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EDITOR'S HIGHLIGHT

New perspectives on sub-seasonal xylem anatomical responses to climatic variability

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Key message
Quantitative wood anatomy represents a tool to investigate paleoclimatic signals on a seasonal to sub-seasonal basis.

Increasing the temporal resolution of dendroclimatic reconstructions is crucial to produce reliable climatic projections and evaluate the effect of climate change on vegetation (Jones et al. 2009). A number of different approaches have been proposed to reveal intra-annual climatic signal encoded in tree-rings, such as splitting ring widths in their spring (i.e. earlywood) and summer components (i.e. latewood) (Griffin et al. 2013), assessing variability of wood chemical (i.e. isotopic composition) (Szejner et al. 2016) and physical properties (i.e. density) (Anchukaitis et al. 2013), or correlating tree-ring series with high-resolution climatic data (i.e. daily) (Land et al. 2017). Quantitative Wood Anatomy (QWA), the assessment of xylem cellular features and their environmental significance, represents one of the most promising tools to investigate paleoclimatic signals on a seasonal to sub-seasonal basis (Garcia-Gonzalez and Fonti 2006; Kiorapostolou et al. 2018). Belokopytova et al. (2018, this issue) show that upon proper normalization of xylem anatomical structures measured across tree-rings, it is possible to unveil specific zones of maximum climatic response. They show how tracheid features are finely tuned with seasonal temperature and precipitation variability throughout the entire ring, and how climate-anatomy relationships within ring zones can match the timing of wood formation.

Future climate variability is expected to display more frequent and harsh extreme events, which might produce a stronger impact on natural systems than long-term changes in average conditions (Fischer and Knutti 2015; Coumou et al. 2018). For example, severe seasonal water limitations associated with warmer temperatures are expected to produce a wide range of responses in natural and human systems (Allen et al. 2015). Regions characterized by recurring droughts and/or pronounced seasonality in precipitation are ideal locations to investigate plant responses to current and past hydroclimatic variability (Camarero et al. 2010; Ren et al. 2018; Ziaco and Biondi 2016), providing crucial information to calibrate vegetation and climatic models (Mankin et al. 2017). Several studies have shown that wood anatomy may carry significant and temporally stable climatic signal even when ring-widths show low sensitivity to climate (Liang et al. 2013; Ziaco et al. 2016), and QWA can be particularly effective in tracking climatic extremes (Carrer et al. 2016). Furthermore, time series of anatomical parameters allow to test the stability of climate–growth relationships from a mechanistic perspective, which might help to explain the decoupling of summer temperature variability from ring growth documented in the high-latitude forests from the 1960s and known as the "divergence problem" (Briffa et al. 1998; D'Arrigo et al. 2008), as well as non-linear associations between climate and tree growth (Liang and Camarero 2018). Given the number of parameters that can be directly (i.e. lumen area, lumen diameter, cell wall-thickness) or indirectly measured and unambiguously crossdated, QWA offers great opportunities for exploring new paleoclimatic proxies and potentially modeling several climatic parameters from a same location with unprecedentedly high temporal resolution.

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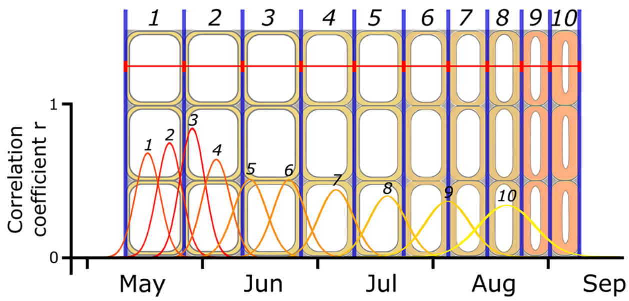

Fig. 1 Theoretical representation of the intra-ring variability of seasonal climatic signals detected according to the approach proposed by Belokopytova et al. (2018, this issue). Each ring is normalized to a common number of n cells, and then divided into n zones (vertical blue lines), each one with the width of a single cell, and not of equal width as proposed by Castagneri et al. (2017). *n* time series of a given anatomical parameter, i.e. cell diameter (red line) are developed for each position and then correlated with moving averages of daily climatic data of a given climatic parameter, i.e. temperature (see Belokopytova et al. 2018). Correlation for each section is generally shifted temporally depending on the timing of formation of each section

Traditionally, xylem anatomical features measured along radial files have been normalized depending on their position across the ring and then displayed as “tracheidograms” (Vaganov 1990) in order to enhance the seasonal sensitivity of xylem cellular features. It has recently been proposed to compartmentalize each ring into equal width sections and measure anatomical features in each section to identify, through correlation with moving averages of daily climatic data, portion specific timeframes of maximum climatic sensitivity (Castagneri et al. 2017). However, depending on the number of cells forming the ring, both techniques can occasionally fail to identify the proper seasonal window of climatic signal by excessively stretching or compressing cellular measurements during the normalization or signal compartmentalization procedures. Belokopitova et al. (2018) propose a distortion-free approach to tree ring compartmentalization where tracheid measurements are normalized using a constant cell number *n* (as in tracheidograms), and then each cell is treated as an independent section. Average anatomical parameters recorded at each position (i.e. for each *n*th cell) can be combined into annually resolved time series and correlated against local climatic and environmental records (Fig. 1). The method proposed by Belokopytova et al. (2018) still allows to distinguish earlywood, latewood and transition zone properties, making it suitable for comparison with existing reconstructions.

Xylem features are largely determined by the conditions at the time of their formation, which means that while tree-rings encode the average climatic conditions over an entire growing season, tracheid parameters (i.e. lumen diameter, cell wall-thickness) present short-term linkages with meteorological variables (Deslauriers and Morin 2005; Liang and Eckstein 2006). Xylem morphogenesis is tightly connected to the kinetic of cellular division and differentiation and, therefore, with the phenology of cambial activity (Cuny et al. 2014). Shifting cambial phenology has been observed in boreal and temperate environments (Rossi et al. 2014), but less is known for semi-arid environments where the timing of wood formation is driven by a combination of thermal and moisture conditions (Ren et al. 2018) or predominantly by water availability in hyperarid regions (Ziaco et al. 2018). The intra-annual analysis of climate sensitivity performed by Belokopytova et al. (2018) suggests that their single-cell normalization procedure could bypass the limitations of an equal width intra-ring sectioning, making it possible to extend retrospective inferences on cambial phenology in species characterized by higher phenological plasticity and frequent Intra Annual Density Fluctuations (IADFs).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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