annual wood formation processes. Norway spruce trees were studied in detail during the growing season 2009 with weekly sampling of microcores, high resolution point-dendrometers and wood anatomical analysis. The combination of the applied techniques allowed us to convert the spatial scales of radial tracheid diameter profiles to seasonal time scales and to synchronize fluctuations in intra-annual cell diameter profiles. This spatiotemporal information was used to validate the recently introduced software MICA (*Multiple interval-based curve alignment*). In comparison to the conventional approach of averaging profiles of tree ring variables, the MICA aligned profiles exhibit a significantly higher synchronicity of the averaged data points. We also demonstrate two new features in the MICA application that enable to extrapolate spatiotemporal information between intra-annual profiles for the construction of robust mean (consensus) profiles that are representative for the population dynamics. By using a set of complementary techniques in an integrated approach, this study highlights a new methodological framework that can contribute to a better understanding of the environmental control of wood formation during the growing season.

1. Introduction

Annually resolved tree ring measures such as tree ring width, early or late wood proportions, isotope ratios or maximum late wood density have long been identified as powerful proxies that provide valuable ecological information and insights into the responses of forest ecosystems to climatic extreme events (Spiecker, 1995; Kirdyanov et al., 2008; Tegel et al., 2014). An enhanced understanding of the impact of ecological factors on tree growth can be obtained by analyzing the intra-annual variability of tree ring characteristics and the seasonal radial growth dynamics. The methodology for investigating intra-annual wood formation dynamics has advanced considerably during recent years and progress can be observed in sampling and laboratory techniques as well as in respect to image and data analyses (Rossi et al., 2006; Gärtner and Schweingruber, 2013; von Arx and Carrer, 2014; Gonzalez-Benecke et al., 2015). Most frequently used and established methods are measurements of the (radial or circumferential) stem size variations with dendrometers, the assessment of cambial cell divisions and cell differentiation with microcores and quantitative analysis of xylem anatomy with semiautomatic image analysis systems. Despite the commendable advance in the applied methodology, intra-annual growth research still is considered as laborious, time-consuming or technically demanding. Furthermore, the insight into the processes of xylogenesis remains fragmentary, in particular if the different methods and techniques are not applied in combination.

Dendrometers are instruments that are able to measure changes in stem radius or stem circumference in high spatial and temporal resolution (Drew and Downes, 2009). However, previous studies have demonstrated that it is difficult to make reliable statements about onset and cessation of cambial cell divisions and seasonal radial growth dynamics based on the analysis of dendrometer data alone (Deslauriers et al., 2007; Mäkinen et al., 2008). Reversible

* Corresponding author.
E-mail address: d.stangler@yahoo.de (D.F. Stangler).

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changes in stem dimension caused by stem hydrological fluctuations are intermingled with irreversible growth components, which in turn are not solely composed of new layers of xylem tissue as also phloem and periderm can be produced and degrade simultaneously (Prislan et al., 2013).

In contrast to dendrometer data, microcoring allows to assess xylem production separately from other tissue types and to identify cell differentiation phases in the developing tree ring. Microcore studies operate at a lower temporal resolution of mostly weekly intervals between the sampling dates. As the raw data contain a considerable amount of noise due to the variability in accumulated growth and cell numbers between consecutively taken samples, deterministic growth functions are commonly fitted to the data and used to model the seasonal wood formation dynamics (Rossi et al., 2003; Michelot et al., 2012).

Measurements of wood anatomical features within tree rings such as radial tracheid diameter, lumen width, lumen area, or wall thickness can be used to compute intra-annual wood anatomical profiles or so called tracheidograms (Vaganov, 1990; Rathgeber et al., 2006). Several studies have already successfully demonstrated that it is feasible to use dendrometer data or model-based approaches for converting the spatial scale of intra-annual tree ring data, such as wood density profiles, sequences of wood anatomical variables or isotope signatures, into a seasonal time scale (Skomarkova et al., 2006; Vaganov et al., 2009; van der Maaten et al., 2012). By attributing time stamps to intra-annual profiles of tree ring features, also the mechanisms that determine the formation of an intra-annual density fluctuation (IADF) within a tree ring could be analyzed more rigorously. IADFs are characterized by anomalous variations in wood density and xylem cell structure within a tree ring and a wide range of exogenous and endogenous factors has been identified to control their occurrence (Rigling et al., 2001; Vieira et al., 2009; Gonzalez-Benecke et al., 2015).

The *Multiple interval-based curve alignment* (MICA) is an innovative method that uses warping functions to align characteristic time-specific patterns such as IADFs in selected microstructure wood density profiles, with the aim to identify and preserve common environmental signals in the generated intra-annual chronologies (Bender et al., 2012). Despite the fact, that the underlying theory of the MICA approach is plausible and intuitive to understand, the a priori assumption that the aligned microstructural patterns in the wood density profiles are triggered by the same temporal sequence of environmental factors during the growing period has not been tested yet. Furthermore, it has not been investigated or quantified so far, how much the strength of the environmental signal increases if the MICA method is applied.

The main objective of this study was to evaluate the synergetic potentials of combining established methods like dendrometer measurements, microcoring and quantitative wood anatomical analysis with the MICA approach. For this purpose, the dendrometer data was used to convert spatial scales of radial tracheid diameter profiles to seasonal time scales. The data of the microcores hereby provided a rather accurate estimation of the initiation and cessation of seasonal radial growth. Furthermore, new features within the MICA application are demonstrated that allow the transfer of this laboriously acquired spatiotemporal information between different wood anatomical profiles. In a final step we have used the aggregated spatiotemporal profiles to exemplify the relationships between short-term shortages in soil water availability and seasonal fluctuations in radial tracheid diameters. In this feasibility study we focused on submontane Norway spruce (*Picea abies* L. Karst.) during the growing season 2009. Norway spruce has been selected as study species due to its high relevance for the European forest and wood sector and its known sensitivity to drought and climatic extreme events (Spiecker, 1995; Spiecker, 2002).

2. Material and methods

2.1. Study site and tree selection

The study site is located on a gentle slope with westerly aspect at an elevation of 450 m above sea level in the Black Forest, a low mountain range in South-Western Germany, approximately 7 km south of the city of Freiburg im Breisgau (47°57′25.44″N, 7°52′5.12″E). The mature groupwise mixed-species forest stand is dominated by *Abies alba*, *Pseudotsuga menziesii*, *Fagus sylvatica* and *P. abies* with an age of approximately 70–80 years. According to the forest site classification, the site unit is a submontane *Abieti–Fagetum* forest on moderately fresh, gritty loam with humus types mull and mullmoder on predominating cambisols. Five healthy looking Norway spruce trees with a diameter at breast height (dbh) in the range of 50–60 cm were selected as sample trees from the dominant and co-dominant stand layer to study in detail the intra-annual wood formation dynamics during the growing season 2009. Although all five sample trees were used for wood anatomical analyses, dendrometer measurements and microcoring were restricted on two of the five sample trees.

2.2. Dendrometer measurements

Electronic point dendrometers with stainless steel body and a linear displacement transducer, manufactured by Trans-Tek Inc. (Connecticut, USA), were mounted in the beginning of April 2009 on two (PcAb1, PcAb2) of the five sample trees in 1.40 m stem height with the sensors placed perpendicular to the stem axis and to the slope to minimize influences of compression wood formation. The sensors register changes in the stem radial displacement with a measurement accuracy of 1 μm. These changes, which are triggered by swelling and shrinking of mainly non-lignified tissues and growth processes, are converted into electric signals, which were recorded and stored by a data logger (type 21X, Campbell Scientific, Logan, USA) in 15 min intervals. Due to technical problems, the dendrometer time series contain a one week data gap between the 8th and 15th of May 2009.

2.3. Microcore sampling

Microcores were sampled with the Trephor tool (Rossi et al., 2006) on the same trees that were selected for dendrometer measurements. Previous studies have shown that radial growth dynamics and tree ring phenology can vary considerably around the stem circumference (e.g., Hauser, 2003). To optimize compatibility with the dendrometer measurements, microcores were extracted in an extraction field that was limited to one quarter of the stem circumference with the dendrometer located in its center (see Appendix Fig. A.1). Microcores were sampled sequentially along rows from left to right in the extraction field at 30 cm vertical distance between the first extraction row and the dendrometer sensor. After reaching the end of the first row on the right side of the extraction field, subsequent rows again started from the left at a vertical distance of 10 cm to the previous row. Within the rows, the distances between the microcore sampling locations were 2.5 cm in the horizontal and vertical direction, respectively. This sampling design was based on findings by Forster et al. (2000) who stated that injuries caused by the extraction of a 1.5–2.5 mm diameter core by the comparable increment puncher, stimulate growth and facilitate callus formation in an area of about ±10 mm in vertical and ±2 mm in horizontal direction around the wound. Microcoring on the two sample trees was conducted from 1st of April until 2nd of October in 2009. Microcores were sampled two times per week in April and late August/early September in order to determine onset- and cessation of radial growth at relatively high accuracy. During the