



ORIGINAL ARTICLE

Dendroclimatic potential of dendroanatomy in temperature-sensitive *Pinus sylvestris*Jesper Björklund^{a,*}, Kristina Seftigen^{a,b,c}, Patrick Fonti^a, Daniel Nievergelt^a, Georg von Arx^a^a Swiss Federal Institute for Forest Snow and Landscape Research WSL, Birmensdorf Switzerland^b Regional Climate Group, Department of Earth Sciences, University of Gothenburg, Sweden^c Georges Lemaître Centre for Earth and Climate Research, Université Catholique de Louvain, Louvain-la-Neuve, Belgium

ARTICLE INFO

Keywords:

Maximum latewood density (MXD)

Temperature reconstruction

Quantitative wood anatomy

Pinus sylvestris

Northern Fennoscandia

Tree-ring anatomy

ABSTRACT

The most frequently and successfully used tree-ring parameters for the study of temperature variations are ring width and maximum latewood density (MXD). MXD is preferred over ring width due to a more prominent association with temperature. In this study we explore the dendroclimate potential of dendroanatomy based on the first truly well replicated dataset. Twenty-nine mature living *Pinus sylvestris* trees were sampled in North-eastern Finland at the cool and moist boreal forest zone, close to the latitudinal tree line, where ring width, X-ray MXD as well as the blue intensity counterpart MXBI were compared with dendroanatomical parameters. Maximum radial cell wall thickness as well as anatomical MXD and latewood density appeared to be the most promising parameters for temperature reconstruction. In fact, these parameters compare favorably to MXD derived from X-ray techniques as well as MXBI, in terms of shared variation and temperature correlations across frequencies and over time. The reasons for these results are thought to be the unprecedentedly high measurement resolution of the anatomical technique, which provide the optimal resolution – the cell – whereas X-ray techniques have a slightly lower resolution and BI techniques even lower. While the results of this study are encouraging, further tests on longer and multigenerational chronologies are required to more generally and fully assess the dendroclimate potential of anatomical parameters.

1. Introduction

Tree-ring based climate proxies have an outstanding position in current paleoclimatology because they are annually resolved with an absolute dating-accuracy, and in direct consequence, because their performance as climate predictors can be statistically tested for robustness (e.g., Briffa, 1999; Jones et al., 2009). If the trees' ring-characters exhibit high shared variation, quantified through average pair-wise correlations, the so-called Rbar statistic (Briffa and Jones, 1990; Wigley et al., 1984), it indicates that the targeted trees have been exposed to, and record, similar environmental signals (Fonti et al., 2010; Fritts, 1976; Jones et al., 2009; Vaganov et al., 2011). This further implies that fewer trees are needed to explore the imprinted climatic targets (manifested through a higher expressed population signal (EPS), Wigley et al., 1984). However, regardless of the most well-informed sampling strategy, and established common signals, it is still necessary to empirically determine the character and the strength of the tree growth response to climate (Briffa, 1999). This is commonly assessed via correlation with monthly or daily climate variables (Fritts,

1976; Biondi and Waikul, 2004; Meko et al., 2011). Causality is further strengthened if significant correlations can be soundly interpreted (e.g., based on studies of cambial activity, and kinetics (e.g., Rossi et al., 2006; Cuny et al., 2014; Seo et al., 2008)). It is moreover encouraging if the proxy-climate link displays a high fidelity at lower frequencies (decadal to centennial scales) (*sensu* Büntgen et al., 2011; Matskovsky and Helama, 2014). The lower frequency link is critical for the ability of independently withheld data to pass recommended statistical tests, i.e., reduction of error (RE), coefficient of efficiency (CE), mean squared error (MSE) etc. (National Research Council, 2007) for model verification (Cook and Kairiukstis, 1990; Fritts, 1976). In fact, despite observed high Rbars, it can still be difficult to determine a robust statistical climate association. The climatological growing season length may exhibit some inter-annual fluctuations and could confound the identification of a stationary target season (Frank et al., 2007; Vaganov et al., 1999). This concerns in particular predictors that are responsive towards short target seasons. Climate forcing may not be as severe and rather invoke non-linear relationships with tree growth (Björklund, Rydval et al., 2019), or change over time and cause instability in

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Received 5 June 2019; Received in revised form 9 January 2020; Accepted 30 January 2020

Available online 06 February 2020

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dominant limiting factors (Tumajer et al., 2017). It is thus clear that an array of aspects needs to be explored when determining the climate reconstruction potential of tree-ring parameters.

The most frequently and successfully used tree-ring parameters for the study of temperature variations at high latitudes and altitudes are ring width (RW) and maximum latewood density or simply maximum density (MXD) (e.g., Esper et al., 2018). RW is an easy-to-measure parameter (e.g., Grissino-Mayer, 1997), but quite complex to use due to considerable inherent non-climatic information, such as age and size trends (Cook and Kairiukstis, 1990; Weiner and Thomas, 2001), biological memory effects (Esper et al., 2015; Fritts, 1976), external disturbances (Rydval et al., 2018) or simply unexplained variability (Cook, 1985). Moreover, the temperature period of greatest influence is rather short, often only one month (Björklund et al., 2017; Briffa et al., 2002). An earlier onset of the growing season can invoke non-linear growth responses in cell production (Rossi et al., 2013), and thus the ring width–climate relationship is particularly susceptible to distortion. However the timing of cell formation (cambial phenology) can be observed (e.g., Rossi et al., 2006; Seo et al., 2008; Castagneri et al., 2017) and the cell contribution to the ring width is straightforward (Vaganov et al., 2006) making this parameter relatively easy to mechanistically interpret. In contrast, MXD is quite complex to measure (Björklund et al., 2019b), but easier to use in temperature reconstructions because the non-climatic variation is more limited (Franke et al., 2013; Briffa et al., 2004; Rydval et al., 2018; Esper et al., 2015). Furthermore, the temperature period of greatest influence extends over a longer period, often up to six months and is very distinctly imprinted (Björklund et al., 2017), arguably making it relatively more robust over time and across frequencies (George and Esper, 2019). However, the mechanistic understanding of this parameter is rudimentary. This is highlighted by the large temporal mismatch between formation of the cells defining maximum density and the commonly observed correlation patterns of this parameter (Vaganov et al., 2006).

The use of wood anatomical parameters (quantitative wood anatomy, QWA; von Arx et al., 2016v) could potentially alleviate this conundrum. However, measurement schemes of wood anatomical parameters assigned to dated tree-rings (dendroanatomy or tree-ring anatomy) have been hampered by time-consuming approaches resulting in low replication of trees, rings, and cells per ring measured. This has basically meant that dendroanatomy has yet an unrealized potential within dendroclimatology compared to traditional tree-ring parameters. Dendroanatomy is measured using the base-unit of wood – the cell – and as such features an unprecedented resolution (Björklund et al., 2019). A wide range of parameters can be obtained and explored (e.g., Prendin et al., 2017), and the mechanistic link between climate and growth response is simplified using the cell characteristics with their direct structure-function link of xylem cells (Hacke et al., 2015). Although the use of dendroanatomy can already showcase strong summer temperature signals of latewood cell wall thickness (Carrer et al., 2018; Fonti et al., 2013; Sidorova et al., 2012; Wang et al., 2002; Yasue et al., 2000; Panyushkina et al., 2003), directly comparable results with RW and MXD in terms of replication and performance is still outstanding. Fortunately, the most severe methodological limitations have recently been mitigated with new analytical tools to facilitate the production of long chronologies (Prendin et al., 2017; von Arx et al., 2016v; von Arx and Carrer, 2014v).

In this study we explore the dendroclimate potential of Scots pine in Northern Finland on the first truly well replicated dendroanatomical dataset. Northern Fennoscandia is among, or even the most, prominent region where temperature sensitive trees can be found (George, 2014) and as such, an appropriate test bed. To increase the informative value of the experiment, we directly compare the anatomical parameters against the state-of-the-art parameter of MXD from the Walesch Electronic Dendro2003 technique (Eschbach et al., 1995), but also to the corresponding parameter MXBI derived with the accessible blue intensity technique (McCarroll et al., 2002), as well as with basic RW.

First, we evaluate the shared variation among trees and the link with climate for a range of anatomical parameters, and then we short-list the most suitable parameters for additional experiments, such as required replication of trees to achieve the generally accepted EPS threshold of > 0.85 (Wigley et al., 1984), frequency fidelity and time stability to a common temperature target. We contrast each of these analyses against results obtained for MXD, MXBI and RW. Results are finally discussed on the prospect of using these parameters in high-quality temperature reconstructions.

2. Material and methods

2.1. Tree-ring material

Twenty-nine mature living *Pinus sylvestris* trees were sampled in North-eastern Finland at the cool and moist boreal forest zone, close to the latitudinal tree line (200 m a.s.l., 68.9 °N 28.2 °E). This sampling concord with the principle of limiting factors (Fritts, 1976) targeting temperature sensitive trees, where the sampling region belongs to the most suitable places in the world for temperature reconstruction (e.g., Büntgen et al., 2011; Esper et al., 2012; Linderholm et al., 2015; Melvin et al., 2013). The trees were felled and cut at 2.7 m stem height as a part of a logging operation coordinated by the Finnish Forest Research Institute (METLA) in 2014, and miniature logs (ca. 30 cm axial log length) were selected for data analysis. In total, two radii (averaged to represent the tree) per tree were analyzed and compared in this study using X-ray, blue intensity and anatomical measurement techniques. Each data set per technique was constructed with unique and randomly selected radii from the logs, making the results statistically nearly identical (Björklund et al., 2019). Initially, the tree-rings in the wood material were visually cross-dated (*sensu* Yamaguchi, 1991), and the dating of ring-width measurements was statistically verified with the software COFECHA (Holmes, 1983).

2.2. Dendroanatomical analysis

The anatomical data was produced by firstly cutting thin sections of 15 µm thickness using a sledge microtome (Gärtner et al., 2015) with Feather N35 disposable blades (Feather Safety Razor Co., Ltd., Osaka, Japan). Sections were stained with safranin-astrablue to increase contrast and permanently fixed with Canada balsam. Images of the sections were then captured with a camera (Canon EOS 650D, Canon Inc., Tokyo, Japan) mounted on a microscope (Olympus BX41, Olympus Corp., Tokyo, Japan) at a resolution of 2.36 pixels/µm. Multiple overlapping images were stitched to an overall composite image of the anatomical sample using the image-stitching software PTGui (New House Internet Services B.V., Rotterdam, NL; von Arx et al., 2016v). The software ROXAS v3.1 was used to automatically detect anatomical structures of all tracheid cells (75–100 radial files per ring) and annual ring borders. The output was summarized as different cell anatomical dimensions, such as lumen, outer cell and cell wall dimensions, catalogued with position within each dated tree ring (von Arx and Dietz, 2005v; von Arx and Carrer, 2014v). The measurement of the thickness of all four cell walls, i.e., two tangential and two radial walls per tracheid were provided (Prendin et al., 2017), as well as anatomical density, i.e. the percentage of wall area of each cell. From the anatomical technique, inter-annual time series of several tracheid parameters were produced (see Fig. 1). Cells of each ring were assigned to 10-µm wide bands parallel to the ring borders, and the value corresponding to the 75th percentile of the respective parameters was used for each band. A percentile instead of averaging approach was chosen to avoid the negative impact of outliers, and the 75th percentile was considered to represent the fusiform tracheid cells cut through their axially central part. The bands track the ring borders, and the band width, where the ring is differently wide, was accordingly reduced (increased) in narrower (wider) parts of the ring, while still averaging to a band width of

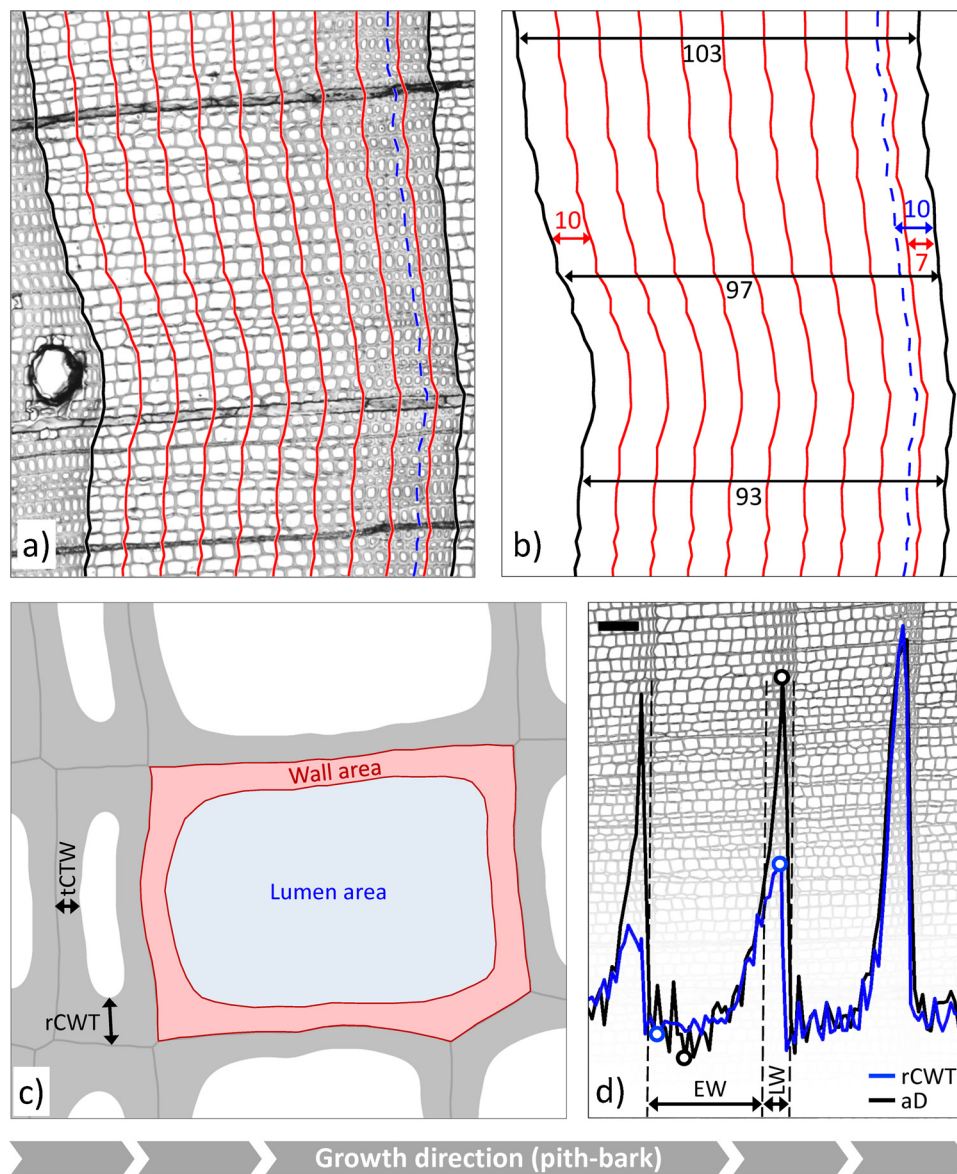


Fig. 1. Explanatory figure of measured parameters and measurement technicalities. a) and b) Visualization of the algorithm used to create intra-annual profiles of anatomical parameters based on cell position in the ring. Cells are here assigned to on average 10 unit wide bands (in the analysis we use 10 µm bands) (red lines) parallel to the ring borders (black lines) based on their center coordinates. Anatomical parameters are then calculated as the 75th percentile in each band. Bands are not allowed to cross ring borders and thus never include cells from two adjacent rings. To avoid a truncated narrower last band towards the ring borders (7 units in the b) example), the terminal band (blue dashed line) is defined as the 10 units adjacent to the terminal ring border. This means that cells in the overlapping part of the last and second-last band are included in both bands. c) Illustration of the basic tracheid dimensions used in this study: rCWT – radial cell wall thickness (i.e., the walls running in radial direction in a cross-sectional view), tCWT – tangential cell wall thickness (walls running in tangential direction in a cross-sectional view), lumen area and wall area. Anatomical density (aD) of each cell is defined as the ratio of wall area to overall cell area (sum of wall and lumen area). d) Exemplary 10-µm-resolution intra-annual profiles for rCWT (blue curve) and aD (black curve). Maximum and minimum values for each parameter (circles) are extracted for each ring, whereas means for earlywood (EW) and latewood (LW) are obtained by averaging the values of the bands assigned to EW and LW, respectively. Scale bar in (d): 100 µm (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

10 µm (see Fig. 1a and b). Bands were not allowed to cross ring borders and thus were never including cells from two consecutive rings. To avoid a truncated narrower last band towards the ring borders, the terminal bands were defined as the 10 µm adjacent to the respective ring border. This means that some cells were included in both the last and second-last band of a ring where they overlapped.

2.3. X-ray and blue intensity data

The blue intensity data was produced using the standard protocol according to Campbell et al. (2011). Samples were refluxed in a soxhlet with ethanol during 24 h to remove extractives, and surfaced by hand with sand paper with gradually finer grit (last round 400–600 grit). Digital images were produced with a flatbed scanner at 1600 dpi resolution (Epson Expression XL10000 Series) calibrated with SilverFast Ai professional scan software using the calibration target IT8.7/2. The images were analyzed with the commercial software WinDendro™. The X-ray density data was produced using the DENDRO2003 – Walesch Electronic measurement setup (Eschbach et al., 1995) according to standard protocols developed over the years at WSL (Schweingruber et al., 1988). Similarly to BI, the samples were extracted in a soxhlet and were exposed to a stationary soft X-ray source in a room with

controlled environment (50 % RH at 20 °C). Analogue film X-ray negatives were developed for analysis in the DENDRO2003 densitometer. From the X-ray and blue intensity techniques, inter-annual time-series of MXD, the corresponding MXBI, and RW were derived.

2.4. Statistical analysis

The common signal among trees for each specific tree-ring parameter was established with the Rbar statistic (Wigley et al., 1984). The association with climate was determined with Pearson correlations against monthly temperature data (Fritts, 1976). Precipitation was tested but results were insignificant and are not presented further here. Prior to Rbar and temperature correlation, both tree-ring and temperature data were high-pass filtered with cubic smoothing splines (50 % frequency response cut-off at 10 years) (Cook and Peters, 1981). The tree-ring data were correlated with local monthly temperature data retrieved from the CRUTEM4 (5° gridded monthly dataset; Osborn and Jones, 2014). The grid-point centered over the sampling-site comprised data spanning 1876 to the present. The Rbar statistic was also established over this time period. Using only 137 years ensures directly comparable Rbar analyses to climate correlations, and considerably decreases the amount of juvenile/core-wood (Pereira et al., 2003) in the

analysis (see Fig. S1 for sample replication). The minimum replication of trees (two cores per tree) during this period was 21. The common signal was further explored on selected anatomical, as well as reference (X-ray and BI-based) parameters, in terms of how many trees are needed to meet the arbitrary $\text{EPS} > 0.85$ criterion across different frequencies: high-pass filtered data with 50 % frequency cut-off at 10, 67, 150 and 300 years, as well as with raw data (no filter), and moreover with low-pass filtered data (data represented by cubic smoothing splines with a 50 % frequency cut-off at 4, 6, 8 and 10 years). There are > 800 possible pair-wise correlation permutations using 29 trees, and we chose to calculate the $\text{EPS} > 0.85$ sample number requirement for the 5th percentile as well as 25th percentile (R_{P5} and R_{P25} respectively) to roughly simulate quite unfortunate sampling subsets/outcomes and thus conservative expected sample number requirements. For context, R_{bar} , as the name implies, is calculated on the average pair-wise correlation and R_{P5} the 5th percentile of pair-wise correlations.

Moreover, similarly treated data was correlated against the most suitable target season (monthly aggregate of temperature) for the chosen parameters. When data was smoothed to explore the lower-frequency fidelity to the temperature target, substantial degrees of freedom are lost, and the significance levels at $\alpha < 0.01$ were accordingly adjusted to the new effective sample sizes (Dawdy and Matalas, 1964). Finally, the time-stability of the association between the suitable target seasons and tree-ring parameters was investigated with moving window correlations starting at year 1876 with 48-year windows incrementally moved 10 years until 2013. Here only high-pass filtered data were used (50 % cut-off at 10 years), because of short length of the windows.

3. Results

We screened a total number of 10 anatomical parameters (Fig. 2), and MXD from BI and X-ray techniques, as well as RW, earlywood width and latewood width derived from the anatomical survey. Parameters of cell wall dimensions, particularly in the latewood tend to have quite high R_{bar} (> 0.5), whereas parameters of lumen and external cell dimensions, particularly in the earlywood, display lower R_{bar} (substantially lower than 0.5) (Fig. 2). The highest R_{bar} was found for maximum radial cell wall thickness (Max. rCWT) and anatomical MXD (aMXD) (Fig. 1), at 0.72 and 0.61 respectively. The most prominent temperature signals were found for Max. rCWT, aMXD and anatomical

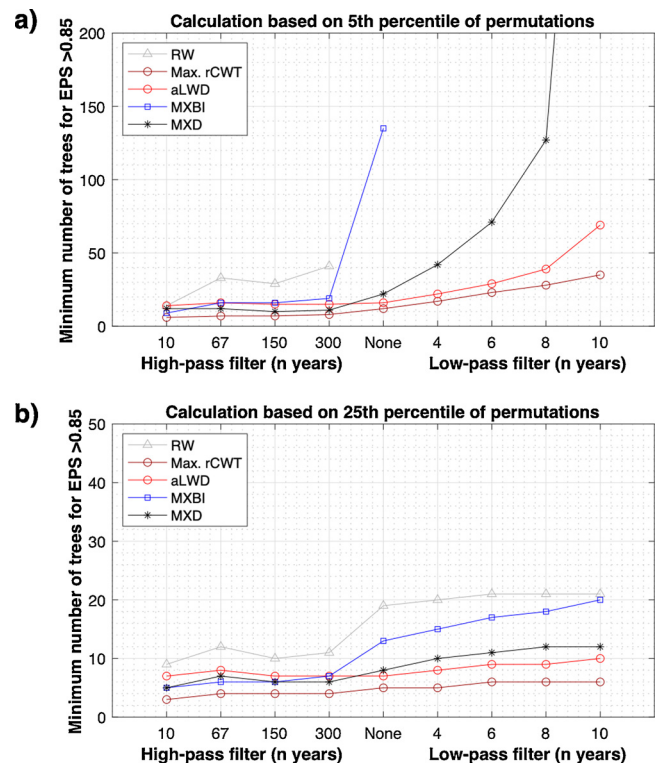


Fig. 3. Development of replication requirement across frequencies to achieve $\text{EPS} > 0.85$ for RW, MXD, MXBI, aLWD and Max. rCWT. a) display the results from using the 5th percentile of all > 800 possible permutations of pairwise correlations R_{P5} . b) display the results from using the 25th percentile of pairwise correlations R_{P25} . The replication requirement to reach $\text{EPS} > 0.85$ increases if lower frequencies are of interest. If more than 1000 series are needed to achieve $\text{EPS} > 0.85$, points are not plotted in the graphs.

latewood density (aLWD) (Fig. 2). In addition, inverse strong responses were found for the related latewood lumen area parameter, although accompanied by a substantially lower R_{bar} . The X-ray and BI based MXD parameters also displayed high R_{bar} and prominent temperature responses. Significant correlations with temperature were obtained for the months of April through September for these parameters, whereas ring width was significantly correlated only with July. For a more in-

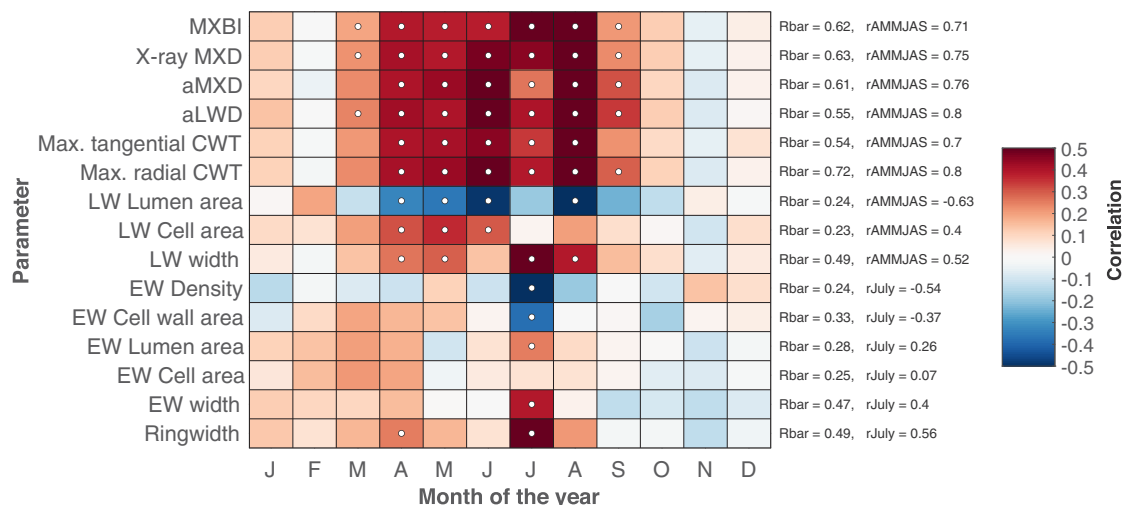


Fig. 2. Monthly temperature correlations of a range of ring anatomical and width parameters. EW and LW refer to earlywood and latewood respectively. To the right in the figure, R_{bar} for each parameter, as well as April–September (AMJJAS) or July target season correlations can be found. Both tree-ring and instrumental data have been 10-year high-pass filtered. White dots indicate months with significant correlations at $\alpha < 0.01$. At the top, statistics for the X-ray MXD and MXBI parameters are inset for comparison.

depth interpretation of the small differences between the April through September temperature correlations of anatomical, X-ray and BI-based MXD parameters, we refer to Björklund et al., 2019. The earlywood density displayed an almost inverse response to temperature compared to RW. The Max. rCWT and aLWD parameters were short-listed for further analyses because of promising combination of high Rbar and pronounced temperature responses.

All possible > 800 pair-wise correlations of trees for the parameters show that Max. rCWT is slightly higher inter-correlated (unfiltered data) than aLWD, Xray MXD, MXBI and RW in that order (Fig. S2). This pattern appears to be consistent also when parameters are compared across different frequencies (Fig. 3a and b). In an “unfortunate” case scenario where the hypothetical sampling campaign could have targeted some of the least correlative trees (R_{p5}), still less than 15 trees would suffice to capture the expressed population signal of > 0.85 for all parameters, except for RW that needs c. 15–25 trees at high frequencies. When only the multi-annual to decadal scale variability is considered, the amount of trees needed is drastically increased, whereby Max. rCWT is the only parameter that requires less than 50 trees at decadal scales. When taking a less conservative estimate of R_{p25} – where the field campaign has been more successful, but not excellent by any standard – around 5 trees are needed at higher frequencies, and at decadal scales, 6–12 trees are needed depending on parameter, whereby Max. rCWT again requires the least amount. MXBI is slightly worse and needs around 20 trees at decadal scales, similar to RW.

When non-RW parameters are correlated with the April–September target season (AMJJAS), and RW is correlated with the target season of July, the anatomical parameters display once more a bit higher correlations than the X-ray MXD and MXBI data, and substantially better than RW at high frequencies (Fig. 4). While MXBI and X-ray MXD decline in correlations across lower frequencies, the anatomical parameters do not. In fact, both anatomical parameters explain over or nearly 60 % of the variance at all tested frequencies and over 60 % of the variance when no filter at all is applied, whereas X-ray MXD explain 46 % and MXBI explain 30 % respectively. It is not possible to test the proxy–temperature link at lower frequencies because the effective sample size becomes so low that adjusted significance levels will be above 1 and impossible to pass.

The moving window correlation using high-pass filtered data showed that the anatomical data had slightly higher correlations than the traditional tree-ring parameters at every time slice, and stayed above $r = 0.71$ ($R^2 = 50\%$) throughout the full period (Fig. 5). The

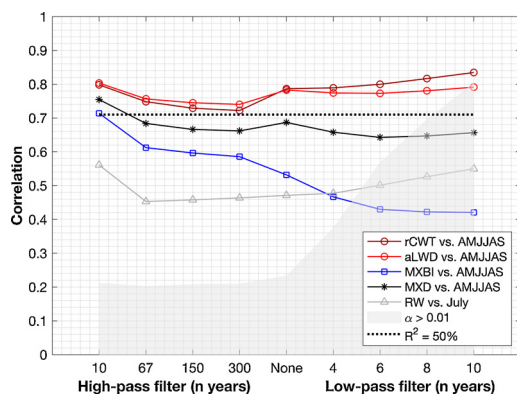


Fig. 4. Stability of temperature signal across frequencies. High-pass filtered time series express residual frequency variability when subtracting an n -year smoothed curve from the raw data. Low-pass filtered time series express the frequencies of the n -year smoothed curve. Both tree-ring data and temperature targets have been treated identically. When calculating correlation coefficient for raw and smoothed data the significance level, at $\alpha = 0.01$, was adjusted to the loss of effective sample size (Dawdy and Matalas, 1964). Results including confidence intervals for the same parameters correlated with AMJJAS as well as JJA temperature target seasons can be found in Fig. S3 and S4.

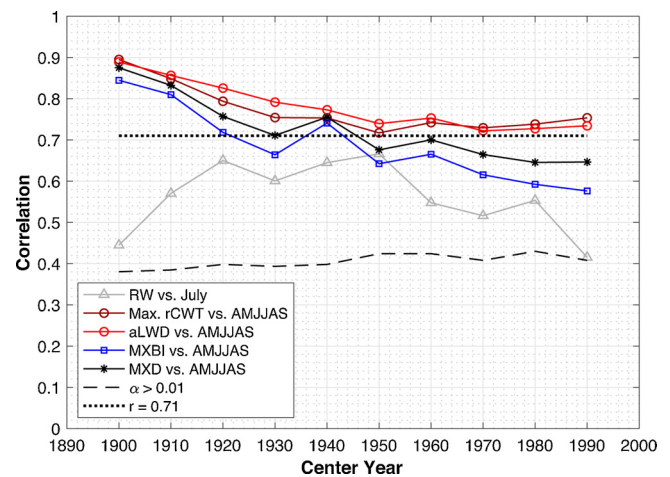


Fig. 5. Stability through time of Pearson correlations between target season temperatures and various traditional and anatomical tree-ring parameters, where both tree-ring and instrumental data have been 10-year high-pass filtered. Base-length of every correlation window is 48 years incrementally moved 10 years through the time period of 1876–2013. Results including confidence intervals for the same parameters correlated with AMJJAS and JJA temperature target seasons can be found in Fig. S5 and S6.

traditional parameters fail at explaining 50 % of the temperature variance in the recent half of the record. While all the non-RW parameters displayed a similar development of coefficients through time, the RW had a different pattern. On average the correlations were lower, but peaked in the mid-century time slice in contrast to the others that display the highest correlations early in the records, where Max. rCWT peaks at $r = 0.9$.

4. Discussion

4.1. Dendroanatomical parameters show potential on annual to decadal scales

MXD is frequently described, with sound basis, as a superior parameter to RW for temperature reconstruction purposes (e.g., Björklund et al., 2019; George and Esper, 2019). Because of this, authors routinely call for more investments in new MXD data production to strengthen local, hemispheric and global temperature reconstructions (e.g., Jones et al., 2009; Briffa et al., 2004; Wilson et al., 2016; Esper et al., 2018; George and Esper, 2019). Therefore it is particularly interesting to note here that MXD or LWD derived from anatomical measurements and other anatomical parameters such as Max. rCWT compare favorably to MXD derived from X-ray techniques and MXBI. The statistic of EPS firmly establishes the acceptable replication of trees needed in every year at a specific observed shared variation (Wigley et al., 1984). Not only was the observed shared variation of the best anatomical parameters for our target species in Northern Finland very high, but it also appeared to be surprisingly stable across frequencies, a feature of great importance but very rarely tested (Jones et al., 2009). A common criticism of tree-ring data in a paleo-climatological context is its ability to represent multi-decadal and longer timescales of climatic targets (Rydval et al., 2018; Jones et al., 2009). If decadal scale variation, as tested with the Rbar statistic in Fig. 3, is of a higher quality using anatomy-based analytical techniques, it stands to reason that centennial and multi-centennial scale variation also would be more likely to exhibit these favorable properties. Moreover, the connection with a common temperature target was also observed to be particularly strong with the dendroanatomical parameters. Not only was the inter-annual link pronounced, but the fidelity again persisted across frequencies. The time stability of the link was also robust, explaining > 50 % of the variance in every time-slice. In summary, the tested features in this

study indeed provided encouragement for using dendroanatomical parameters, but there remain many more dimensions to explore. These dimensions include alternative species, geographical areas and climatological limitations, and perhaps the most pressing and important property, long time-periods.

4.2. Can the tested dendroanatomical parameters by-pass the problem of standardization?

In fact, the most severe critique concerning climatic reconstruction via tree-ring data is directed towards the longest time-scales. Traditional tree-ring standardization, i.e., the harmonization of means and variance, place fundamental limit on the characterization of climatic fluctuations when they are manifested at longer time-scales than the typical life span of the trees, the “segment length curse” (Cook et al., 1995). There are methods to overcome this arithmetic limitation. One alternative is to neutralize statistically shared age-trends while conserving relative average growth rates (regional curve standardization, RCS) (e.g., Briffa et al., 1992). Because trees are living organisms and arguably have the ability to adapt to the environment, and because they can exhibit different growth rates due to micro-site conditions, it is a substantial challenge to extract useful multi-generational information from trees. This is particularly relevant for small sample sizes commonly used in dendroclimatology (Melvin and Briffa, 2011). At lower frequencies, tree-ring parameters are known to contain a substantial fraction of non-climate related variance (von Storch et al., 2004; Esper et al., 2005; Fonti et al., 2009). This variance can be separated into i) persistent ontogenetic trends that are age or size related (Carrer et al., 2015). ii) Amplified responses to environmental variability (so-called biological memory effects; Esper et al., 2015) – effects that arise from physiological processes such as carbohydrate storage that partly decouples carbon assimilation from carbon allocation to tree-ring growth (Matalas, 1962; DeSoto et al., 2016; von Arx et al., 2017v). iii) Stand related disturbances from wind-throws, insect outbreaks and wild fires etc. (Dale et al., 2001) and iv) unexplained variability (Cook, 1985). Moreover, the sampling of deadwood on the ground to extend chronology lengths places a further uncertainty on climatologically representative growth rates because slow-growing trees tend to be preserved longer than fast-growing trees, potentially leading to a “modern sampling bias” (Melvin, 2004). When non-climate variation is prominent, pressure is placed on replication requirements and/or dynamism (data-adaptability of used functions) of standardization techniques, where more dynamic standardization techniques are connected to greater risks of dampening and distorting long-term environmental trends and spectral properties (e.g., Esper et al., 2002; Franke et al., 2013). If replication is determined sufficient to use conservative approaches, such as RCS, this approach can still invoke systematic biases near the beginnings and ends of tree-ring chronologies (Cook and Peters, 1997; Briffa and Melvin, 2011; Melvin and Briffa, 2008), and is associated with a prominent inflation of the uncertainty in multi-generational mean level estimates (Briffa, 1999).

Therefore it is again very interesting to note that the dendroanatomical parameters performed excellently even when no standardization was applied (*sensu* Carrer et al., 2018, 2017) (see Fig. 6 where all untreated mean chronologies are stacked for visual inter-comparison, and comparison with relevant temperature target seasons).

Although reduced non-climatological information and reduced need for dynamism or standardization altogether are valuable attributes in a climate proxy, it is not a guarantee that average growth rates are more homogenous (variation invoked mainly by climate) in dendroanatomical data. But if they were, the narrower distributions, and thus confidence bands of long mean chronologies, would be extremely attractive for paleoclimatologists (Briffa, 1999; Jones et al., 2009). The important next step is thus to sample many generations using high-resolution anatomical techniques to make further tests for ontogenetic trends, presence of disturbance expressions, biological memory and

distribution around average growth rates across generations.

4.3. Unprecedented measurement resolution is the key to the dendroanatomy potential

What could then be the reason for the modest but still conspicuously detected favorable attributes of anatomical LWD or MXD as well as the Max. rCWT? In terms of MXD or LWD, the only real differences between X-ray or BI techniques compared to anatomical techniques, is i) that cell wall density is not considered in anatomical techniques, and ii) that effective measurement resolutions are different (Björklund et al., 2019). Variation in cell wall density is not generally observed among tree species (Stamm and Sanders, 1966). Variation is also limited moving from earlywood to latewood (Decoux et al., 2004). Nonetheless, even if there were some important variation in cell wall density at inter-annual ring level, it does not appear to have a positive effect on the climate signal strength, fidelity across time or across frequencies, because the X-ray MXD parameter perform slightly worse than anatomical counterparts on all tested features.

However, there are with high likelihood prominent differences in effective measurement resolution among the techniques, where anatomical techniques provide the optimal resolution – the cell – and X-ray techniques have a slightly lower effective resolution and BI techniques even lower (Björklund et al., 2019). The spatial measurement resolution will affect the amplitude of the measurement profile. In practice, this means that MXD values in rings where only one or a few rows of latewood cells are present, will be relatively suppressed and slightly alter the inter-annual variation of MXD time-series – an increased similarity to RW can be observed (Björklund et al., 2019). MXD measured at lower resolution than the cell thus behave and exhibit features more related to RW, likely influencing features such as Rbar and temperature signal over time and across frequencies. The relatedness to RW may also entail an inherited age-trend from RW (RW's are narrow at older ages, and thus high MXD's at older ages are similarly muted). This line of argumentation is further consistent with the fact that the largest difference in temperature correlation between anatomical and established techniques are observed when the rings in the chronologies are oldest. Moreover, if established MXD data inherit age-trends from RW, an unstandardized comparison with temperature would likely reduce the fidelity across lower frequencies, as was also observed in this study. Note that these effects are even more prominent for the BI based MXBI data with the lowest measurement resolution. Max. rCWT appears to be the explored cell parameter with the purest temperature signal. Similar results are also presented in Carrer et al. (2018). If dendroanatomical parameters were to be exploited for temperature reconstructions, it appears as Max. rCWT should provide the best low-frequency results.

4.4. Concluding remarks

The cost and effort of producing an anatomical parameter-chronology for climate reconstruction is only justifiable as long as the environmental information gained could not be obtained more easily from ring widths or densities (*sensu* Hughes, 2002; Gagen et al., 2011). It is of little consequence that fewer samples are needed, because it will, at least in the near future, be economically advantageous to produce more data with established techniques. It is furthermore not critical if high-frequency fidelity to temperature is insignificantly higher. However, if the low-frequency variability is of a higher quality and if there is no need for standardization (except for removing the juvenile or corewood phase as is sometimes advocated with tree-ring isotope parameters (Young et al., 2011)), this would indeed justify the extra effort. It is premature to conclude from this single study whether dendroanatomical parameters are worth the effort and cost, but results are encouraging, motivating further tests on longer and multigenerational chronologies.

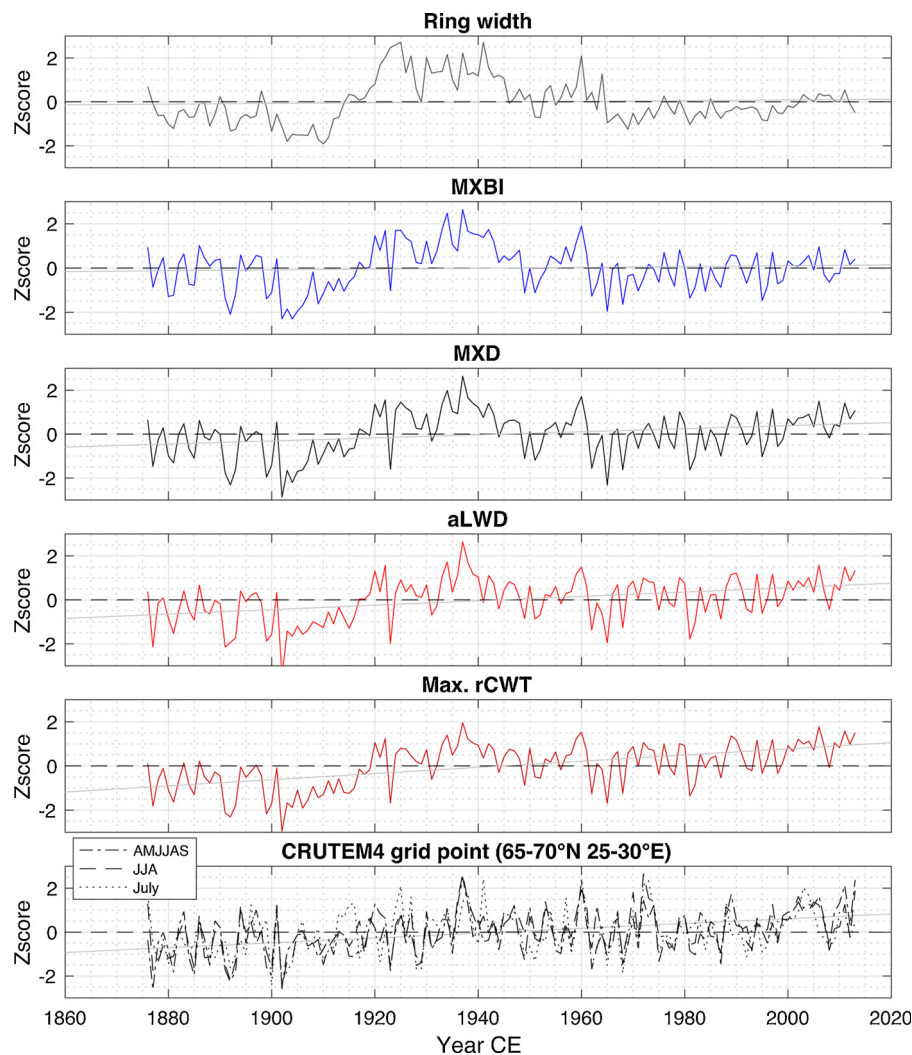


Fig. 6. Visual comparison of shortlisted parameter chronologies. Light grey solid line represents the overall trend of the data where the dashed black line provides zero-line contrast. Raw data with median and one standard deviation chronologies, as well as data aligned by cambial age can be found in Fig. S7 and S8.

Declaration of Competing Interest

None.

Acknowledgments

We sincerely thank two anonymous reviewers for valuable critique to an earlier version of the manuscript. The work executed by J.B., K.S., G.v.A. and D.N. was mainly funded by the Swiss National Science Foundation (Project XELLCIM no. 200021_182398) awarded to G.v.A. G.v.A. was also supported by a grant from the Swiss State Secretariat for Education, Research and Innovation SERI (SBFI C14.0104). P.F. was supported by the Swiss National Science Foundation (grant no. 150205, LOTFOR).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.dendro.2020.125673>.

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