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Climate signal age effects in boreal tree-rings: Lessons to be learned for paleoclimatic reconstructions

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ABSTRACT

Age-related alternation in the sensitivity of tree-ring width (TRW) to climate variability has been reported for different forest species and environments. The resulting growth-climate response patterns are, however, often inconsistent and similar assessments using maximum latewood density (MXD) are still missing. Here, we analyze climate signal age effects (CSAE, age-related changes in the climate sensitivity of tree growth) in a newly aggregated network of 692 *Pinus sylvestris* L. TRW and MXD series from northern Fennoscandia. Although summer temperature sensitivity of TRW ($r_{All} = 0.48$) ranges below that of MXD ($r_{All} = 0.76$), it declines for both parameters as cambial age increases. Assessment of CSAE for individual series further reveals decreasing correlation values as a function of time. This declining signal strength remains temporally robust and negative for MXD, while age-related trends in TRW exhibit resilient meanderings of positive and negative trends. Although CSAE are significant and temporally variable in both tree-ring parameters, MXD is more suitable for the development of climate reconstructions. Our results indicate that sampling of young and old trees, and testing for CSAE, should become routine for TRW and MXD data prior to any paleoclimatic endeavor.

1. Introduction

The ability of trees to form annually resolved rings in extra-tropical environments allows paleoclimatologists to develop annually resolved and absolutely dated climate reconstructions over several centuries to sometimes even millennia (Briffa et al., 2008; Büntgen et al., 2011b, 2013; Esper et al., 2007; Esper et al., 2012; Graumlich, 1993; Grudd et al., 2002; Helama et al., 2002; Linderholm and Gunnarson, 2005; Myglan et al., 2012; Schneider et al., 2015; Trouet et al., 2009; Villalba, 1990). The most frequently used tree-ring parameters, TRW and MXD, therefore provide the backbone of high-resolution paleoclimatology (Büntgen et al., 2013; Esper et al., 2007; Graumlich, 1993; Trouet et al., 2009; Villalba, 1990).

The underlying principle for these reconstructions is a temporal consistent climate sensitivity of tree growth (Fritts, 1976; Speer, 2010). This assumption is considered acknowledged not only over time and space (Büntgen et al., 2009; Esper and Frank, 2009) but also over cambial tree age. While the first two arguments remain under persistent scrutiny for many sites and species (Cook et al., 2004; D'Arrigo et al., 2006; Frank et al., 2007b; Ljungqvist et al., 2012), the latter assumption has not yet been explored in a systematic manner.

At the same time, age-dependent changes in raw TRW values are a well-known feature, associated with geometrical constraints of adjoining new rings to an increasing stem-radius/basal increment (Cook et al., 1990). These trends are present less pronounced in MXD data as geometrical constraints are negligible, though the gradually increasing tracheid and lumen sizes might reduce MXD values with increasing tree age/size (Carrer et al., 2015). In contrast to TRW, MXD has been reported to contain stronger temperature signals and enhanced signal-to-noise ratios in the high-frequency domain, compared to TRW (Briffa et al., 2002; Büntgen et al., 2015; Frank et al., 2007a). Due to lower biological memory (i.e.

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lower autocorrelation), MXD from cold environments typically exhibits higher correlation coefficients with summer temperature deviations (Esper et al., 2015).

In addition, it has been demonstrated that TRW-based climate reconstructions are, to a certain degree, constrained by age-related biases (Szeicz and MacDonald, 1994). Several studies have recently analyzed these climate signal age effects (CSAE) in TRW, revealing a better agreement between climate variation and the growth of old trees (Carrer and Urbinati, 2004; Esper et al., 2008; Linares et al., 2013; Yu et al., 2008). Other studies using different sites and species, however, found growth-climate relationships to be stronger in younger tree-rings (Dorado Liñán et al., 2011; Rozas et al., 2009). An overview on CSAE, including all previously mentioned cases and others (Linderholm and Linderholm, 2004; Rossi et al., 2008) is provided in Table 1. While sometimes pondered negligible (Dorado Liñán et al., 2011; Esper et al., 2008; Linderholm and Linderholm, 2004), CSAE can significantly impact the climate sensitivity of tree growth (Carrer and Urbinati, 2004; Linares et al., 2013; Rossi et al., 2008; Rozas et al., 2009; Yu et al., 2008). Varying prerequisites in earlier studies (Fig. 2), nonetheless, aggravate any straightforward comparison of the individual, and often contradicting findings. Furthermore, testing for CSAE in MXD has been broadly ignored.

Since age is closely related to tree size and height, disentangling this connection is challenging. Increased size can stimulate secondary growth, due to higher light accessibility and reduced competition (Bond, 2000). On the other hand, it can also lead to secondary growth reductions (Ryan and Yoder, 1997), due to hydraulic constraints in water transport and increased respiration (Meinzer et al., 2011; Schweingruber, 1996). Xylogenesis depends on cambial cell division, cell expansion and the growth of secondary cell walls (Schweingruber, 2007), which are intrinsically controlled by gene expression and hormonal signals (Meinzer et al., 2011), and extrinsically by environmental factors, including temperature or precipitation (Deslauriers et al., 2008). Several functional and physiological processes are affected by tree age, including a reduced foliar efficiency, lower photosynthetic rates, delayed onset of reproduction, and shorter growing seasons (Bond, 2000; Day et al., 2002; Rossi et al., 2008; Thomas, 2011). These age-related changes support the assumptions, that varying physiological processes should result in different levels of climate sensitivity throughout a tree's lifespan.

Here, we analyze CSAE in a unique *Pinus sylvestris* L. network from northern Fennoscandia. This dataset of 692 MXD and TRW measurement series from young and old trees provides ideal conditions for the re-organization of data by cambial age, the assessment of CSAE at both, the site and tree level, as well as parameter-specific and age-related comparisons of growth-climate response patterns.

2. Material and methods

2.1. Tree-ring data

Five well replicated MXD datasets from several sites across northern Sweden and Finland are used (Fig. 1). This compilation is part of a wider Northern Fennoscandian Network (NFN), previously developed to reconstruct changes in regional summer temperatures (Büntgen et al., 2011a; Esper et al., 2012; Schneider et al., 2014). A total of 692 cores were taken from *Pinus sylvestris* trees, spanning the period 1475–2006 (exceeding ten series in each year). Data include different tree ages ranging from 1 to 612 years. Sample replication ranges from 99 to 198 cores per site. TRW was measured with an accuracy of 0.01 mm using a LinTab measurement device and corresponding TSAP software (Rinn, 2007), and all rings were absolutely dated and verified by crossdating using the COFECHA

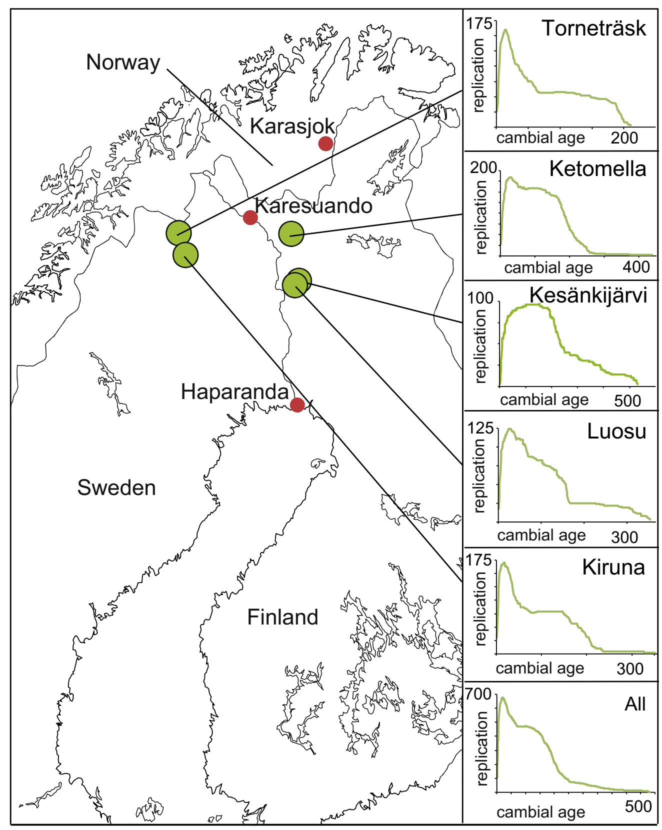

Fig. 1. Tree-ring sites (green circles), sample replication (panels on the right) and meteorological stations in Karasjok (1876–2011 period), Karesuando (1879–2011), Haparanda (1860–2009; red circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Published work associated with Climate Signal Age Effects (CSAE).

Publication	Region	Species	# Age-classes	# Cores (min/max)	Age-effects	Best responding age-class
Carrer and Urbinati, 2004	Eastern Italian Alps	*Larix decidua* *Pinus cembra*	4	7/60	Yes	old
Dorado Liñán et al., 2011	Spanish Pyrenees South-east Spain	*Pinus uncinata* *Pinus nigra*	2	8/18	No	young
Esper et al., 2008	Swiss Alps	*Pinus cembra*	3	35/128	No	old
Linares et al., 2013	Moroccan Atlas	*Cedrus atlantica*	2	50/60	Yes	old
Linderholm and Linderholm, 2004	Scandinavian Mountains	*Pinus sylvestris*	5	5/10	No	varies with time
Rossi et al., 2008	Eastern Italian Alps	*Larix decidua* *Pinus cembra* *Picea abies*	2	15/15	Yes	middle aged
Rozas et al., 2009	Central Spain	*Juniperus thurifera*	5	18/66	Yes	young
Yu et al., 2008	Qilian Mountains China	*Sabina przewalskii*	5	16/34	Yes	old

software (Holmes, 1983). Annual MXD values were obtained from high-resolution X-ray densitometry at the Swiss Federal Research Institute WSL in Birmensdorf (Eschbach et al., 1995).

Biologically induced, non-climatic trends associated with juvenile growth/density variations were removed using Regional Curve Standardization (RCS) (other detrending techniques reveal similar results), applied via the ARSTAN program (Cook, 1985; Cook et al., 1995; Esper et al., 2003; Fritts, 1976). Curve estimation was achieved by using negative exponential functions or linear fits with negative slopes. Index values were computed as residuals. Only TRW data were power-transformed prior to detrending as MXD does not contain any substantial spread-versus-level relationship (Cook and Peters, 1997). Chronologies were calculated using the robust bi-weight mean, and temporal variance changes stabilized considering sample size and varying interseries correlations (Rbar) (Frank et al., 2007b). Chronology signal strength was estimated by calculating Rbar and the Expressed Population Signal (EPS) statistics over 31-year moving intervals with an overlap of 30 years (Wigley et al., 1984).

With respect to previously published age-class grouping categories (Table 1), a total of 30 MXD and 30 TRW age-class subset chronologies were calculated by using the software Spotty (Esper et al., 2009). Site chronologies were considered to evaluate the influence of local environmental factors versus age.

2.2. Growth-climate relationships and age effects

Monthly data from the three longest nearby meteorological stations with monthly resolution (Haparanda, Karasjok, Karesuando) were utilized to generate seasonal and annual temperature means over the common period 1879–2006. Climate response patterns were estimated using *Pearson's* correlation coefficients (r) between the MXD and TRW records (i.e. two main chronologies, ten site chronologies, 60 age-class chronologies, 1384 individual timeseries) and June–August (JJA) temperature means (Büntgen et al., 2011a; D'Arrigo et al., 2008; Esper et al., 2012; Schneider et al., 2014, 2015). The frequency-dependent reliability of growth-climate relationships were analyzed by applying high- (HP) and low-pass (LP) filters to the proxy and the target data, using 31-year smoothing splines and residuals thereof. Climate correlations of individual core samples were aligned by biological/cambial age (Esper et al., 2003) and we fitted linear regression functions to estimate positive or negative slopes in CSAE trends and associated significance levels (Fritts, 1976).

We evaluated the temporal robustness of CSAE by splitting the common period 1879–2006 into nine equidistant periods of 40 consecutive years with a lag of 11 years. The evaluation of CSAE trends during pre-defined periods of marked warming and cooling, as well as the more trend-free episodes in-between, required calculating 1st differences of the 11-year low-pass filtered JJA temperature. To quantify the linear regression functions and explain the coherency between growth-climate linkages and cambial age, we performed analyses of variance (ANOVA) for a single factor and established significance estimation using the associated p-values.

3. Results

3.1. Age- and site-related chronologies

CSAE has been addressed in several studies considering a variety of methods and presenting differing results including decreasing (Dorado Liñán et al., 2011) and increasing (Carrer and Urbinati, 2004) climate signal strength with tree aging (overview in Table 1). These differences are related to several factors aggravating comparability: The studies are based on samples from different ecosystems and species, include changing numbers of age-classes ranging from 2 to 5, and numbers of tree samples averaged in age-class chronologies changes dramatically among (and partly within) studies. Sample replication of some age-classes varies considerably from $n_{min} = 7$ to $n_{max} = 60$ (Carrer and Urbinati, 2004), or generally, include just a few trees ranging from 5 to 10 trees (Linderholm and Linderholm, 2004). Some of the differences among existing studies might therefore be due to these differing setups. The identified best-responding age-class also varies from youngest (Dorado Liñán et al., 2011; Rozas et al., 2009), to middle-aged (Linderholm and Linderholm, 2004) and oldest (Carrer and Urbinati, 2004; Linares et al., 2013).

The published age-class chronologies consider different thresholds making it difficult to compare existing studies (Fig. 2). Age-classes range from only 30 years (Linares et al., 2013: age50–80) to 200 years (Yu et al., 2008: age1–200), so that the different age-class chronologies represent different life-stages of trees. Overall, only two out of nine studies considered juvenile age-classes <100 years (Esper et al., 2008; Rossi et al., 2008), while the threshold "100" is used in another three publications (Carrer and Urbinati, 2004; Linderholm and Linderholm, 2004; Rozas et al., 2009). Consideration of these thresholds with age-aligned data (Fig. 2 upper panel) clearly shows how differing portions of juvenile and adult TRW and MXD data are captured, limiting the comparability of varying, pre-defined age-class systems.

The application of all previously published age-class categorizations to the NFN dataset reveals a general trend of decreasing temperature correlations with increasing cambial age (Fig. 3). MXD shows a higher coherency with JJA temperatures than TRW. Highest correlations are recorded in the youngest age-classes ($r_{MXD1-150} = 0.78$, $r_{TRW1-200} = 0.49$), though these values only slightly exceed the values when using all data ($r_{MXDall} = 0.76$, $r_{TRWall} = 0.48$). Cross-parameter differences appear to be most pronounced in the older age-classes ($r_{MXD500-612} = 0.47$, $r_{TRW400-500} = 0.10$).

These findings are, however, constrained by the changing numbers of MXD and TRW samples averaged in the various age-class chronologies (top panel in Fig. 3). Some age-class categories divide the data into small sections, thereby reducing minimum replication down to only 12 ($n_{age201-250}$) or 14 samples ($n_{age\ 50-80}$), while other schemes result in much better replicated sub-set chronologies (e.g. $n_{age176-250} = 97$, $n_{age63-123} = 129$). In four cases ($n_{age251-325} = 8$, $n_{age326-430} = 7$, $n_{age251-340} = 9$, $n_{age500-612} = 10$), minimum replication of the age-class chronologies falls below the commonly accepted threshold of >10 samples. In addition, replication within most age-classes varies in increments of ten or up to >400 series (e.g. $\Delta n_{age151-200} = 427$, $\Delta n_{age300-400} = 418$), due to the amount of 128 consecutive years within the calibration period and simultaneously adapted cambial ages, that lead to the inclusion or exclusion of data within the age-class categories and thresholds. Overall, the comparison of climate signals among age-class and site chronologies (last column in Fig. 3) reveals a higher variability of correlation values among the different age-classes than between the five sites. While this indicates the importance of CSAE compared to commonly assessed between-site differences, this conclusion is limited by severe replication changes between the various age-class chronologies.

3.2. Individual series and trends

Using individual core series (rather than age-class chronologies) supports the estimation of CSAE unbiased by changes in replication (Fig. 4). This assessment reinforces climate signals to be stronger in MXD (than TRW), a finding that holds true in all frequencies, and

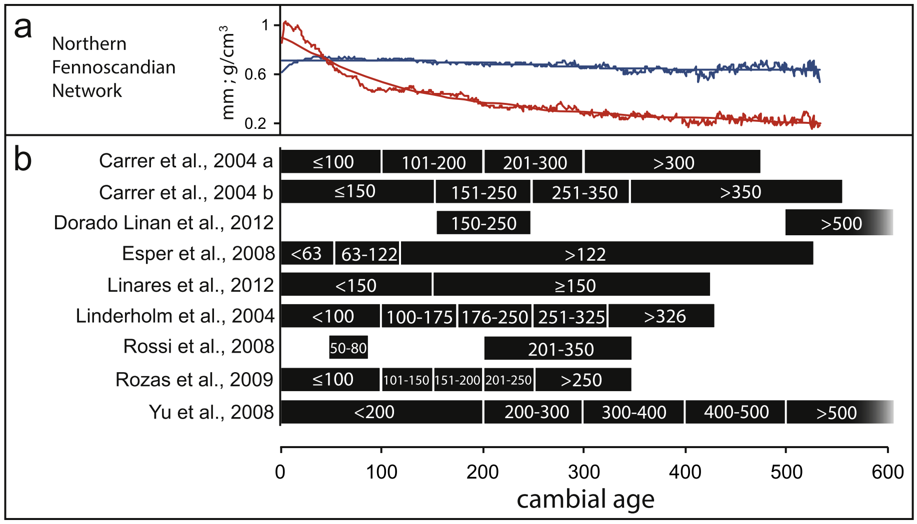

Fig. 2. Age-class categorizations in previous studies and regional curves. **a** Regional curves (MXD in blue, TRW in red) of the NFN; **b** Cambial age-class boundaries as used in studies in CSAE. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

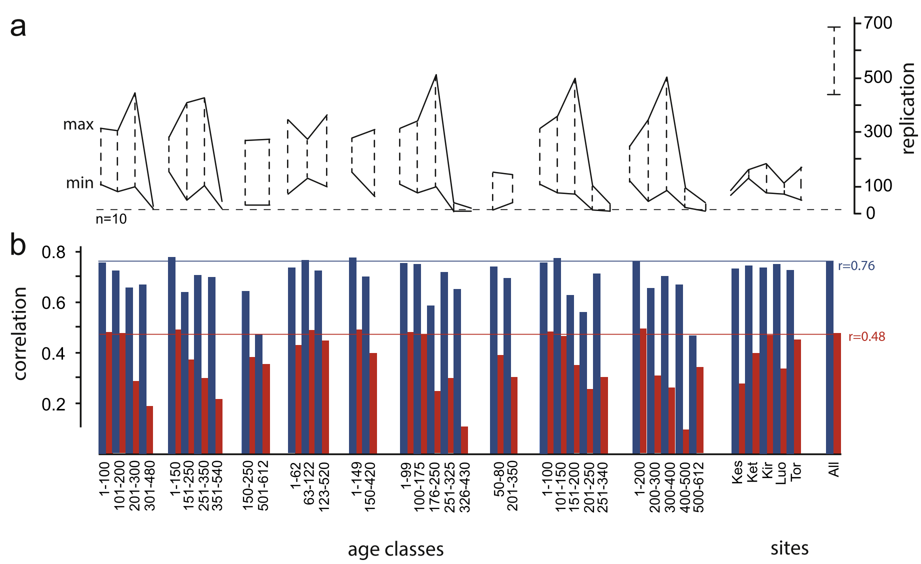

Fig. 3. CSAE in pines from Fennoscandia using published age-class boundaries. **a** Minimum and maximum replication of age-classes chronologies during the 1879–2006 calibration period **b** Correlations with JJA temperatures for MXD (blue) and TRW (red) age-class chronologies over the 1879–2006 period, colored horizontal lines indicate correlation coefficients using all samples. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

over various cambial ages and time periods. Linear trend functions demonstrate JJA temperature signal strength to change with individual tree age. The trends are significant in MXD at $p = 0.006$ for the original data and $p = 0.001$ for the high-pass filtered data, showing robust, decreasing centennial gradients of $g_{MXDOriginal} = -0.028$ and $g_{MXDHP} = -0.026$ over the 1879–2006 common period. In TRW, climate signal strength depends on cambial age in all frequencies. The linear trends are less pronounced though, and decrease with age in the original ($g_{TRWoriginal} = -0.028$) and low-pass filtered data ($g_{TRWLP} = -0.013$) but increase in the high-passfiltered data ($g_{TRWHP} = +0.014$).

CSAE in MXD is more robust over time, since correlations in a split calibration approach comprising nine equidistant periods (40 consecutive years with a lag of 11 years) exhibit steadily decreasing values with age throughout the calibration interval (Fig. 5). Whereas the slopes of the linear trends vary from $g_{MXD1956-1995} = -0.003$ to $g_{MXD1967-2006} = -0.040$, they remain negative in all periods in both the original and the high-pass filtered data (Fig. 6). In comparison, the TRW data not only correlates weaker with JJA temperature, but also the CSAE slopes also change throughout the calibration interval (Fig. 5). Only six of the nine calibration periods show negative trends, ranging from $g_{TRW1934-1973} = -0.010$ and to $g_{TRW1901-1940} = -0.047$. The three remaining periods yield positive trends with the highest value reached at $g_{TRW1956-1995} = +0.048$. However, the high-pass filtered TRW data reveals a more coherent pattern, with all periods exhibiting positive, and remarkable trends (Fig. 6). Whereas for the high frequency data the mean gradient of all sub-periods resembles the common period results, this is not the case in the original data, where the negligible trend from the sub-periods contrasts the significant negative trend over the full calibration period 1879–2006.

An assessment of the NFN in association with warming and cooling periods over the last 130 years suggests that CSAE is

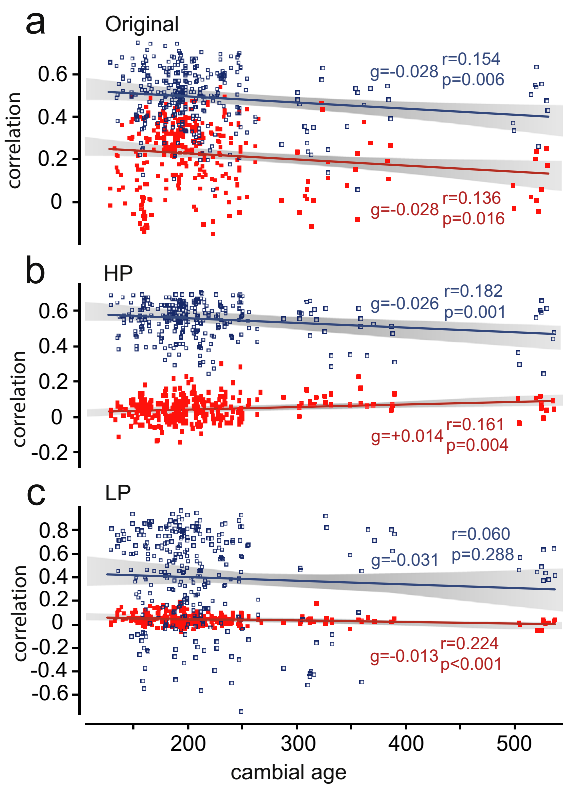

Fig. 4. Growth-climate relationships of individual trees over the 1879–2006 period. **a** RCS detrended MXD (blue) and TRW series (red, n = 317) correlated against JJA temperatures and linear regressions fitted to the correlation values. Shaded areas indicate 95% confidence limits for the predicted linear regression. With g = regression slope over 100 years, r = correlation coefficient and p = significance level **b** Same as in **a** but for high-pass filtered MXD and TRW series **c** Same as in **a** but for low-pass filtered data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

influenced by the temporally changing environmental conditions, a finding that seems to hold true for both TRW and MXD (Fig. 7). While MXD shows higher correlations and generally decreasing CSAE trends throughout the 1879–2006 calibration period, the TRW signal displays the previously detected oscillation between negative and positive CSAE trends, which can be differentiated in five periods: Two periods of consecutive summer temperature warming (1904–1938 and 1984–2006), two periods of weak trends (1879–1903 and 1961–1983), and one period associated with summer cooling (1939–1960).

The most pronounced CSAE trends, in both tree-ring parameters, are apparent in the recent period 1984–2006 ($g_{1984-2006} = -0.075$, $p < 0.001$), characterized by strong summer temperature warming (Fig. 8). Also the second warming period from 1904 to 1938 is characterized by significant negative trends in both datasets ($g_{MXD1904-1938} = -0.034$, $g_{TRW1904-1938} = -0.060$, $p < 0.001$). During the period of consecutive summer temperature cooling, CSAE is effectively non-existent in both, MXD and TRW. Finally, during periods with no clear temperature trend, CSAE is less distinct/homogeneous: During 1879–1903, the MXD trend is significant ($g_{MXD1879-1903} = -0.026$, $p < 0.01$), whereas the TRW trend is not. During 1961–1983, the TRW trend is significant ($g_{TRW1961-1983} = +0.046$, $p < 0.001$), but MXD trend is not.

In summary, climate sensitivity of MXD and TRW decline with increasing cambial age. These general tendencies are, however, modified by the differing warming and cooling trends throughout the past 130 years. Gradual summer temperature warming enhances CSAE, whereas decadal scale cooling removes this bias.

4. Discussion

At best, tree-ring chronologies comprise all cambial ages of tree-rings. However, the age distribution as a function of time displays variations, which take place not only in the calibration but also in the reconstruction period. Early reconstruction periods are typically represented by young tree-rings, while cambial ages increase towards older trees in the 20th century calibration period. Here we assessed the influence of changing tree age on climate signals using age-class chronologies and individual series. For this analysis, well-replicated datasets composed of young and old trees are required to minimize replication biases. However, such datasets are rare for TRW as most sampling strategies mostly focused on dominant and old trees (Nehrbass-Ahles et al., 2014). Due to the time-consuming procedure of MXD measurements, the dataset presented her is unique as it includes all cambial ages.

4.1. Data structure and characteristics

Splitting the MXD and TRW data into several age-classes considering schemes from previous studies from differing ecological and climatological settings, yielded inconsistent results. By comparing the diverse length of some age-class categories it becomes obvious that a physiological cause in terms of changes in growth or density rates can be excluded when using these age-class chronologies. CSAE estimates are sensitive to different age-class thresholds, especially as these thresholds lack a physiological background. Particularly for the juvenile episode of tree-growth, large age-class categorizations of >100 years appear inadequate, since many physiological changes occur during this life-span (Meinzer et al., 2011). Generally, thresholds rather appear estimated as adaptation to the commonly used decimal numeral system (e.g. age-class 1–50, 1–100, 1–150, etc.) or to the age span of the samples at hand, thus, raising the question whether some datasets fulfill the requirements of studying CSAE. An evenly distributed mix of young and old trees is needed to assess differences during the 20th century calibration period. Additionally, replication changes between the age-class chronologies may affect results and cannot easily be distinguished from CSAE. However, results suggest a gradual decrease of climate sensitivity with increasing age in both TRW and MXD. Replication changes limit this conclusion, particularly for the older age-classes, although the large dataset includes a high amount of young and old trees.

Exploring individual core series, instead of age-class chronologies, helped to mitigate uncertainties related to replication changes and age-class thresholds, and confirmed the gradual decrease of climate sensitivity with increasing age. The calculation of linear trends also enabled an estimation of CSAE gradients per unit of age and accompanying significance levels. CSAE trends were significant in MXD and TRW (except for low-pass filtered MXD data), although they may not explain large fractions of variance in the data.

In contrast to the robust negative gradients in MXD, TRW climate correlations decrease with age only in the low-pass filtered data. The high-pass filtered data exhibits higher correlation values with increasing cambial age. In the original data, including both high- and low-frequency variance, the trend is again negative containing the strongest gradient. TRW is typically connected with high autocorrelation values and biological memory (Esper, 2015), incorporating a stronger low-frequency component, leading to superimposed negative trend in the original data (Büntgen et al., 2015; Fritts, 1976). However, this decreasing trend with age is not temporally robust, since results from split calibration approaches do not reflect results over the common period, which was also

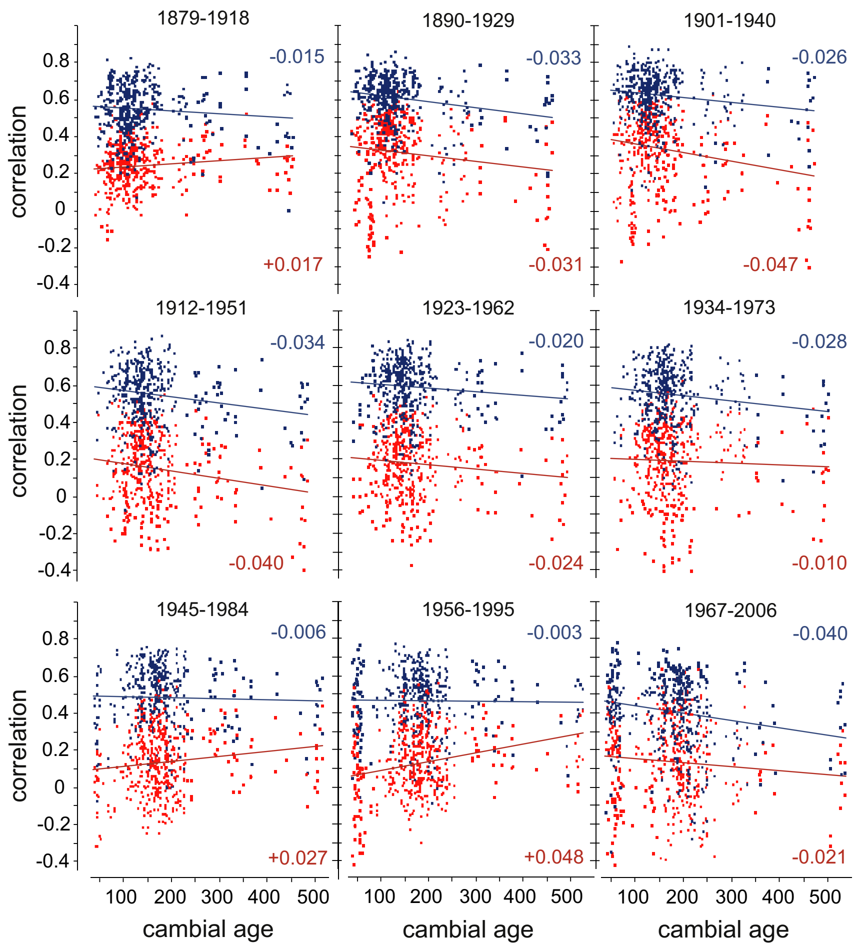

Fig. 5. Growth-climate relationships of individual trees over equidistant periods (40 years, lag: 11-year lags). RCS detrended MXD (blue) and TRW (red) correlated against JJA temperature and linear trends as in Fig. 4. The numbers of correlations ranges from n = 418 to n = 456. Values in blue and red indicate the regression line slopes per 100 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

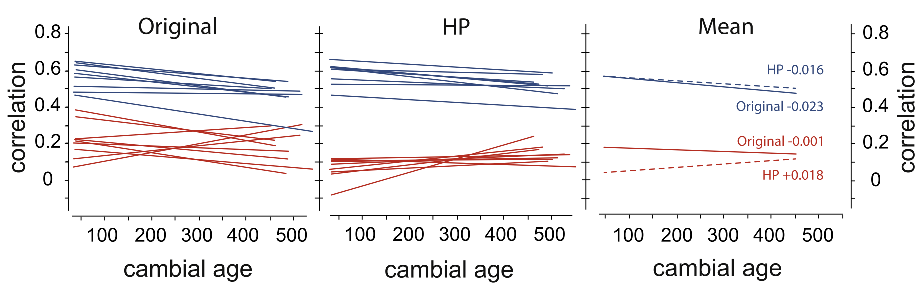

Fig. 6. CSAE trends. Left: Linear trends of RCS detrended MXD (blue) and TRW data (red) for correlations against JJA temperature in equidistant periods (40 years, 11-year lags). Middle: Linear trends from using high-pass filtered tree-ring and temperature data. Right: Mean trends of the original and high-pass filtered data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

detected by Linderholm and Linderholm (2004). Cambial age seems to have a frequency-dependent impact on climate signals in TRW, which seems to be absent in MXD. Particularly in the low-frequency domain, MXD contain no significant CSAE trends, thereby reinforcing the strength of this tree-ring parameter for climate reconstruction purposes. This conclusion is supported by the temporal robustness of CSAE trends in MXD, which remain significant and independent of frequency domain.

The significance of CSAE in both tree-ring parameters, MXD and TRW, is related to temporal changes in JJA temperatures over the past 130 years. Whereas warming periods seem to support negative CSAE trends, cooling periods appear to be associated with insignificant CSAE trends. In other words, older trees tend to mirror warming trends in their tree-rings to a smaller extent than younger trees. Particularly the pronounced warming in the most recent period seems to be linked to the strongest CSAE trends. Due to the typical age-structure consisting of oldest living trees and tree-rings in the most recent period together with the decreasing tree-ages back in time, CSAE can play an important role when establishing climate signals in the late calibration period and may add another factor to ongoing debate about divergence effects in Northern European tree-ring networks (D'Arrigo et al., 2008; Esper and Frank,

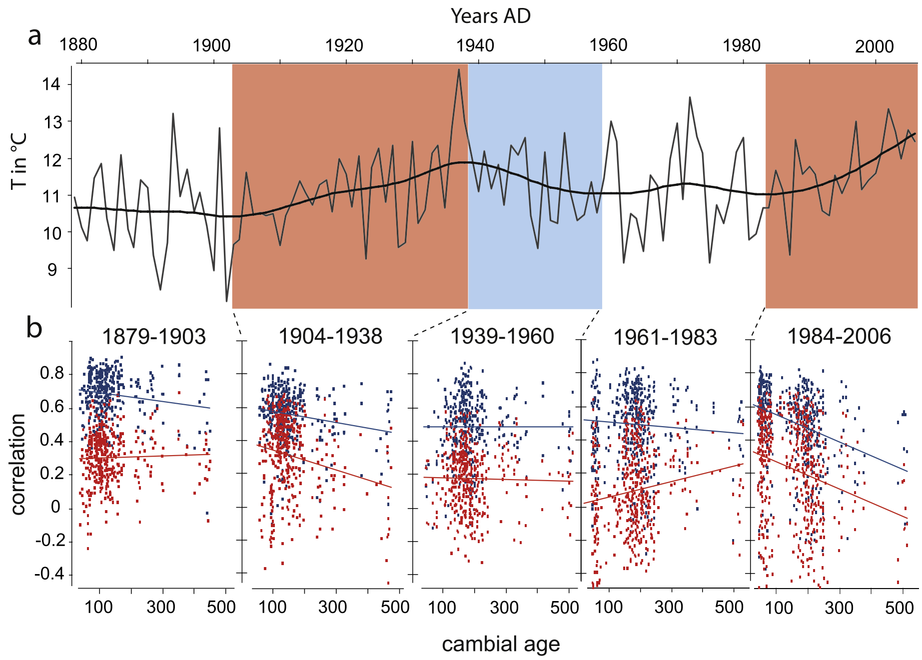

Fig. 7. CSAE during warming, cooling and trend-free periods. **a** Mean JJA temperatures from Haparanda, Karasjok and Karesuando over the 1879–2006 period. Bold curve is a 30 year smoothing spline. Colors indicate warming (red), cooling (blue) and trend-free periods (white), calculated from smoothed (11-year spline) and 1st-differenced temperatures of smoothed temperature data (30 year spline) **b** RCS detrended MXD (blue) and TRW series (red) correlated against JJA temperature during warming, cooling and trend-free periods. Straight lines are linear regression trends. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

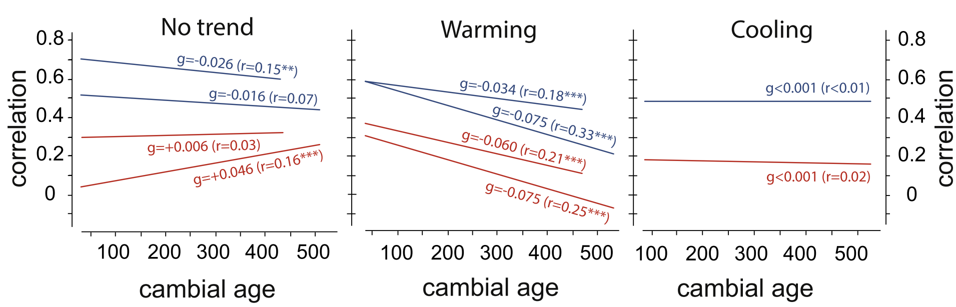

Fig. 8. CSAE trends during warming, cooling, and trend-free periods of RCS detrended MXD (blue) and TRW series (red) from correlations against regional JJA temperatures. Left panel shows results for the trend-free periods 1879–1903 and 1961–1983. Middle panel shows results for warming periods 1904–1938 and 1984–2006. Right panel shows results for the cooling period 1939–1960, g = regression slope over 100 years, r = correlation coefficient, and significance level: *(p < 0.05), ** (p < 0.01), ***(p < 0.001). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2009).

4.2. Physiological processes

For the first time we demonstrate that the decrease of temperature sensitivity with increasing cambial age is a significant component in MXD and TRW timeseries from *Pinus sylvestris* in Northern Fennoscandia. Previously reported physiological changes throughout the trees' lifespans seem to affect cambial activity and cell-wall thickness, and their sensitivity to environmental influences. Generally, younger trees tend to prolong the vegetation period at the greater risk of mortality to enhance stem growth in competition for light (Bond, 2000; Day et al., 2002). Contrary, the vegetation period of older trees appear to be shorter, since these trees are well established, access to light is granted by fully formed canopies and competition is of no substantial importance (Rossi et al., 2008).

The interdependency of age-related vegetation period length and seasonal response patterns may contribute to the explanation of CSAE. The JJA period considered here is the best responding season when all trees of this study are included. Our results indicated that by prolonging this season, e.g. to May–September, CSAE appear overall even larger, with young rings correlating better ($r_{MXD1-100} = 0.73$, $r_{TRW1-100} = 0.47$) than old rings ($r_{MXD500-600} = 0.43$, $r_{TRW500-600} = 0.22$). A season shortening to only July leads to less pronounced trends in climate correlations: Older age-classes display higher or similar correlations to July temperatures compared to younger classes ($r_{MXD1-100} = 0.56$, $r_{MXD500-612} = 0.60$, $r_{TRW1-100} = 0.49$, $r_{TRW500-600} = 0.48$). The JJA season was chosen here, as it showed the strongest correlations among sites and proxies, and was previously considered in the climate reconstructions from the region (Büntgen et al., 2011a; Esper et al., 2012; Schneider et al., 2014). The estimated CSAEs may, however, be a masked expression of the temporal shift of age-related growth seasonality.

Generally, MXD and TRW data are derived from the same tree-rings, but are controlled by differing physiological processes. MXD is closely related to cell-wall thickness, which is primary linked to lignification (Schweingruber, 1996). TRW relates closely to the number of cells and their tracheid area (Schweingruber, 1996). In young trees, cells are usually smaller, due to the shorter root-leaves path length and associated hydraulic constraints linked to tree height (Ryan and Yoder, 1997; West et al., 1999). In climatologically favorable periods, the cambium is prone to produce more cells, thereby enlarging TRW. However, older and taller trees produce only few larger cells per ring and increase to a lesser degree their number under favorable conditions, due to slower and shorter xylogenesis (Rossi et al., 2008). This makes older trees more complacent, especially during warming periods (Carrer et al., 2015). In contrast, shorter cooling trends seems to affect both, young and old trees. Cell wall thickening (MXD) is usually not that tightly bound with such hydraulic constraints, and age- and height-related changes thereof. CSAE in this parameter probably only results from the shortening of the vegetation period. The phenomenon appears to be temporally more robust, and can probably be more easily avoided by creating datasets with an evenly distributed age-structure, i.e. be including high numbers of samples of all cambial ages.

5. Conclusions

Analyzing a northern Fennoscandian MXD and TRW network, we show that climate signal age effects are overall larger than the differences in summer temperature response among different tree sites. However, if we use all data, including all age-classes, the mean chronologies display only marginally lower correlations against temperature data compared to the best responding age-class chronology. On an individual tree level, the relationships between climate and MXD and TRW are age-dependent, except for the low-pass filtered MXD data (though reduced degrees of freedom need to be considered here). Decreasing climate correlations with increasing cambial age appear to be a temporally robust feature in MXD data, while TRW exhibits a more complex behavior including oscillations between positive and negative CSAE trends, depending on climate states (warming or cooling) and frequency domains (high- and low-pass). Changing climate conditions throughout the past 130 years seem to affect both tree-ring parameters: consecutive warming over several years enhanced CSAE in MXD and TRW, while cooling temperatures seems to minimized this bias.

Generally, the calibration results using MXD data are characterized by higher and temporally more robust correlations, even though also these are decreasing with tree age. CSAE is less important in the low-frequency domain, though degrees of freedom were low when testing this, which is likely important for climate reconstruction purposes. Overall warming temperatures seem to foster CSAE, which is a prominent feature of the most recent period of the calibration interval. Our findings show that CSAE bias the estimation of climate signals and subsequent reconstructions from both MXD and TRW data. CSAE should be studied in climate reconstructions, and can probably be mitigated by a careful selection of sampled trees and inclusion of tree-rings of differing cambial age throughout time.

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