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

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A B S T R A C T

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

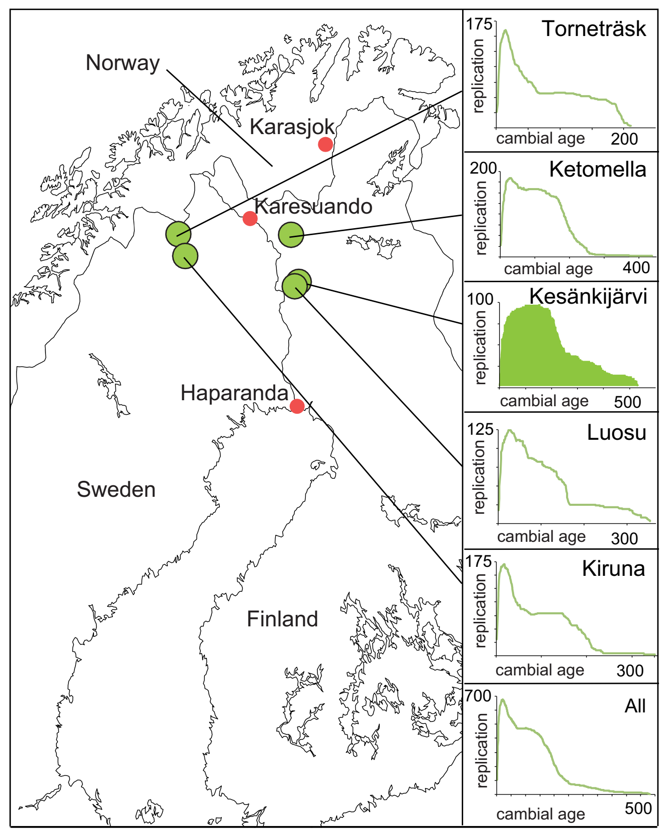

Fig. 1. Tree-ring sites (green circles), sample replication (panels on the right) and meteorological stations in Karasjok (1876–2011 period), Karesuando (1879–2011), Haparanda (1860–2009; red circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the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