



# Size matters—a comparison of three methods to assess age- and size-dependent climate sensitivity of trees

Mario Trouillier<sup>1</sup> · Marieke van der Maaten-Theunissen<sup>2</sup> · Tobias Scharnweber<sup>1</sup> · David Würth<sup>3</sup> · Andreas Burger<sup>1</sup> · Martin Schnittler<sup>3</sup> · Martin Wilmking<sup>1</sup>

Received: 3 June 2018 / Accepted: 17 September 2018 / Published online: 28 September 2018  
© Springer-Verlag GmbH Germany, part of Springer Nature 2018

## Abstract

**Key message** Changes in tree's climate sensitivity during their ontogenetic development is best assessed with stem diameter classes, which can be calculated retrospectively from the cumulative ring width.

**Abstract** Climate affects tree growth but the effect size can be modulated by other variables, including tree's age and size. To assess how climate sensitivity changes over the life of a tree, previous studies mostly stratified trees into age classes, while cambial ring-age stratification (age-band decomposition) was less frequently used. However, trees do not age as other organisms and arguably age is mainly a proxy for size, which in contrast to age has been shown to affect wood anatomy and physiology. Stem diameter classes, calculated from cumulative ring width, could thus facilitate a more direct assessment of size effects. Here we compare these three methods, which differ regarding how they stratify data into age/size classes. We found that using age-band decomposition and cumulative ring-width classes had major advantages over the tree-age method: (a) age and size are decoupled from other temporal changes, like atmospheric CO<sub>2</sub> concentration or nitrogen deposition, which excludes potential biases. (b) Shifts in climate sensitivity occur earlier than estimated by the tree-age method. (c) Younger/smaller classes can be assessed. Furthermore, direct comparison supports that size, rather than age, alters climate sensitivity. Therefore, the cumulative ring-width method appears to be the best approach to assess the effect of ontogenetic changes on a tree's climate sensitivity. Understanding how climate sensitivity changes when trees get older and larger is important for forest ecology and management, climate reconstructions, global carbon models and can help to study age and height limitations of trees.

**Keywords** Dendrochronology · Climate sensitivity · Tree age · Tree height · Hydraulic limitation hypothesis

## Introduction

### Tree-age related development

Age appears to have no direct effect on tree physiology, or at least aging of trees is very different from aging in many other organisms (Bond 2000; Thomas 2002). In particular, the cambial meristem does not show signs of tissue senescence, as it was shown with reciprocal-grafting experiments: Transplanting shoot tips from young to old trees and vice versa showed that the shoot tips adopt the characteristics of the rootstock (Bond et al. 2007). Similarly, size, not cellular senescence, is responsible for declining growth with age (Mencuccini et al. 2005). Instead of aging, trees develop continuously, through stages of seedlings, juveniles, mature and old growth (Thomas 2002). Next to changes in the root systems and stem diameter, height growth is probably the

Communicated by Wieser.

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00468-018-1767-z>) contains supplementary material, which is available to authorized users.

✉ Mario Trouillier  
trouillier@posteo.de

<sup>1</sup> Landscape Ecology and Ecosystem Dynamics Working Group, Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany

<sup>2</sup> Forest Growth and Woody Biomass Production, TU Dresden, Dresden, Germany

<sup>3</sup> General and Special Botany Working Group, Institute of Botany and Landscape Ecology, University of Greifswald, Greifswald, Germany

most apparent developmental change of trees. Because of that, previous studies also used size-related parameters, instead of age, to consider the effect of ontogenetic development in the assessment of long-term growth trends (Luis et al. 2009; Bontemps and Esper 2011). Evolutionary, height growth developed because it is a selective advantage for plants in the competition for light. However, this competitive advantage appears to come with a trade-off cost (King 1990; Koch et al. 2004). Various physiological and morphological changes occur related to height growth, for example leaf morphology (Koch et al. 2004) or annual primary growth (shoot length) (Day et al. 2002). One of the main costs of increased height is increased hydraulic resistance (Ryan and Yoder 1997; Ryan et al. 2006). Wood anatomy in particular seems to play an important role in height-related changes in the hydraulic conductivity of the xylem (Carrer et al. 2015). As first described in ‘Sanio’s law’ (Sanio 1872), conduit area increases with distance from apex. Mencuccini et al. (2007) evaluated ‘Sanio’s law’ and developed a model that accounts for the xylem construction costs relative to the photosynthetic gain, to describe wood anatomical changes with tree height. This illustrates why tree height, rather than age is of interest when physiological processes are studied and why wood anatomy has recently seen recognizable methodological advances (Rossi et al. 2006; Gärtner and Nievergelt 2010; von Arx and Carrer 2014). Tree height thus plays an important role for tree physiology, but long time series of height increment data are rarely available to study its effect directly. Stem diameter and age, on the other side, can be easily calculated retrospectively from tree-rings and are useful proxies for tree height and allow to study how height modulates environmental effects on tree growth.

### Modulation of tree’s climate sensitivity

Climate-growth relationships are the foundations of dendroecology as well as dendroclimatology. It is crucial for both fields to quantify exactly how the various dendrochronological parameters like tree-ring width, wood density or isotope concentrations are related to specific climatic variables. However, as it was formulated so elegantly by Briffa et al. (1996), “trees are not thermometers or raingauges”, which emphasizes the high complexity of tree growth. The analyses presented in this article thus contribute to a growing body of literature that explores how a tree’s climate sensitivity is modulated. Even though this complexity of tree growth has long been recognized (Cook and Kairiukstis 1990; Vaganov et al. 2006), many studies still assume that trees show the same climate sensitivity in the past as they do in the present, often referred to as the ‘uniformitarian principle’ (Fritts 1976; Cook and Kairiukstis 1990). However, as argued by Wilmking et al. (2017b), frequently reported changes in climate sensitivity, the so called ‘divergence problem’

(D’Arrigo et al. 2008; Williams et al. 2011), rather reflect an incomplete understanding of tree growth, not the invalidity of this principle. Consequently this article contributes to these discussions by exploring how tree age and size affects climate-growth correlations.

There has been a general increase in the number of studies that report modulations of a tree’s climate sensitivity by various parameters like competition (Piutti and Cescatti 1997; Wang et al. 2016; Gleason et al. 2017), nitrogen deposition (Ibáñez et al. 2018) and CO<sub>2</sub> concentration (Nicolussi et al. 1995). However, long time-series of climate sensitivity modulating variables like competition (forest structure) or nutrient status are rarely available, which makes studying these effects difficult. Tree-age and size effects on the other side, can be studied using age or stem-diameter data, obtained from tree-rings, as proxies.

This article focuses on the structural changes happening to a tree as it develops continuously over time and compares three methods that aim to assess how age and size modulate a tree’s climate sensitivity. Such changing climate sensitivity with age or size can have important implications for the study of tree growth, survival, reproduction, carbon sequestration models as well as for climate reconstructions (Fritts 1976; Cook and Kairiukstis 1990; Briffa et al. 1998; Jump et al. 2006; Babst et al. 2014; Zhang et al. 2015; Price et al. 2015; Sullivan et al. 2017).

## Materials and methods

### Tree-ring data

Assessing age- and size-dependent climate sensitivity requires large data sets, ideally with several hundred trees. We took advantage of a large white spruce (*Picea glauca* (Moench) Voss) treeline dataset from the Brooks Range, Alaska, originally sampled in 2012 (Eusemann et al. 2016) and updated in 2015 and 2016 (Wilmking et al. 2017a) summing up to 452 individual trees. For this data set, all trees in a plot of 100 × 200 m with a diameter at breast height (DBH) of > 5 cm were cored at the lowest possible height (~40 cm). One or two cores were extracted from each tree and DBH, diameter at coring height (DCH), tree height, and coring height were recorded. Along two 110 m transects, diameter at the root–shoot boundary and height was measured of all seedlings and saplings (DBH < 5 cm). Additionally, we collected 20 disks (cookies) of five different height classes each (0–30 cm, 31–60 cm, ..., 121–150 cm). Cores from trees sampled in 2012 and seedling cookies were sanded with increasingly finer grits, while the surface of cores sampled in 2015 were prepared with a core microtome (Gärtner and Nievergelt 2010). Samples were then scanned with an Epson Perfection V700 Photo flatbed scanner with 3200dpi and

ring widths were measured with Coorecorder 8.1 (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). The measurements were cross-dated visually and with CDendro 8.1 (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). Ring-width measurements were then loaded into R 3.1 (R Core Team 2015) with the *dplR* package (Bunn 2008) and detrended with a 30-year cubic smoothing spline with a 50% frequency cut-off to create a dimensionless tree-ring index (TRI). Additionally we removed autocorrelation ('prewhitening'). Ring ages were corrected for coring height based on the age–height relationships of the sampled seedlings. Similarly, stem diameters in each year, that were calculated from cumulative ring width, were corrected for coring height based on the seedling age and stem diameter at the root–shoot boundary. To assure that our plot setup did not pose a bias we assessed age, DBH, and tree height distribution along the treeline gradient.

### Age and size class methods

In this study, we compare three methods for the assessment of age- and size-related changes in climate sensitivity. The methods differ in how they stratify the tree-ring data, which are either based on (1) tree age, (2) cambial ring age, also known as age-band decomposition (ABD) and (3) stem diameters calculated from the cumulative ring width (CRW). (4) For the direct comparison of size- and age effects, we combined cambial ring age and cumulative ring width methods by distinguishing fast- and slow-growing trees:

(1) The first approach, that is most frequently applied to assess age-modulated climate sensitivity, calculates tree age from the number of tree rings and then divides all trees into age classes (Carrer and Urbinati 2004; Yu et al. 2008; Esper et al. 2008; Vieira et al. 2009; Rozas et al. 2009). This means that in each year the same tree subset is used to calculate the class average. (2) Briffa et al. (2001) introduced age-band decomposition (ABD), which uses the cambial ring age to create age classes. Despite the apparent similarity to the tree-age method, ABD leads to a fundamentally different data subset for each age class, because ABD selects for each year tree-rings from a different subset of trees, illustrated in Fig. 1. (3) Similar to ABD, we created stem-diameter classes based on the cumulative ring width, similar to size-class isolation used for the assessment of long-term growth trends (Bowman et al. 2013; Peters et al. 2015). Analogue to the ABD method, tree rings rather than trees are used to create classes. Often cores did not hit the pith and no pith-offset estimates were included in the dataset. Thus we used the diameter at coring height and calculated CRW classes backwards from bark to pith. (4) Lastly, size and age cannot directly be compared because they use different scales. Therefore, to facilitate a direct comparison of age and size methods, we created size data-subsets of age subsets based

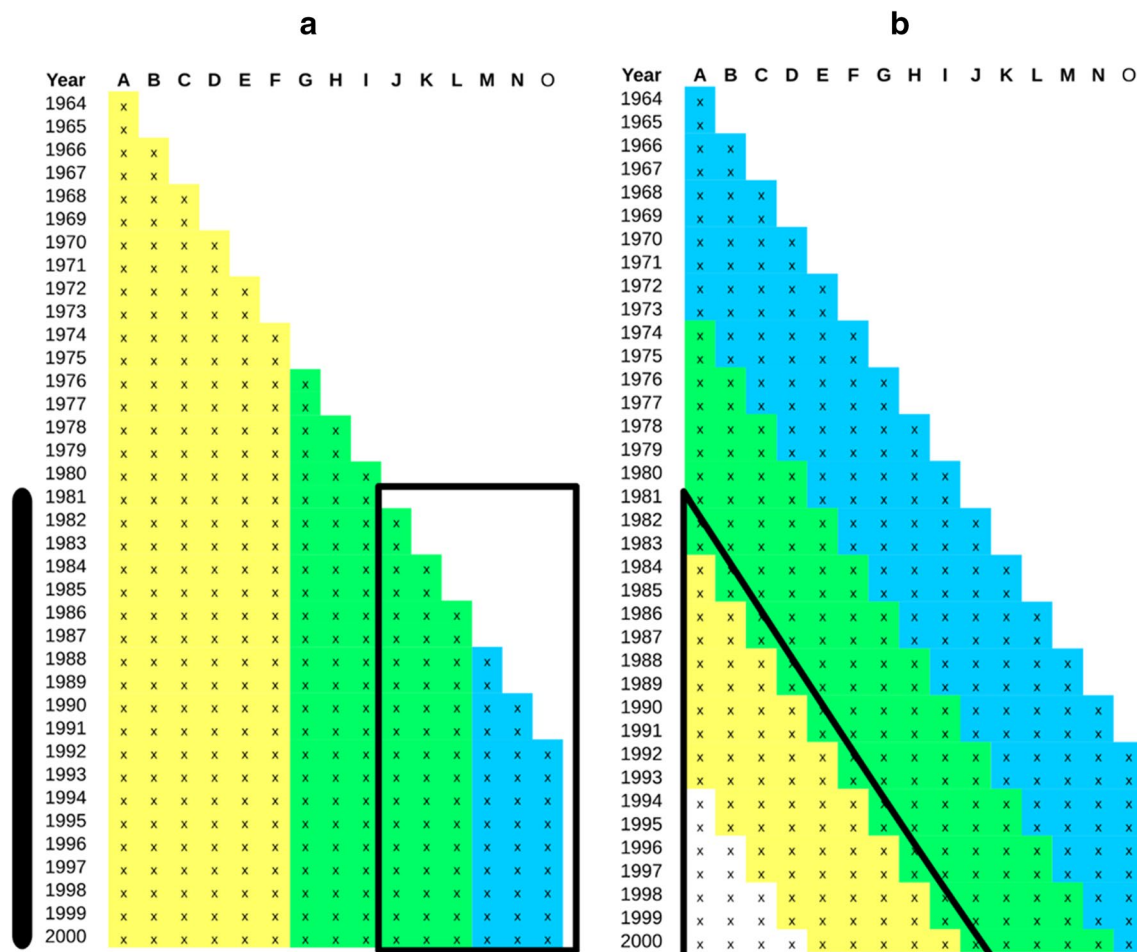
on cambial ring age and cumulative ring width. This allows comparison of climate sensitivity of small and large trees of the same age, by accounting for different growth speeds. Fast- and slow-growing trees were split based on the slope of the linear regression between cambial ring age and cumulative ring width.

For each of the methods, we created overlapping classes of 20 years or 20 mm width with an offset of 1 year or 1 mm (1–20, 2–21, 3–22,...). We used a minimum sample size of 15 trees for each class and year, which resulted in 144 tree-age classes, 147 ABD classes and 151 CRW classes. Because of large sample size requirements when creating CRW classes within ABD classes (4), we had to use 30 year windows and a minimum sample size of  $n = 10$ . We then calculated class chronologies (yearly averages) from the detrended tree-ring data in each class, which we then used for the climate-growth correlations.

### Climate data and climate-growth correlations

Because of limited climate station data in Alaska, particularly in the Brooks Range and in the first half of the twentieth century, we used gridded monthly climate data for the period 1950 till 2009, which was provided by the Scenarios Network for Alaska and Arctic Planning (SNAP 2016). On top of the available data on precipitation, temperature, potential evapotranspiration (PET) and water–vapor pressure, we calculated the standardized precipitation evapotranspiration index SPEI (Vicente-Serrano et al. 2009) including a 'memory' of six and nine previous months (hereafter SPEI6 and SPEI9 which represent drought on different time-scales) with the R package SPEI (Beguería and Vicente-Serrano 2013). Analogue to the tree-ring data, we detrended climate data with a 30-year cubic smoothing spline. Detrending ring width as well as climate data avoids erroneously lower/higher correlation coefficients between both variables because of similar/opposite long-term trends in climate and radial tree growth time-series data. We argue that long-term growth trends can hardly be attributed to single monthly climate variables, because such trends likely exist in multiple climate variables as well as in other environmental variables like atmospheric CO<sub>2</sub> concentration or nitrogen deposition. Therefore, only high-frequency signals were correlated for our analyses.

Similar to the host of studies analyzing climate effects on tree growth, we computed climate-growth correlations (Pearson correlation coefficients) for all climate variables of the previous and the current year and all age and size-class chronologies. In addition to these 'static' correlations, we assessed how climate sensitivity changed over time for each age/size class with moving-window correlations (window width = 31 years, 1 year offset). In the results, we focus on the correlations



**Fig. 1** Schematic illustration of the difference in the subsamples taken to create age-class chronologies: **a** tree-age method, **b** cambial-ring-age method. Individual trees are in columns A–O and colors mark different age classes. The ‘x’ marks the years with ring-width measurements available. The first ‘x’ in each column thus marks the

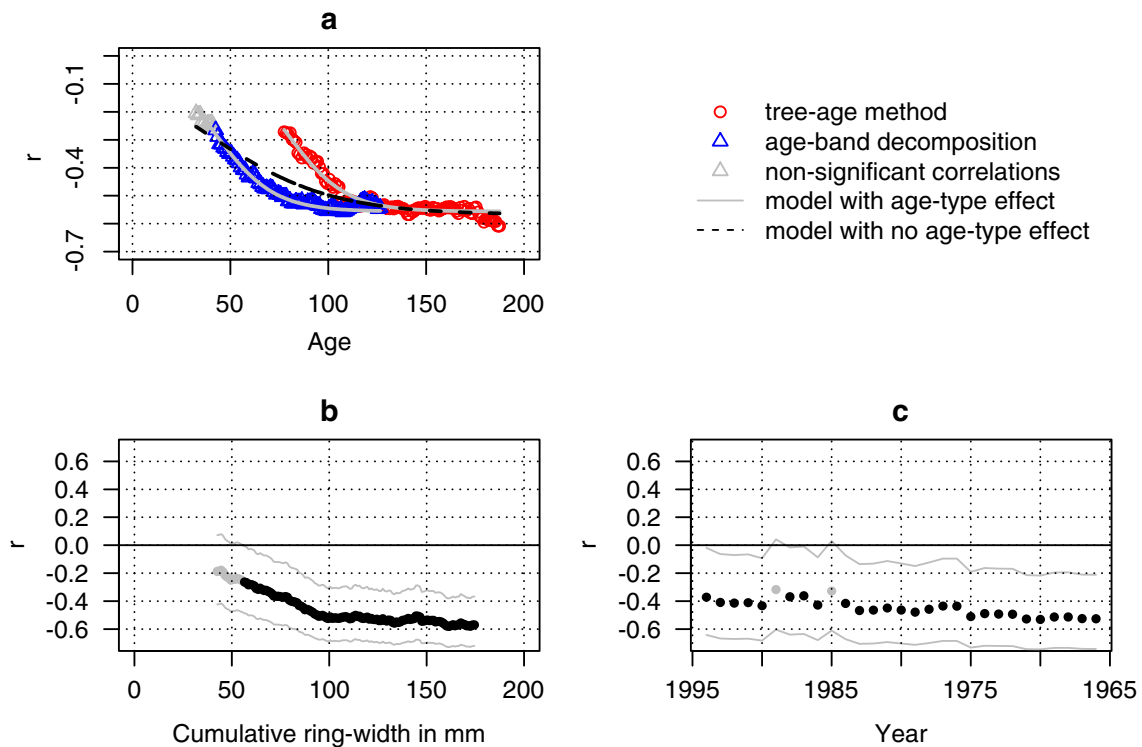
year of the pith and tree age is decreasing from left to right. If climate-growth correlations are calculated with climate data since 1981 (indicated by the black bar on the left) the data in the black frames are dropped

to previous year July temperature as the parameter with the highest significant correlations.

Lastly, we used a non-linear mixed effect model to test if the age-shifts in trees sensitivity to previous year July temperature occurs at a significantly different (earlier) age when using the age-band decomposition method, in contrast to the tree-age method: a three-parametric logistic function was fitted (ML) to the correlation coefficients (Fig. 2a) using the lme4 package in R (Bates et al. 2015) with the age method as random effect (categorical variable) that shifts the function along the  $x$  axis (age).

## Results

The three methods differ in their assessment on how climate sensitivity of trees changes as trees get older and larger. First, the tree age and ABD methods disagree at what age the climate sensitivity changes. In particular, the ABD method finds that these shifts happen at a younger age (Fig. 2a). According to the mixed model this age difference is significant, because when the age method was included as random effect (Fig. 2, solid grey lines) the AIC



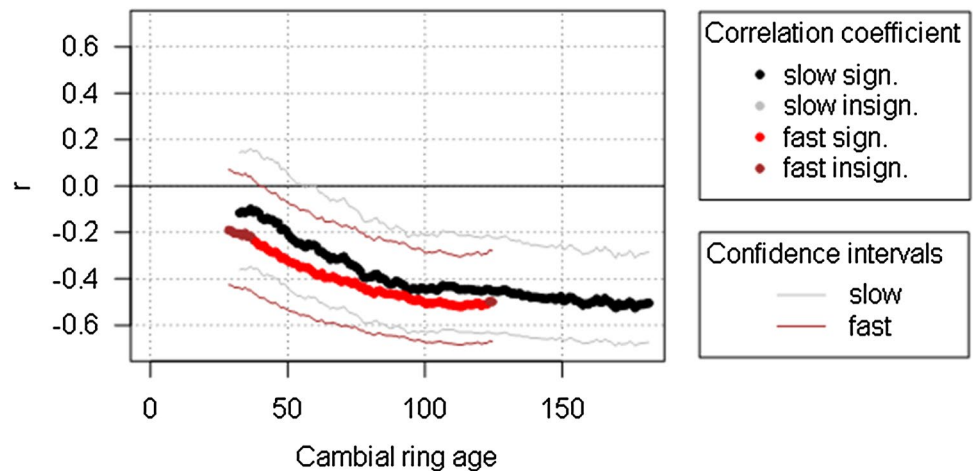
**Fig. 2** Correlations between previous July temperature and the tree-ring index of age classes based on the tree-age method and age-band decomposition (**a**). Lines show the predictions of the non-linear mixed effect model that was used test if the difference between both methods is significant. **b** Climate-growth correlations for stem diam-

eter classes (CRW method), respectively. In addition, moving-window (31 years) climate-growth correlations for the mean site chronology, including all age/size classes are shown (**c**). Grey points indicate insignificant correlations ( $p > 0.05$ ), grey lines in **b** and **c** mark the confidence intervals

was lower ( $-1105.3$ , in contrast to  $-622.5$ , black line, without this effect). This age lag approximates half the length of the climate data period used in the climate correlations and is connected to the fact that with the tree-age method, age in the selected classes increases with time, contrary to the ABD and CRW methods. For the same reason, the tree-age method appears to be able to assess

older age classes than the ABD method. The youngest-age classes on the other hand, are not covered by the tree-age method. This is important because pronounced changes in climate sensitivity were mostly detected in younger/smaller classes. The CRW method appears to perform very similar to the ABD method (Fig. 2b, c). However, in direct comparison, the CRW method generally appears to be a

**Fig. 3** Direct comparison of correlations between tree-ring indices with previous year July temperature of thicker (fast growing) and thinner (slow growing) trees of the same age. At the same age, larger trees show stronger climate correlations

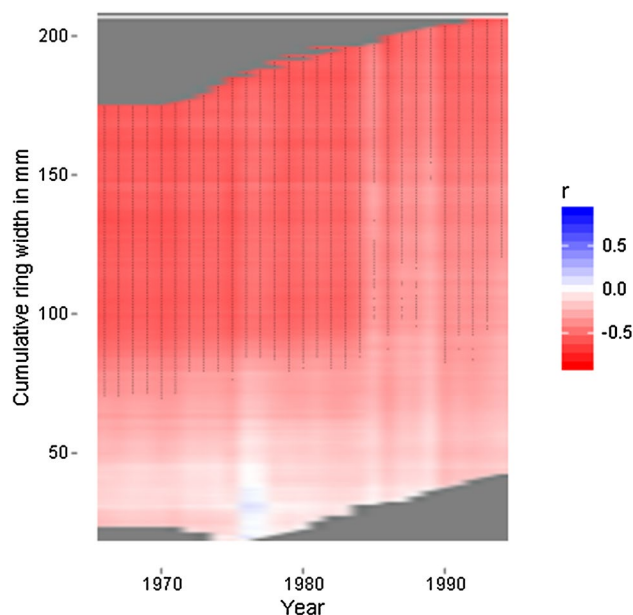




slightly better predictor of changes in climate-growth correlations: Fig. 3 directly compares climate sensitivity of small (slow growing) and large (fast growing) trees of the same age. In particular, larger trees showed stronger correlations with previous July temperature than smaller trees of the same age. This indicates that changes in climate sensitivity are more likely size- than age-related.

Climate-growth correlations with previous July temperature were stable over time but varied for other climate variables like previous year May temperature (S3 p. 103). This could be due to changes in the growth-limiting factor ('divergence problem') or due to low quality of the climate data, particularly further back in time when fewer climate stations were available. Lastly, we thus assessed a potential divergence problem with double moving-window correlations over (1) CRW classes and (2) calendar years. Figure 4 shows exemplarily for previous year July temperature that correlations with tree growth were relatively strong and stable throughout time for larger CRW classes while correlations for smaller classes were not significant.

The association between age, DBH and tree height was analyzed to assess if age and stem diameter generally are appropriate proxies for tree height, because tree height is assumed to have a direct effect on tree growth. Generally DBH and tree height were more closely associated with each other than with tree age (Fig. S1), indicating that trees have different growth speeds, and that rather stem diameters (like CRW) should be used as proxy for tree size and height.



**Fig. 4** Correlation matrix showing CRW class-specific sensitivity to previous year July temperature in each time period. Black dots mark significant correlations ( $p < 0.05$ ) and show that larger CRW classes showed relatively stable climate-growth correlation over time

In addition to previous July temperature, which showed one of the strongest climate-growth correlations at our study site, S3–S5 show the assessment for all 144 monthly climate variables. This allows a more complete description of white spruce' climate sensitivity at our study site and shows how the three methods performed, respectively.

## Discussion

### Method comparison

The ABD and the CRW methods had three major advantages over the most frequently applied tree-age method: (1) arguably most importantly, the ABD and CRW methods quantify only the pure age/size effect on climate sensitivity because these methods decouple aging and size increment from the temporal change of other variables like  $\text{CO}_2$  concentration or additional climate variables. Other variables can thus not overlay and bias these effects. (2) The ABD method more correctly identifies a shift in climate sensitivity at a younger age than the tree-age method, most likely, because the tree-age method does not decouple age from time. For example, correlating age class 80–100 with 50 years of climate data actually means that in the beginning of the 50-year long climate time series, the trees within this age class are only 30–50 years old. Consequently, the tree-age method erroneously stretches shifts in climate-growth correlations toward an older age. This delay approximates half the length of the climate data, in our example, 25 years. (3) The tree-age method cannot compute climate-growth correlations for age classes younger than the length of the climate data. For example, one cannot correlate tree-ring chronologies of 30-year old trees with 50 years of climate data, because it would require to drop 20 years from the correlation. Because of this effect only few studies using the tree-age method considered age classes below 100 years (Konter et al. 2016), where a lot of ontogenetic development takes place. The ABD and CRW methods are not affected by this bias and can assess even youngest ages/sizes. This is particularly important because in the first decades of a tree, height growth is strongest (Ryan et al. 2006) and the described height-related changes in climate sensitivity thus appears likely.

Our direct comparison supports previous studies that found size, not age, to be the cause of physiological changes in trees: At the same age, larger trees showed stronger climate-growth correlations in cases where climate sensitivity increased with age and weaker correlations in case correlations decreased with age. In our analysis, this effect appears relatively weak (difference in Pearson's  $r$  of about 0.1). However, because of sample size limitations we only could separate two size classes per age (fast and slow growing trees). It thus appears likely that the most extreme growth speed

differences, like 5% quantiles, would show much stronger differences in climate sensitivity of trees with the same age. We thus conclude that cumulative ring width should be used in future studies to explore size effects. This also is the logical consequence from previous studies that showed how tree height affects wood anatomy (Mencuccini et al. 2007; Carrer et al. 2015) and thus tree physiology and the fact that stem diameter (CRW) is closely related to tree height (Fig. S1 c).

### Size- and age-related changes in climate sensitivity

Climate correlations can either increase or decrease with size and age (Carrer and Urbinati 2004; Rozas et al. 2009; Konter et al. 2016), which points towards different mechanisms driving such changes. Higher climate sensitivity of taller and older trees is mostly found with moisture-related parameters like precipitation, SPEI or temperature-induced drought stress (Carrer and Urbinati 2004; Bond et al. 2007; Linares et al. 2013). This increased sensitivity of old trees to drought stress is in line with wood anatomical studies (Mencuccini et al. 2007; Petit et al. 2011) and the ‘hydraulic limitation hypothesis’ (Ryan and Yoder 1997; Ryan et al. 2006), reporting an increasing hydraulic resistance with height. In addition, changes in the position of a tree within a stand might lead to such effects (Mériani and Lebourgeois 2011). Once understory trees reach the canopy position, their more-exposed crown might cause a higher drought susceptibility. However in the sparse boreal forest of our study this effect is probably rather small.

Higher climate sensitivity of smaller and younger trees on the other side could be related to prolonged vegetation periods reported for smaller trees (Bond 2000; Day et al. 2002; Deslauriers et al. 2003; Rossi et al. 2008; Rathgeber et al. 2011; Zeng et al. 2018). This is also supported by our white spruce dataset, where young/small trees showed stronger correlations with shoulder season climate (e.g., previous year May temperature, S3 p. 103). However, further research with more species and climatic regions is required to come to general conclusions regarding climate signal size-effects. Likely these effects are highly species and site- dependent. For example, under dry climate but at sites with groundwater access, small trees might show higher correlations with precipitation because they have shallower root systems and no access to the groundwater yet.

### Methodological challenges and potential biases

The ABD and CRW methods require large sample sizes that might impede the use of these methods. To some extent both methods can be adjusted for lower sample sizes using wider age classes (20 years in this study) and lower minimum sample sizes ( $n = 15$  in this study), though, this will of course reduce the accuracy of the explored age and size effects.

We thus recommend that future fieldwork campaigns that aim at exploring age and size effects should sample several hundred, ideally  $> 500$  trees per site, including seedlings, saplings, and dead trees. When using the ABD or CRW methods to explore age and size effects samples should be corrected for coring height based on sampled seedlings and for pith offset, either based on offset-estimates or stem diameters at coring height. Not accounting for this will bias any correlation towards the correlation values of younger/smaller classes. The assessment of the books range dataset for example could be biased because no pith-offset estimates were available. While this problem could be avoided with the CRW method using measurements of the diameter at coring height and calculating past stem diameters from the bark to the pith, this was not possible for age estimates. It could thus be that changes in the climate sensitivity of the analyzed white spruce in the Brooks Range occurs at a somewhat older age.

Even though the ABD and CRW method decouple age from other temporal changes, for example in climate or atmospheric  $\text{CO}_2$  concentration, there are still potential biases left, in particular environmental gradients within study sites like the treeline in our study site. Figure S2 shows that the oldest and largest trees are only found towards the forest edge of the plot. Because climate sensitivity is usually assumed to be highest at the tree-line edge (Fritts 1976; Cook and Kairiukstis 1990), old tree-line edge trees could be underrepresented. However, this age and size gradient is relatively weak and mainly caused by a few old trees and a few trees at the tundra edge, thus we assume this to have little effect on our results.

### Applications

Our findings support that size rather than age affects a tree’s climate sensitivity. Consequently cumulative ring-width classes appear to be a promising tool for various research questions: Forest management techniques that aim to reduce competition for water (Callaway and Walker 1997; Allen et al. 2010; Bottero et al. 2017; Gleason et al. 2017) by reducing stem density already consider tree sizes, not age. In unmanaged forests self-thinning due to water stress (Wang et al. 2016) should be studied in relation to tree size. Research on treeline shifts related to climate change (Harsch and Bader 2011; Körner 2012; Jochner et al. 2017), can benefit from better understanding size specific climate sensitivity by identifying which size classes are suffering or profiting the most from climate changes. Old forests are reported to be carbon sinks (Knobl et al. 2003; Luyssaert et al. 2008), but the role of tree height on carbon accumulation is less clear. Climate reconstructions crucially depend on stable climate-growth correlations, thus shifts in the tree-size distribution

of the samples over time could bias climate reconstructions (Carrer and Urbinati 2004). On the other side, the climate signal could potentially be increased and reconstruction accuracy improved by only using the most sensitive CRW classes. In conclusion, the CRW method appears to be a very promising tool to explore a variety of different research questions related to trees, forests, and climate change.

**Author contribution statement** MT, TS, DW, AB and others collected the data. MT ran all analyses and drafted the first manuscript version. All authors discussed methodological details and the wider implications of age- and size-related climate sensitivity. All authors contributed to the draft and gave final approval for publication.

**Acknowledgements** This project was funded by the German Research Foundation (DFG) within the Research Training Group RESPONSE (DFG RTG 2010). We would like to thank Glenn Juday, Ryan Jess, and Jamie Hollingsworth for supporting our work and their expertise. Furthermore, we thank Jelena Lange, Renate Hefner, Franziska Eichhorn and Brook Anderson for their assistance during fieldwork, and two anonymous reviewers for comments that helped improving an earlier version of this manuscript.

## Compliance with ethical standards

**Conflict of interest** We declare that there are no conflicts of interest.

**Data archiving** All data will be uploaded to the international tree-ring database (ITRDB).

## References

- Allen CD, Macalady AK, Chenchouni H et al (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For Ecol Manag* 259:660–684. <https://doi.org/10.1016/j.foreco.2009.09.001>
- Babst F, Alexander MR, Szejner P et al (2014) A tree-ring perspective on the terrestrial carbon cycle. *Oecologia* 176:307–322. <https://doi.org/10.1007/s00442-014-3031-6>
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw*. <https://doi.org/10.18637/jss.v067.i01>
- Beguéría S, Vicente-Serrano SM (2013) SPEI: calculation of the standardised precipitation-evapotranspiration index. R Package Version 1
- Bond BJ (2000) Age-related changes in photosynthesis of woody plants. *Trends Plant Sci* 5:349–353. [https://doi.org/10.1016/S1360-1385\(00\)01691-5](https://doi.org/10.1016/S1360-1385(00)01691-5)
- Bond BJ, Czarnomski NM, Cooper C et al (2007) Developmental decline in height growth in Douglas-fir. *Tree Physiol* 27:441–453. <https://doi.org/10.1093/treephys/27.3.441>
- Bontemps J-D, Esper J (2011) Statistical modelling and RCS detrending methods provide similar estimates of long-term trend in radial growth of common beech in north-eastern France. *Dendrochronologia* 29:99–107. <https://doi.org/10.1016/j.dendro.2010.09.002>
- Bottero A, D'Amato AW, Palik BJ et al (2017) Density-dependent vulnerability of forest ecosystems to drought. *J Appl Ecol*. <https://doi.org/10.1111/1365-2664.12847>
- Bowman DMJS, Brien RJW, Gloor E et al (2013) Detecting trends in tree growth: not so simple. *Trends Plant Sci* 18:11–17. <https://doi.org/10.1016/j.tplants.2012.08.005>
- Briffa KR, Jones PD, Schweingruber FH et al (1996) Tree-ring variables as proxy-climate indicators: problems with low-frequency signals. In: *Climatic variations and forcing mechanisms of the last 2000 years*. Springer, Berlin, pp 9–41
- Briffa KR, Schweingruber FH, Jones PD et al (1998) Trees tell of past climates: but are they speaking less clearly today? *Philos Trans R Soc Lond B Biol Sci* 353:65–73. <https://doi.org/10.1098/rstb.1998.0191>
- Briffa KR, Osborn T, Schweingruber F et al (2001) Low-frequency temperature variations from a northern tree ring density. *J Geophys Res*. <https://doi.org/10.1029/2000JD900617>
- Bunn AG (2008) A dendrochronology program library in R (dplR). *Dendrochronologia* 26:115–124. <https://doi.org/10.1016/j.dendro.2008.01.002>
- Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78:1958–1965. [https://doi.org/10.1890/0012-9658\(1997\)078%5B1958:CAFASA%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078%5B1958:CAFASA%5D2.0.CO;2)
- Carrer M, Urbinati C (2004) Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology* 85:730–740. <https://doi.org/10.1890/02-0478>
- Carrer M, von Arx G, Castagneri D, Petit G (2015) Distilling allometric and environmental information from time series of conduit size: the standardization issue and its relationship to tree hydraulic architecture. *Tree Physiol* 35:27–33. <https://doi.org/10.1093/treephys/tpu108>
- Cook ER, Kairiukstis LA (eds) (1990) *Methods of dendrochronology*. Springer, Dordrecht
- D'Arrigo R, Wilson R, Liepert B, Cherubini P (2008) On the 'Divergence Problem' in Northern Forests: a review of the tree-ring evidence and possible causes. *Glob Planet Change* 60:289–305. <https://doi.org/10.1016/j.gloplacha.2007.03.004>
- Day ME, Greenwood MS, Diaz-Sala C (2002) Age- and size-related trends in woody plant shoot development: regulatory pathways and evidence for genetic control. *Tree Physiol* 22:507–513. <https://doi.org/10.1093/treephys/22.8.507>
- Deslauriers A, Morin H, Urbinati C, Carrer M (2003) Daily weather response of balsam fir (*Abies balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Québec (Canada). *Trees* 17:477–484. <https://doi.org/10.1007/s00468-003-0260-4>
- Esper J, Niederer R, Bebi P, Frank D (2008) Climate signal age effects—evidence from young and old trees in the Swiss Engadin. *For Ecol Manag* 255:3783–3789. <https://doi.org/10.1016/j.foreco.2008.03.015>
- Eusemann P, Schnittler M, Nilsson RH et al (2016) Habitat conditions and phenological tree traits overrule the influence of tree genotype in the needle mycobiome—*Picea glauca* system at an arctic treeline ecotone. *New Phytol* 211:1221–1231. <https://doi.org/10.1111/nph.13988>
- Fritts HC (1976) *Tree rings and climate*. The Blackburn Press, Caldwell
- Gärtner H, Nievergelt D (2010) The core-microtome: a new tool for surface preparation on cores and time series analysis of varying cell parameters. *Dendrochronologia* 28:85–92. <https://doi.org/10.1016/j.dendro.2009.09.002>
- Gleason KE, Bradford JB, Bottero A et al (2017) Competition amplifies drought stress in forests across broad climatic and compositional gradients. *Ecosphere*. <https://doi.org/10.1002/ecs2.1849>



- Harsch MA, Bader MY (2011) Treeline form—a potential key to understanding treeline dynamics. *Glob Ecol Biogeogr* 20:582–596. <https://doi.org/10.1111/j.1466-8238.2010.00622.x>
- Ibáñez I, Zak DR, Burton AJ, Pregitzer KS (2018) Anthropogenic nitrogen deposition ameliorates the decline in tree growth caused by a drier climate. *Ecology* 99:411–420. <https://doi.org/10.1002/ecy.2095>
- Jochner M, Bugmann H, Nötzli M, Bigler C (2017) Among-tree variability and feedback effects result in different growth responses to climate change at the upper treeline in the Swiss Alps. *Ecol Evol* 7:7937–7953. <https://doi.org/10.1002/ece3.3290>
- Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Glob Change Biol* 12:2163–2174. <https://doi.org/10.1111/j.1365-2486.2006.01250.x>
- King DA (1990) The adaptive significance of tree height. *Am Nat* 135:809–828. <https://doi.org/10.1086/285075>
- Knohl A, Schulze E-D, Kolke O, Buchmann N (2003) Large carbon uptake by an unmanaged 250-year-old deciduous forest in Central Germany. *Agric For Meteorol* 118:151–167. [https://doi.org/10.1016/S0168-1923\(03\)00115-1](https://doi.org/10.1016/S0168-1923(03)00115-1)
- Koch GW, Sillett SC, Jennings GM, Davis SD (2004) The limits to tree height. *Nature* 428:851–854. <https://doi.org/10.1038/nature02417>
- Konter O, Büntgen U, Carrer M et al (2016) Climate signal age effects in boreal tree-rings: lessons to be learned for paleoclimatic reconstructions. *Quat Sci Rev* 142:164–172. <https://doi.org/10.1016/j.quascirev.2016.04.020>
- Körner C (2012) Alpine treelines: functional ecology of the global high elevation tree limits. Springer, Basel
- Linares JC, Taïqui L, Sangüesa-Barreda G et al (2013) Age-related drought sensitivity of Atlas cedar (*Cedrus atlantica*) in the Moroccan Middle Atlas forests. *Dendrochronologia* 31:88–96. <https://doi.org/10.1016/j.dendro.2012.08.003>
- Luis MD, Novak K, Čufar K, Raventós J (2009) Size mediated climate–growth relationships in *Pinus halepensis* and *Pinus pinea*. *Trees* 23:1065–1073. <https://doi.org/10.1007/s00468-009-0349-5>
- Luyssaert S, Schulze E-D, Börner A et al (2008) Old-growth forests as global carbon sinks. *Nature* 455:213–215. <https://doi.org/10.1038/nature07276>
- Mencuccini M, Martínez-Vilalta J, Vanderklein D et al (2005) Size-mediated ageing reduces vigour in trees. *Ecol Lett* 8:1183–1190. <https://doi.org/10.1111/j.1461-0248.2005.00819.x>
- Mencuccini M, Hölttä T, Petit G, Magnani F (2007) Sanio's laws revisited. Size-dependent changes in the xylem architecture of trees. *Ecol Lett* 10:1084–1093. <https://doi.org/10.1111/j.1461-0248.2007.01104.x>
- Mérian P, Lebourgeois F (2011) Size-mediated climate–growth relationships in temperate forests: a multi-species analysis. *For Ecol Manag* 261:1382–1391. <https://doi.org/10.1016/j.forec.2011.01.019>
- Nicolussi K, Bortenschlager S, Körner C (1995) Increase in tree-ring width in subalpine *Pinus cembra* from the central Alps that may be CO<sub>2</sub> related. *Trees* 9:181–189. <https://doi.org/10.1007/BF00195270>
- Peters RL, Groenendijk P, Vlam M, Zuidema PA (2015) Detecting long-term growth trends using tree rings: a critical evaluation of methods. *Glob Change Biol* 21:2040–2054. <https://doi.org/10.1111/gcb.12826>
- Petit G, Anfodillo T, Carraro V et al (2011) Hydraulic constraints limit height growth in trees at high altitude. *New Phytol* 189:241–252. <https://doi.org/10.1111/j.1469-8137.2010.03455.x>
- Piutti F, Cescatti A (1997) A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. *Can J For Res* 27:277–284. <https://doi.org/10.1139/x96-176>
- Price DT, Cooke BJ, Metsaranta JM, Kurz WA (2015) If forest dynamics in Canada's west are driven mainly by competition, why did they change? Half-century evidence says: climate change. *Proc Natl Acad Sci* 112:E4340–E4340. <https://doi.org/10.1073/pnas.1508245112>
- R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rathgeber CBK, Rossi S, Bontemps J-D (2011) Cambial activity related to tree size in a mature silver-fir plantation. *Ann Bot* 108:429–438. <https://doi.org/10.1093/aob/mcr168>
- Rossi S, Anfodillo T, Menardi R (2006) Trephor: a New tool for sampling microcores from tree stems. *IAWA J* 27:89–97. <https://doi.org/10.1163/22941932-90000139>
- Rossi S, Deslauriers A, Gričar J et al (2008) Critical temperatures for xylogenesis in conifers of cold climates. *Glob Ecol Biogeogr* 17:696–707. <https://doi.org/10.1111/j.1466-8238.2008.00417.x>
- Rozas V, DeSoto L, Olano JM (2009) Sex-specific, age-dependent sensitivity of tree-ring growth to climate in the dioecious tree *Juniperus thurifera*. *New Phytol* 182:687–697. <https://doi.org/10.1111/j.1469-8137.2009.02770.x>
- Ryan MG, Yoder BJ (1997) Hydraulic limits to tree height and tree growth. *Bioscience* 47:235–242. <https://doi.org/10.2307/1313077>
- Ryan MG, Phillips N, Bond BJ (2006) The hydraulic limitation hypothesis revisited. *Plant Cell Environ* 29:367–381. <https://doi.org/10.1111/j.1365-3040.2005.01478.x>
- Sanio K (1872) Über die Grosse der Holzzellen bei der gemeinen Kiefer (*Pinus silvestris*). *Jb Wiss Bot* 8:401–420
- SNAP (2016) Scenarios network for Alaska and arctic planning. <http://ckan.snap.uaf.edu/dataset>. Accessed 28 July 2016
- Sullivan PF, Pattison RR, Brownlee AH et al (2017) Limited evidence of declining growth among moisture-limited black and white spruce in interior Alaska. *Sci Rep* 7:15344. <https://doi.org/10.1038/s41598-017-15644-7>
- Thomas H (2002) Ageing in plants. *Mech Ageing Dev* 123:747–753. [https://doi.org/10.1016/S0047-6374\(01\)00420-1](https://doi.org/10.1016/S0047-6374(01)00420-1)
- Vaganov EA, Hughes MK, Shashkin AV (2006) Growth dynamics of conifer tree rings: images of past and future environments. Springer, Berlin, Heidelberg
- Vicente-Serrano SM, Beguería S, López-Moreno JJ (2009) A multi-scalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J Clim* 23:1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>
- Vieira J, Campelo F, Nabais C (2009) Age-dependent responses of tree-ring growth and intra-annual density fluctuations of *Pinus pinaster* to Mediterranean climate. *Trees* 23:257–265. <https://doi.org/10.1007/s00468-008-0273-0>
- von Arx G, Carrer M (2014) ROXAS—a new tool to build centuries-long tracheid-lumen chronologies in conifers. *Dendrochronologia* 32:290–293. <https://doi.org/10.1016/j.dendro.2013.12.001>
- Wang Y, Pederson N, Ellison AM et al (2016) Increased stem density and competition may diminish the positive effects of warming at alpine treeline. *Ecology* 97:1668–1679. <https://doi.org/10.1890/15-1264.1>
- Williams AP, Xu C, McDowell NG (2011) Who is the new sheriff in town regulating boreal forest growth? *Environ Res Lett* 6:041004. <https://doi.org/10.1088/1748-9326/6/4/041004>
- Wilmking M, Buras A, Eusemann P et al (2017a) High frequency growth variability of White spruce clones does not differ from non-clonal trees at Alaskan treelines. *Dendrochronologia* 44:187–192. <https://doi.org/10.1016/j.dendro.2017.05.005>
- Wilmking M, Scharnweber T, van der Maaten-Theunissen M, van der Maaten E (2017b) Reconciling the community with a concept—the uniformitarian principle in the dendro-sciences. *Dendrochronologia* 44:211–214. <https://doi.org/10.1016/j.dendro.2017.06.005>

- Yu G, Liu Y, Wang X, Ma K (2008) Age-dependent tree-ring growth responses to climate in Qilian juniper (*Sabina przewalskii*). *Trees* 22:197–204. <https://doi.org/10.1007/s00468-007-0170-y>
- Zeng Q, Rossi S, Yang B (2018) Effects of age and size on xylem phenology in two conifers of Northwestern China. *Front Plant Sci.* <https://doi.org/10.3389/fpls.2017.02264>
- Zhang J, Huang S, He F (2015) Half-century evidence from Western Canada shows forest dynamics are primarily driven by competition followed by climate. *Proc Natl Acad Sci* 112:4009–4014. <https://doi.org/10.1073/pnas.1420844112>