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When trees don’t act their age: size-deterministic tree-ring standardization for long-tern trend estimation in shade-tolerant trees

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Abstract

With increasing awareness of the consequences of climate change for global ecosystems, the focus and application of tree-ring research has shifted to reconstruction of long-term climate-related trends in tree growth. Contemporary methods for removing the biological growth-trend from tree-ring series (standardization) are ill-adapted to shade-tolerant species, leading to biases in the resultant chronology. Further, many methods, including regional curve standardization (RCS), encounter significant limitations for species in which accurate age estimation is difficult. In this study we present and test two tree-ring standardization models that integrate tree size in the year of ring formation into the estimation of the biological growth-trend. The first method, dubbed size deterministic standardization (SDS), uses tree diameter as the sole predictor of the growth-trend. The second method includes the combined (COMB) effects of age and diameter. We show that both the SDS and COMB methods reproduce long-term trends in simulated tree-ring data better than conventional methods – this result is consistent across multiple species. Further, when applied to real tree-ring data, the COMB method is more parsimonious than its than RCS. We recommend the inclusion of tree size in the year of ring formation in future tree-ring standardization models, particularly when dealing with shade-tolerant species, as it does not compromise model parsimony and allows for the inclusion of unaged trees.

1 Introduction

Tree-rings have long-served as a record of environmental change in forest ecosystems. Early dendrochronological studies used tree-ring chronologies from climate sensitive species to elucidate the dynamics of growth-climate relationships and reconstruct climate anomalies from periods before the existence of instrumental records. However, with increasing awareness of the consequences of climate change for global ecosystems, the focus and application of tree-ring research has shifted to reconstruction of low-frequency climate related trends in tree growth (Gedalof and Berg 2010, Boisvenue and Running 2006, Jacoby and D'Arrigo 1997). As it stands, previous optimism regarding the benefits of carbon fertilization for forest growth (Battipaglia et al. 2012, Norby et al. 2005) has been quelled by a lack of consistent evidence in real forests. While many studies have noted increases in long-term growth rates over time in temperate forests (Gedalof and Berg 2010, Huang et al. 2007, Martinelli 2004) others suggest no change (Giguère-Croteau et al. 2019, Camarero et al. 2015, Granda et al. 2014, Silva et al. 2010, Peñuelas et al. 2011). Further, in boreal and drought prone species, growth decline (Chen et al. 2017, Dietrich et al. 2016, Girardin et al. 2012, Silva and Anand 2013) and increased mortality (Herguido et al. 2016, Liang et al. 2016) in response to climate stress have been prevalent. Central to all these studies is the assumption that long-term growth-trends can be accurately and unbiasedly estimated from tree-ring data.

As it stands, accurate estimation of long-term growth-trends in forests may be limited by poorly adapted tree-ring standardization (age-trend removal) methods (Briffa et al. 1996) and inappropriate sampling methods (Nehrbass-Ahles et al. 2014, Brienen et al. 2012). Early standardization methods (i.e. conservative detrending) were designed to maintain high-frequency variation in tree-ring series and discard long-term, low-frequency variation. It is accepted that these methods are inappropriate for estimating long-term climate related growth-trends (Briffa 1992); however, they are still used in situations where contemporary standardization methods are not applicable due to restrictive data requirements (e.g. Villalba et al. 2012, Gedalof and Berg 2010, Geoff Wang et al. 2006). More recently, the use of regional curve standardization (RCS), and its many variants, as well as the conversion of tree-ring widths to basal area increments (BAI) have become commonplace (Peters et al. 2015). But, due to the difficulties in separating

https://doi.org/10.5194/bg-2019-210
Preprint. Discussion started: 13 June 2019

climate related trends that vary on long time scales from those related to biological tree growth and/or succession-related environmental change, neither of these methods are likely to produce accurate estimates of external forcing when trees from only a single age/size class are sampled (Brienen et al. 2012, Briffa and Melvin 2011). While increased awareness of sample biases has led to better prescriptions for study design (see Nehrbass-Ahles et al. 2014, Brienen et al. 2012), systematic tests of the ability of these models to accurately reproduce long-term trends are limited (e.g. Sullivan et al. 2016, Peters et al. 2015, Esper 2010).

RCS remains the standard method for estimating long-term growth-trends in tree-ring data (Helama et al. 2017). However, the standard RCS approach encounters large limitations for many species in which accurate age estimation is difficult. Additionally, we suggest the inherent assumption of RCS that biological growth-trends are sufficiently determined by tree age may not be appropriate in all species. More specifically, this assumption is problematic for shade-tolerant trees. Shade-tolerant species exhibit relatively low low-light mortality and thus can persist in forest understories for variable amounts of time before release from overstory light suppression. In these cases, traditional age-deterministic models exhibit high variance, and thus low precision, in the period following tree establishment and leading up to the age when most trees have been released from suppression (Fig. 1). This period of ill-fit means that trees which are released relatively early (or late) from light suppression will exhibit inflated (or deflated) growth relative to the chronology. As a result, the final chronology will show less agreement than would be expected in a shade-intolerant species. Even more problematic, if trees are sampled according to minimum size thresholds, the youngest trees in the chronology are likely to be early-release trees leading to an artificial inflation of modern growth rates in the final chronology. While modifications to traditional RCS that address variance in contemporaneous growth rates and regional environmental conditions have been prevalent in shade-intolerant species (see Helama et al. 2017) there has been little to no focus on the improvement of standardization techniques specific to shade-tolerant tree species.

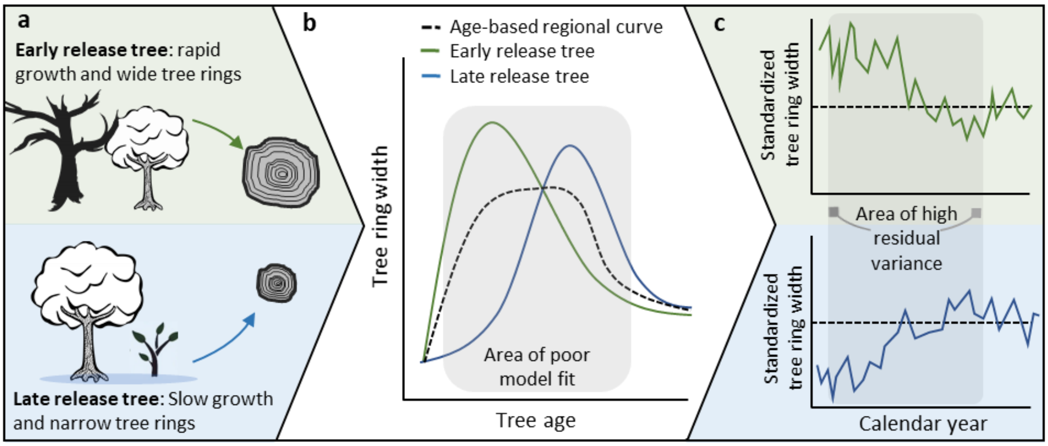

Figure 1: (a) In shade-tolerant species young trees are stochastically released from low-light suppression in the understory. (b) Since release from suppression is not strictly related to tree age, widely used communal age-trend models (RCS) poorly model tree growth in the period following establishment and leading up to the age when most trees have been released from suppression. (c) Poor model-fit in this period implies that the biological growth-trend is not entirely removed from individual series and leads to high residual variance when standardized tree-ring series are aligned according to calendar year.

Alternatively, in the field of forest growth and yield modelling, size, rather than age, deterministic predictive growth models are ubiquitous. It is well understood that tree size regulates the capacity for resource acquisition, namely, light (Canham et al. 2004), water and nutrients (Homann et al. 2000), resource allocation (Lehnebach et al. 2018) and metabolic costs (West et al. 2001). As such, the notion of radial growth being deterministic according to size rather than age is logical from both a physiological and ecological perspective. We propose that a size-deterministic model for tree-ring standardization may be more appropriate than traditional RCS for shade-tolerant tree species. The application of size-deterministic models has been limited, with few examples of tree size in a given year being incorporated into BAI models (e.g. Marqués et al. 2016, Camarero et al. 2015, Nock et al. 2011, Martínez-Vilalta et al. 2008) and even fewer of uniquely size-based tree-ring models (e.g. Bontemps and Esper 2011). Further, there have been no systematic evaluations of the ability of size-based models to accurately estimate long-term trends in tree-ring series.

We present two tree-ring standardization models that integrate tree size in the year of ring formation into estimation of the biological growth-trend. The first model uses tree diameter as the sole predictor of the communal growth-trend while the second includes the combined effects of both age and diameter. It follows that the objective of this study is to determine the efficacy of both models in estimating long-term growth-trends in their resultant tree-ring chronologies. First, we use modelled tree-ring data from shade-tolerant and intolerant species to make explicit the inappropriateness of age-based models for shade-tolerant trees. Further, we investigate the performance of size-based models relative to contemporary standardization methods in the presence of size thresholds in tree sampling. Last, we apply the developed models to tree-ring data from shade-tolerant temperate species to evaluate model performance relative to contemporary methods on the basis of model-fit and chronology quality statistics.

2 Methods

2.1 Model formulation

Traditional RCS makes two assumptions about tree growth. First that trees of the same species in a given region exhibit a common growth-trend as they age, and second, that growth of an individual tree in a given year is thus a product of its age and common climatic or environmental forcing in that year (Esper et al. 2003, Briffa et al. 1992). We present a variant of the RCS method that uses tree size, measured by diameter at breast height (DBH), in the year of ring formation as the primary determinant of the common biological growth-trend. As with RCS we assume that the relationship between expected growth and tree size is non-linear and can be approximated for a region from a sufficiently large sample of trees from the species in question.

https://doi.org/10.5194/bg-2019-210
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Further, we assume that using a sample of trees from a range of size/age classes ensures estimation of the common trend is not confounded by underlying low-frequency climate or environmental forcing in the chronology (Brienen et al. 2012). The size-based regional curve model, hereafter referred to as the **size deterministic standardization (SDS)** model, takes the following form:

$$(1)\ E(RW_{y,i}) = B_o + f_1(DBH_{y,i}) + e_{yi}$$

Where $E(RW_{yi})$ represents the expected ring width of a given tree (i) in year (y), and f_1 represents a non-linear function relating DBH of a given tree (i) in year (y) to $E(RW_{yi})$. The non-linear relationship is estimated using penalized spline fitting techniques in a generalized additive model (GAM). Under this paradigm the model residuals (e_{yi}) represent individual standardized ring width indices and, by extension, individual tree response to climatic or environmental forcing. Annual model residuals subject to a robust mean, thus, represent the final standardized chronology. This approach differs slightly from traditional RCS, whereby occasionally standardized ring width indices are produced by division of raw data by the expected value. Calculation of standardized ring width indices by subtraction from the expected value, as in the case of residuals, is now commonly used as it tends to reduce bias in the resultant chronology (Helama et al. 2004) and eases in the formulation of more complex tree-ring standardization models. However, unlike division methods, the subtraction method does not provide any stabilization of variance in the resulting residuals; as such, it may be necessary to use a stabilization procedure (i.e. log transformation, power transformation) on raw ring width data beforehand.

Tree size in a given year can be estimated by outside-in or inside-out techniques. If the pith of a tree is present in the core (or reasonably close to) DBH_y is a simple summation of all previous ring widths since the year of origin, multiplied by two. Alternatively, if the pith is missed, DBH_y can be calculated via subtraction of more modern ring widths (multiplied by two) from the inside-bark diameter. In this case inside-bark diameter is calculated as the measured DBH minus bark thickness (multiplied by two), where bark thickness can be directly measured or estimated using species-specific allometric equations (e.g. Stayton and Hoffman 1970).

Similar to the model formulation for SDS, RCS models were estimated with GAMs of the following form:

$$(2)\ \mathrm{E}(\mathrm{RW}_{yi}) = B_o + f_1(\mathrm{Age}_{yi}) + e_{yi}$$

Where Age_{yi} is the age of an individual tree in a given year and the resultant standardized tree-ring indices are derived from model residuals (e_{yi}).

In addition, a more complex model that integrated independent size and age effects was also evaluated for comparison. This model, hereafter referred to as the **combined model (COMB)**, took the following form:

$$(3)\ \mathrm{E}(\mathrm{RW}_{yi}) = B_o + f_1(\mathrm{Age}_{yia}) + f_2(\mathrm{DBH}_{yi}) + e_{iy}$$

In a large variety of long-lived tree species, accurate age estimation (pith sampling) is difficult or impossible; rendering traditional RCS or combined models inappropriate for all trees sampled. To address this issue, the above model incorporates unaged trees. Here f_1 represents the non-linear function relating age to expected ring width for the subset of all trees that are aged (ia). In this model, ring widths from unaged trees are assigned arbitrary ages which do not contribute to the linear approximation of the smooth term for Age (i.e. $f_1(\mathrm{Age}_{yia})$ but these trees still contribute to the smooth term for size f_2 (DBH_{yi}). Syntax for missing data in GAMs followed the protocol provided in mgcv (Wood 2011). In this study all GAMs were fit using the mgcv package (Wood 2011) in the R statistical program (v.3.5.0).

In addition to the models presented above we investigated two more contemporary standardization methods; conservative detrending (CD) and BAI. Conservative detrending describes functions (i.e. negative exponentials, straight lines) or flexible splines fit to individual tree-ring series. In this study we use spline fitting techniques rather than modified negative exponentials as they are more appropriate for shade-tolerant tree species. Alternatively, BAI attempts to remove biological growth-trends by converting ring widths from individual trees to estimates of annual basal area growth. For simplicity, untransformed BAI was used to compile chronologies for this study. Both CD and BAI methods were applied using the dplR package (Bunn 2008) in R.

2.2 Simulated tree-ring data

To evaluate the efficacy of each standardization method in detecting long-term trends, we simulated tree-ring data using a well-established gap-phase model. The SORTIE-ND model was chosen over other similar gap-phase models as it better emulates understory light conditions and low-light mortality both of which are central to the notion of age being an inappropriate determinant of growth in shade-tolerant species. For simplicity, a 100% sugar maple (*Acer saccharum)* dominated stand was simulated as sugar maple is a model shade-tolerant species that grows in self-replacing stands. All living trees (>5 cm dbh), (n=3657) in the final year of the model run were used for further analysis. Additionally, to elucidate our claim that age-deterministic growth estimation is more problematic in shade-tolerant species, we completed a similar SORTIE simulation for the shade-intolerant species white pine (*Pinus strobus*). Again, the stand was 100% white pine, standard model parameters were used, and the simulation was run for 1000 years. All living trees (>5 cm dbh), (n=7362) in the final year of the model run were used for further analysis. Additional details regarding model parameters for the SORTIE simulations are provided in the supplementary materials (Suppl. S1).

To simulate a low-frequency climate related growth-trend, a logistic trend was added to raw tree-ring width of individual trees produced by both SORTIE simulations. The logistic trend simulated an initial rapid increase in growth and subsequent levelling off that aimed to represent a period of carbon fertilization and eventual acclimation. The logistic model was applied to the last 100 years of growth and took the following form, where *RWt* represents ring widths with the simulated long-term trend and *RWr* are raw ring widths:

$$(4)\ RWt_{yi} = RWr_{yi} + \frac{0.6*\overline{RW}_i}{1+ae^{-r*y}}$$

The logistic trend parameters (*r*, *a*) were chosen such that increases in growth did not exceed 5% of individual average tree growth per decade.

Sixty trees were randomly selected, without replacement, from the simulated tree populations and subject to each of the five standardization methods (SDS, RCS, COMB, CD, BAI). Model residuals (in the case of RCS, SDS and COMB), and standardized (CD) or transformed (BAI) tree-ring widths were compiled into an annual mean chronology using Tukey's biweight robust mean. The resultant chronologies were then tested for significant correlation with the logistic growth-trend using Spearman's rank correlation coefficient. This process was bootstrap resampled 100 times to produce confidence intervals for correlation coefficients.

To examine the effect of minimum size sampling thresholds on the accuracy of long-term trend reconstruction by each of the standardization methods, we completed the same analysis on trees from the simulated populations that exceeded certain size thresholds. The thresholds employed were 10 cm DBH, which represented a practical minimum size threshold for sampling, and 30 and 50 cm DBH which represented thresholds for mature and dominant trees, respectively. The mean Spearman's rho for all detrending methods and sampling thresholds were compared using two-way ANOVA and post-hoc tests. Further, two-way ANOVA compared the effect of model choice on Spearman's rho between species (sugar maple and white pine).

2.3 Real tree-ring data

We evaluated the appropriateness of the SDS, COMB and RCS models for use in real tree-ring data from shade-tolerant species. We collected tree-ring data from seven mature sugar maple dominated stands in Ontario, Canada (Table 1). Further, tree-ring data sets from the shade-tolerant species red spruce (*Picea rubens*) were obtained from the DendroEcological Network database (https://www.uvm.edu/femc/dendro), (Table 1). Red spruce was chosen as it had sufficient replication across studies in the database. Descriptions of the sampling strategies and data processing methods for all sites considered are provided in either the supplementary materials (Suppl. S2) or in their respective references (i.e. Kosiba 2013, Kosiba 2017). Data was considered suitable for this study if age and DBH estimates were provided and if a minimum 20 trees per site and species were sampled. All cores in which pith offset was estimated to be greater than 10 years were considered unaged. The SDS, RCS, and COMB models were fit to tree-ring data from all site-species combinations and the resultant chronologies were compiled with a robust mean. In all cases models were fit to log-transformed ring widths, as it increased residual homoskedasticity. For simplicity and ease of model comparison we did not fit CD or BAI models to the real tree-ring data set.

Model fits from the SDS, RCS and COMB methods were compared according to Akaike information criterion (AIC) and percent variance explained (R^2). Since model comparison via AIC requires equal sample sizes, reduced data SDS (SDS_{red}) and COMB ($COMB_{red}$) models, which only included aged trees, were also fit. These reduced data models have no practical application but allow for direct AIC comparison between the RCS, $COMB_{red}$ and SDS_{red} models.

Table 1:
Location, sample size, chronology length and source of tree ring data sets used in this study.

Species	Site (code)	Longitude (°)	Latitude (°)	N. trees total	N. trees aged	Length of chronology	Source
Sugar maple (*A. saccharum*)	Toobee Lake (TB)	46.7459	-82.8668	79	67	1750-2015	This study
	Wolf Mtn. (WM)	46.7390	-82.8467	22	18	1827-2015	…
	Roosevelt Road (RS)	47.2852	-79.7063	20	11	1792-2016	…
	Raven Lake (RL)	45.3309	-78.6339	31	19	1864-2015	…
	Freezy Lake (FR)	45.2998	-78.4329	20	11	1887-2015	…
	Kakakise Lake (KK)	46.0554	-81.3317	22	7	1773-2016	…
	Mt. Zion Road (MT)	46.4000	-83.7004	29	15	1777-2015	…
Red spruce (*P. rubens*)	Mt. Mansfield (MTM)	44.3750	-73.8750	111	109	1769-2011	Kosiba et al. (2016)
	Burnt Mtn. (BNT)	44.2068	-72.3515	40	40	1891-2010	Kosiba et al. (2013)
	Mt. Carmel (CAR)	43.7709	-72.9205	41	41	1795-2010	…
	Mt. Ellen (ELL)	44.1656	-72.9221	42	42	1824-2010	…
	Mt. Equinox (EQU)	43.1487	-73.1273	89	89	1857-2010	…
	Mt. Greylock (GRY)	42.6738	-73.1575	44	44	1911-2010	…
	Hubbard Brook (HUB)	43.9577	-71.7350	89	89	1885-2010	…
	Killington Mtn. (KIL)	43.6146	-72.8088	104	103	1742-2010	…
	Mt. Mansfield (MAN)	44.5106	-72.8297	57	57	1767-2010	…
	Mt. Moosilauke (MOO)	44.0056	-71.8215	54	54	1760-2010	…
	Mad River Glen (MRG)	44.1932	-72.9232	36	36	1927-2010	…

Further, we calculated chronology quality statistics including: mean interseries-correlation, expressed population signal (EPS) and signal-to-noise ratio (SNR), for all chronologies.

Differences between model fit statistics and quality indices among models were tested using a linear mixed-effect modelling (LME) approach whereby, model error was specified according to site. This approach is analogous to traditional repeated-measures ANOVA but allows for contrast analysis between models.

3 Results

3.1 Comparisons of methods in simulated data

Bootstrapped correlations for chronologies produced by each standardization method are displayed in Figure 2a for the sugar maple and Figure 2b for white pine.

The sugar maple two-way ANOVA suggested a significant effect of both standardization model (p<0.001) and minimum size sampling threshold (p<0.001) on average correlation. Across all sampling thresholds the SDS model produced chronologies with the highest mean correlation ($\bar{r}_s$=0.972±0.024). Tukey HSD contrasts suggested mean correlation for the SDS model was significantly higher than all other models (p<0.001, all cases) except for the COMB model ($\bar{r}_s$=0.969±0.023), (p=0.993) which produced the second highest mean correlation. BAI produced the third highest mean correlation ($\bar{r}_s$=0.954±0.103) which was not significantly different from the combined model (p=0.61) but was significantly higher than correlations from the two remaining models (RCS and CD), (p<0.001). The CD ($\bar{r}_s$=0.720±0.153) and RCS ($\bar{r}_s$=0.925±0.054) models produced the lowest and second lowest correlations respectively; both were significantly different from each other and all other models (p<0.01, all cases).

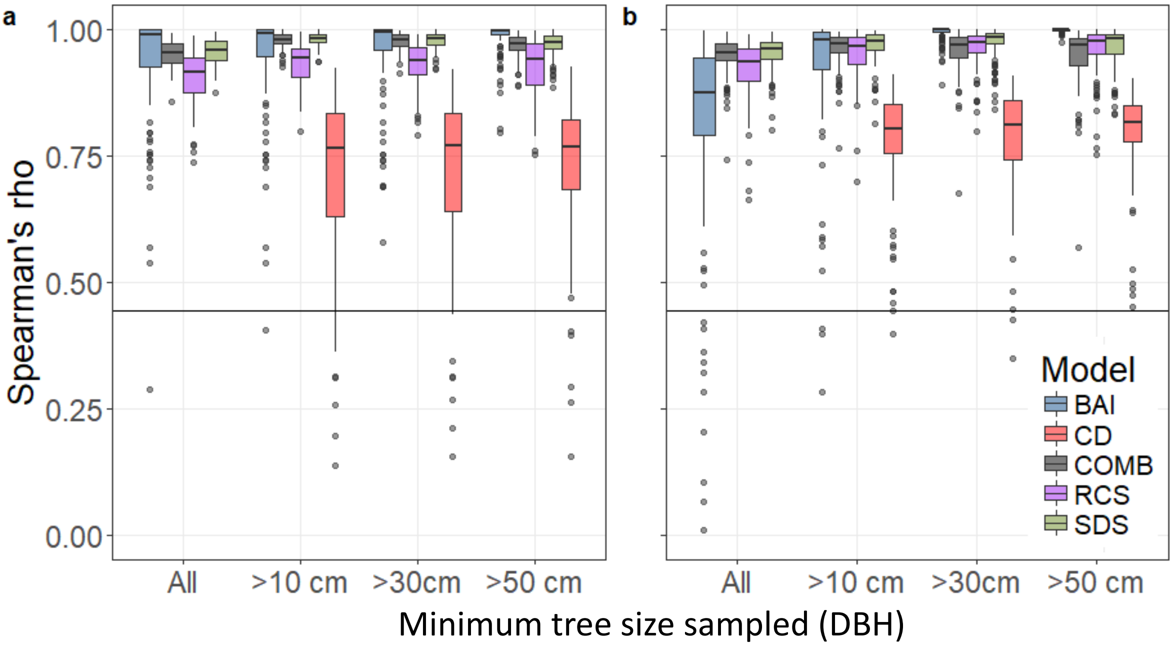

Figure 2: Spearman's rank correlation between chronologies produced by each of the five standardization methods and the imposed logistical trend in simulated (a) sugar maple and (b) white pine tree-ring data. Horizontal axis denotes minimum tree size (DBH) thresholds for sampling from the population.

Contrasts suggested that the significant effect of minimum size threshold was driven by significant differences in correlations between BAI produced chronologies among samples. As evident in Figure 2a, BAI chronologies performed best when size thresholds exceeded 50 cm DBH. At this threshold BAI chronologies produced significantly higher correlations than when all trees were sampled (p=0.002) and marginally significantly higher correlations than when trees >10 cm DBH were sampled (p=0.054). Contrastingly, the SDS, RCS, COMB and CD chronologies produced similar correlations across all minimum size thresholds. Bootstrapped sugar maple chronologies produced by each of the standardization methods are provided in Figure 3a.

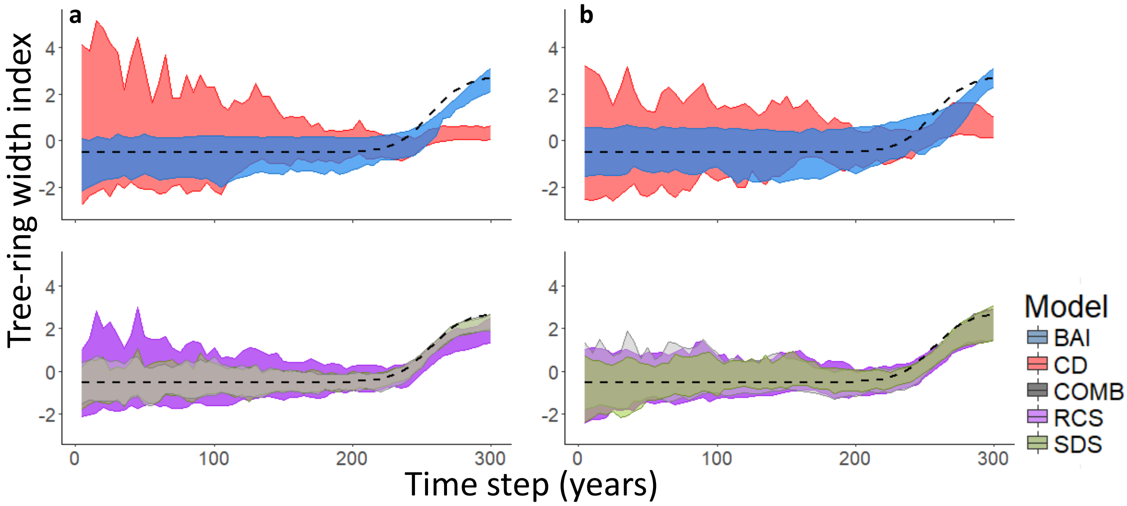

Figure 3: 95% confidence intervals for chronologies produced by each standardization method in SORTIE simulated (a) sugar maple and (b) white pine tree-ring data (Top: BAI, CD; Bottom: SDS, RCS, COMB). Confidence intervals were obtained via bootstrap resampling (rep=100) of 60 trees (>10 cm DBH) from the SORTIE simulated populations. Dotted lines indicate the logistic trend that was added to the raw tree-ring data. For ease of comparison all chronologies and the simulated trend were centred and scaled before plotting.

The white pine two-way ANOVA also suggested a significant effect of both standardization model ($p<0.001$) and minimum size sampling threshold ($p<0.001$) on average correlation. Across all size thresholds the SDS ($\overline{r_s}$=0.965±0.035), COMB ($\overline{r_s}$=0.954±0.037), and RCS ($\overline{r_s}$=0.949±0.049) models produced the highest correlations respectively. Among these, none were significantly different from each other. Again, chronologies produced by CD produced the lowest correlations of all models ($\overline{r_s}$=0.785±0.074), ($p<0.001$, all cases). BAI produced chronologies ($\overline{r_s}$=0.922±0.177) performed significantly worse than SDS, COMB and RCS chronologies and significantly better than CD ($p<0.001$, all cases). Tukey HSD contrasts suggested that the significant effect of minimum size threshold was again driven by significant differences in correlations between BAI produced chronologies among samples. As evident in Figure 2b, BAI chronologies performed significantly better when sampling size thresholds

https://doi.org/10.5194/bg-2019-210
Preprint. Discussion started: 13 June 2019

exceed 30 cm DBH (p<0.001, all cases). However, for BAI chronologies increased size thresholds of 50 cm DBH did not produce significantly higher correlations relative to the 30 cm DBH threshold (p=1.000). Bootstrapped white pine chronologies produced by each of the standardization methods are provided in Figure 3b.

When comparing mean correlations produced by each method between sugar maple and white pine, two-way ANOVA suggested a significant interaction between species and method (p<0.001). Tukey HSD contrasts suggested this effect is driven by significant differences in correlations produced by RCS, BAI and CD between species. More specifically, across all size thresholds RCS and CD produced significantly higher correlations in white pine relative to sugar maple (p=0.011, p<0.001, respectively). Whereas, BAI produced significantly higher correlations in sugar maple (p<0.001).

3.2 Comparisons of methods in real tree-ring data

The standardized partial predictors estimated for each of the SDS, RCS and COMB models fit to the sugar maple and red spruce data are provided in Figure 4. In general, SDS and RCS models suggested rather flat relationships between tree age and size with in average growth (log-transformed) in both species. However, when the effects of age and tree size were considered together in COMB models both showed more distinct relationships with average growth. In the COMB models average tree growth appeared to increase rapidly with tree size and eventually decline as trees exceed 50 cm DBH in both species. Average growth appeared to decline with increasing age before leveling off around 100 years. In both cases the COMB models showed better agreement among sites in small/young trees than the simpler models.

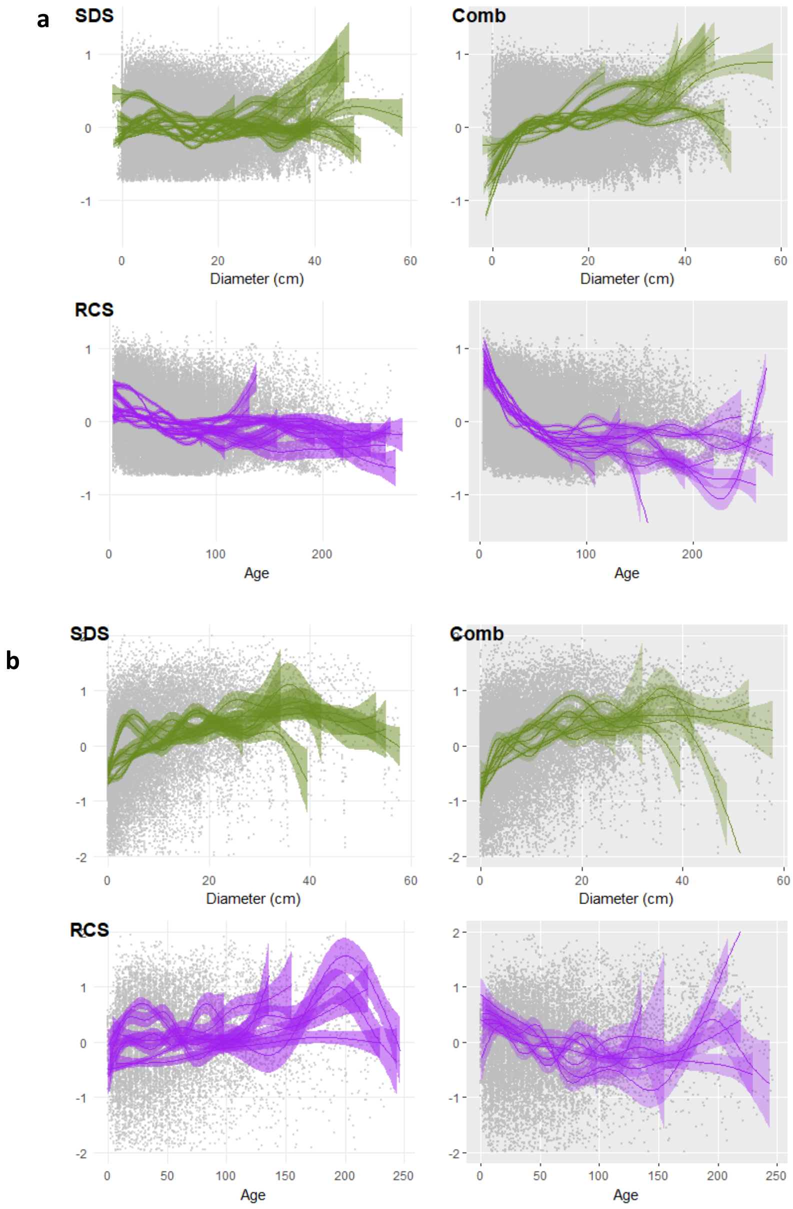

Figure 4: Standardized partial predictors of age (purple) and diameter (green) estimated by GAMs for the SDS, RCS (left) and COMB (right) standardization models for (a) sugar maple and (b) red pine tree-ring data. Ribbons represent 95% confidence intervals of the partial predictors.

In sugar maple, Tukey HSD contrasts suggested no significant differences in the meaningful AIC comparisons after controlling for site differences (Fig. 5a). However, R^2 produced by the COMB models were significantly higher than those produced by both the SDS (p=0.039) and RCS (p<0.001) models, but SDS and COMB were not significantly different from each other (p=0.177), (Fig. 5a). LMEs did not suggest a significant effect of model choice on any of the chronology quality statistics (mean interseries-correlation, SNR, EPS).

In red spruce, the COMB model fits exhibited significantly lower AIC values than the SDS model (p<0.001) after controlling for site differences (Fig. 5b). Similarly, the COMB_{red} model fits exhibited significantly lower AIC vales than the SDS_{red} (p<0.001) and RCS (p<0.001) models, while the SDS_{red} and RCS were not significantly different from each other (p=0.706), (Fig. 5a). Similarly, R^2 produced by the COMB models were significantly higher than those produced by both SDS (p<0.001) and RCS (p<0.001), which were not different from each other (p=0.114), (Fig. 5a). As with sugar maple LME did not suggest a significant effect of model choice on any of the chronology quality statistics.

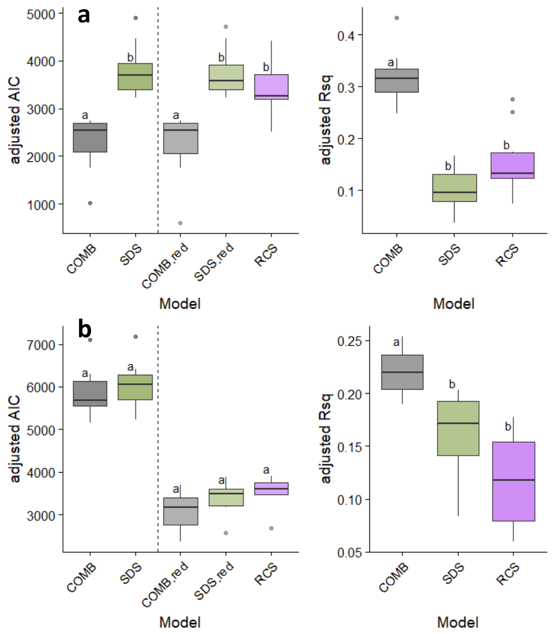

Figure 5: Adjusted AIC and R^2 values for fits of standardization models applied to (a) 7 sugar maple and (b) 11 red spruce tree-ring chronologies. Site-specific error was removed via a mixed modelling approach. Significant differences (a=0.05) between models are indicated with small letters (a, b). Dashed vertical lines signify meaningful pairwise AIC comparisons (i.e. COMB vs. SDS).

4 Discussion

4.1 Size-vs age-deterministic models for long-term trend reconstruction

https://doi.org/10.5194/bg-2019-210
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Using simulated tree-ring data, from the shade-tolerant species sugar maple, we have shown that standardization models which include tree size in the year of ring formation (SDS, COMB) produced chronologies that retain long-term/low-frequency variation better than those produced by models that only include age as a predictor (RCS). Alternatively, in the shade-intolerant species white pine, chronologies produced by the SDS, RCS and COMB models showed no significant difference in their estimation of long-term trends. Further, our analysis suggests that the traditional RCS method performed significantly worse in the shade-tolerant species, sugar maple, than in shade-intolerant white pine.

The finding that size-based standardization models performed well in simulated tree-ring data is not surprising given that the SORTIE model calculates annual tree growth as function of tree size. Thus, the underlying growth-trend would be well-approximated by a flexible curve estimated on the basis of tree size. As such, we use these results solely to elucidate the problematic nature of age-based standardization methods for shade-tolerant species. SORTIE's use of diameter, rather than age, as a determinant of tree growth is not arbitrary; it is well established that tree metabolic processes are directly related to size (West et al. 2001). Additionally, there is little evidence for a unique effect of age on tree growth that is independent of size (Munné-Bosch 2007 (and within)). With the exception of dendrochronological models, the vast majority of individual tree growth and process models are indeed size-based. It follows that the ubiquitous use of age or calendar year in tree-ring standardization methods (RCS, signal-free standardization, C-method, CD, Hugershoff curves) is a practice born out of convenience rather than physiological consideration. As such, we agree with previous accounts that this assumption may be especially problematic in shade-tolerant trees where age and size may not be perfectly correlated (Peters et al. 2015, Bontemps and Esper 2011).

Unfortunately, all systematic comparisons of tree-ring standardization methods in real tree-ring data (e.g. Sullivan et al. 2016) are limited by their inability to validate long-term trends estimated by chronologies. Instead, we evaluate standardization models on the basis of model parsimony. We have shown that in the shade-tolerant species red spruce, COMB models are significantly more parsimonious (estimated by AIC) than simpler models (RCS, SDS). Further, the COMB models explain more variance (estimated by R^2) in tree-ring data regardless of differences in underlying sample sizes. Overall, our results are conservative relative to similar comparisons performed by Nock et al. (2011) in tropical tree species of varying shade-tolerance. Nock et al. (2011) note that LMEs of BAI that included tree diameter had more support than those that included age. In line with discussion above, Nock et al. (2011) attribute this finding to size being a more important determinant of light capture as it relates to tree height and crown size (King et al. 2005). Further, in both red spruce and sugar maple we have shown that tree size and age exhibit stronger relationships with average growth when their unique effects are estimated simultaneously in COMB models rather than alone in SDS and RCS models, respectively. This result is interesting given the high correlation expected between these variables and it may explain why COMB models explained significantly more variance than each of the simpler models. Given the relatively weak trends shown in predictors from both the SDS and RCS, models we suggest that low-frequency variance related to the underlying biological growth-trend may be retained in these chronologies.

Regardless of differences in model fits, the implications for the resultant chronologies remain conservative (Fig. S.2). Similarly, in comparison of RCS and SDS chronologies in common beech (*Fagus sylvatica* L.) Bontemps and Esper (2011) note both chronologies exhibit similar annual variations. The resultant chronology is more likely to be influenced by sample size of the underlying tree population than by choice of standardization model. Tree age can be difficult or impossible to accurately estimate for some trees. In contrast, annual tree size can be reliability estimated from DBH and tree-ring measurements more ubiquitously. We note that in this study only 66% of sugar maple trees could be accurately aged. Since unaged trees are likely to be the oldest trees in the chronology, it follows that RCS chronologies may exhibit poor sample replication (especially in early years) and may be significantly shorter than those produced by SDS or COMB models. This has obvious implications for data quality and suitability. Considerably problematic is the "segment length curse" whereby, almost all standardization methods are ill-equipped to estimate long-term trends on time scales greater than or equal to the length of the chronology itself (Cook et al. 2005). Excessively short RCS chronologies are therefore limited in their application. A large advantage of SDS and COMB models is that they can incorporate otherwise inadmissible tree-ring data.

4.2 BAI and CD methods for long-term trend reconstruction

The finding that CD did not produce accurate long-term trends in simulated tree-ring data is consistent with our expectations (Peters et al. 2015, Briffa et al. 1992). We maintain CD should be avoided if the goal is long-term reconstruction from tree-ring data.

BAI chronologies accurately reproduced long-term trends in simulated tree-ring data. However, our analysis suggests BAI is less reliable when small/young trees are sampled. This was in line with Peters et al. (2015) who note high accuracy and sensitivity of BAI chronologies to imposed long-term trends, but that BAI is likely to produce erroneous trends when the underlying trend is of low signal, as would be the case for young/small trees that have low BAI rates and low climate sensitivity. As presented here, the BAI method imparts a strict relationship between tree size and growth. It has been suggested that this relationship may not account for the entire biological growth-trend (Peters et al. 2015). Accordingly, we caution future studies in their interpretation of BAI trends in low-signal tree-ring series. Alternatively, other studies have explicitly modelled size and/or age effects on BAI using a mixed-effect modelling approach (e.g. Marqués et al. 2016, Camarero et al. 2015, Nock et al. 2011, Martínez-Vilalta et al. 2008). We suggest this approach may better account for species- and site-specific factors that influence expected growth rates, leading to more accurate estimates of long-term trends in the resultant chronology. While our findings regarding the importance of inclusion of size in tree-ring standardization models are presented in the context of raw tree-ring width models, they are also directly relevant to explicit models of BAI.

4.3 Other considerations and future research

It is important to note that the goal of this study was not to explicitly test the effect of sample biases (i.e. modern sample bias, selection bias, etc.) on trend reconstruction, but instead to assess reliability across different underlying sampling distributions. There is now considerable evidence to suggest that the long-standing practice of sampling only dominant trees or trees exceeding a minimum size threshold within a stand leads to considerable bias in the resultant chronology (Nehrbass-Ahles et al. 2014, Brienen et al. 2012, Briffa and Melvin 2011). This bias is consistent across standardization methods (Nehrbass-Ahles et al. 2014). We maintain that in cases of long-term trend reconstruction, stands should be sampled according to the underlying stand age/size distribution, either through use of fixed-plots or random tree selection, regardless of the standardization procedure used.

Our study has suggested that the choice of standardization model (SDS, RCS, COMB) has no discernable effect on indices of chronology quality (EPS, SNR, interseries-correlation). We suggest this finding is a result of the chosen species exhibiting low climate sensitivity (Phipps

1982) and thus, low common signal in the chronology. As such we do not regard this finding as failure of any of the standardization models. We suspect more conclusive results would be found in climate sensitive species. Given the underlying physiological justification of the models presented here, we have no reason to suggest they are not broadly applicable to species of all shade-tolerance levels. We recommend future studies investigate the applicability of SDS and COMB models to both raw tree-ring width and BAI data in wider range of species. That said, shade-tolerant and broadleaf species, and their applicable standardization procedures, are underrepresented in dendrochronological studies (Zhao et al. 2019). We advocate for continued refinement of tree-ring standardization procedures that are relevant to the ecological questions they aim to address.

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References

Battipaglia, G., Saurer, M., Cherubini, P., Calfapietra, C., McCarthy, H. R., Norby, R. J., & Francesca Cotrufo, M.: Elevated CO 2 increases tree-level intrinsic water use efficiency: insights from carbon and oxygen isotope analyses in tree-rings across three forest FACE sites, New Phytol., 197(2), 544-554, 2013.

Boisvenue, C., & Running, S. W.: Impacts of climate change on natural forest productivity–evidence since the middle of the 20th century. Global Change Biol., 12(5), 862-882, 2006

Bontemps, J. D., & Esper, J.: 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(2), 99-107, 2011.

Brienen, R. J., Gloor, E., & Zuidema, P. A.: Detecting evidence for CO2 fertilization from tree-ring studies: The potential role of sampling biases. Global Biogeochem. Cycles, 26(1). 2012.

Briffa, K. R., Jones, P. D., Bartholin, T. S., Eckstein, D., Schweingruber, F. H., Karlen, W., ... & Eronen, M.: Fennoscandian summers from AD 500: temperature changes on short and long timescales. Climate Dyn., 7(3), 111-119, 1992.

Briffa, K. R., Jones, P. D., Schweingruber, F. H., Karlén, W., & Shiyatov, S. G.: Tree-ring variables as proxy-climate indicators: problems with low-frequency signals. In Climatic variations and forcing mechanisms of the last 2000 years (pp. 9-41). Springer, Berlin, Heidelberg, 1996.

Briffa, K. R., & Melvin, T. M.: A closer look at regional curve standardization of tree-ring records: justification of the need, a warning of some pitfalls, and suggested improvements in its application. In Dendroclimatology (pp. 113-145). Springer, Dordrecht. 2011.

Bunn, A. G.: A dendrochronology program library in R (dplR). Dendrochronologia, 26(2), 115-124, 2008.

Canham, C. D., LePage, P. T., & Coates, K. D.: A neighborhood analysis of canopy tree competition: effects of shading versus crowding, Can. J. For. Res., 34(4), 778-787, 2004.

Camarero, J. J., Gazol, A., Tardif, J. C., & Conciatori, F.: Attributing forest responses to global-change drivers: limited evidence of a CO 2-fertilization effect in Iberian pine growth, J. Biogeogr., 42(11), 2220-2233, 2015

Cook, E. R., Briffa, K. R., Meko, D. M., Graybill, D. A., & Funkhouser, G.: The 'segment length curse' in long tree-ring chronology development for palaeoclimatic studies, Holocene, 5(2), 229-237, 1995.

Chen, L., Huang, J. G., Dawson, A., Zhai, L., Stadt, K. J., Comeau, P. G., & Whitehouse, C.: Contributions of insects and droughts to growth decline of trembling aspen mixed boreal forest of western Canada, Global Change Biol., 24(2), 655-667, 2018.

Dietrich, R., Bell, F. W., Silva, L. C., Cecile, A., Horwath, W. R., & Anand, M.: Climatic sensitivity, water-use efficiency, and growth decline in boreal jack pine (Pinus banksiana) forests in Northern Ontario, J. Geophys. Res. Biogeosci, 121(10), 2761-2774, 2016.

Esper, J., Cook, E. R., Krusic, P. J., Peters, K., & Schweingruber, F. H.: Tests of the RCS method for preserving low-frequency variability in long tree-ring chronologies, Tree-Ring Res., 59(2), 81-98, 2003.

Gedalof, Z. E., & Berg, A. A.: Tree-ring evidence for limited direct CO2 fertilization of forests over the 20th century, Global Biogeochem. Cycles, 24(3), 2010.

Geoff Wang, G., Chhin, S., & Bauerle, W. L.: Effect of natural atmospheric CO2 fertilization suggested by open-grown white spruce in a dry environment, Global Change Biol., 12(3), 601-610, 2006.

Giguère-Croteau, C., Boucher, É., Bergeron, Y., Girardin, M. P., Drobyshev, I., Silva, L. C., ... & Garneau, M.: North America's oldest boreal trees are more efficient water users due to increased [CO2], but do not grow faster, Proc. Nat. Acad. Sci., 201816686, 2019.

Girardin, M. P., Bernier, P. Y., Raulier, F., Tardif, J. C., Conciatori, F., & Guo, X. J.: Testing for a CO2 fertilization effect on growth of Canadian boreal forests, J. Geophys. Res. Biogeosci, 116(G1), 2011.

Granda, E., Rossatto, D. R., Camarero, J. J., Voltas, J., & Valladares, F.: Growth and carbon isotopes of Mediterranean trees reveal contrasting responses to increased carbon dioxide and drought, Oecologia, 174(1), 307-317, 2014.

Helama, S., Lindholm, M., Timonen, M., & Eronen, M.: Detection of climate signal in dendrochronological data analysis: a comparison of tree-ring standardization methods, Theor. Appl. Climatol., 79(3-4), 239-254, 2004.

Helama, S., Melvin, T. M., & Briffa, K. R.: Regional curve standardization: State of the art, Holocene, 27(1), 172-177, 2017.

Herguido, E., Granda, E., Benavides, R., García-Cervigón, A. I., Camarero, J. J., & Valladares, F.: Contrasting growth and mortality responses to climate warming of two pine species in a continental Mediterranean ecosystem, For. Ecol. Manage., 363, 149-158, 2016.

Homann, P. S., McKane, R. B., & Sollins, P.: Belowground processes in forest-ecosystem biogeochemical simulation models, For. Ecol. Manage., 138(1-3), 3-18, 2000.

Huang, J. G., Bergeron, Y., Denneler, B., Berninger, F., & Tardif, J.: Response of forest trees to increased atmospheric CO2, CRC Crit. Rev. Plant Sci., 26(5-6), 265-283, 2007.

Jacoby, G. C., & D'Arrigo, R. D.: Tree-rings, carbon dioxide, and climatic change, Proc. Nat. Acad. Sci., 94(16), 8350-8353, 1997.

King, D. A., Davies, S. J., Supardi, M. N., & Tan, S.: Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia, Funct. Ecol., 19(3), 445-453, 2005.

Kosiba, A. M., Schaberg, P. G., Hawley, G. J., & Hansen, C. F.: Quantifying the legacy of foliar winter injury on woody aboveground carbon sequestration of red spruce trees, For. Ecol. Manage., 302, 363-371, 2013.

Kosiba, A. M., Schaberg, P. G., Rayback, S. A., & Hawley, G. J.: Comparative growth-trends of five northern hardwood and montane tree species reveal divergent trajectories and response to climate, Can. J. For. Res., 47(6), 743-754, 2017.

Lehnebach, R., Beyer, R., Letort, V., & Heuret, P.: The pipe model theory half a century on: a review, Ann. Bot., 121(5), 773-795, 2018.

Liang, E., Leuschner, C., Dulamsuren, C., Wagner, B., & Hauck, M.: Global warming-related tree growth decline and mortality on the north-eastern Tibetan plateau, Clim. Change, 134(1-2), 163-176, 2016.

Marqués, L., Camarero, J. J., Gazol, A., & Zavala, M. A.: Drought impacts on tree growth of two pine species along an altitudinal gradient and their use as early-warning signals of potential shifts in tree species distributions, For. Ecol. Manage., 381, 157-167, 2016.

Martinelli, N.: Climate from dendrochronology: latest developments and results, Glob. Planet. Change, 40(1-2), 129-139, 2004.

Martínez-Vilalta, J., López, B. C., Adell, N., Badiella, L., & Ninyerola, M.: Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions, Global Change Biol., 14(12), 2868-2881, 2008.

Munné-Bosch, S.: Aging in perennials, Crit. Rev. Plant Sci., 26(3), 123-138, 2007.

Nehrbass-Ahles, C., Babst, F., Klesse, S., Nötzli, M., Bouriaud, O., Neukom, R., ... & Frank, D.: The influence of sampling design on tree-ring-based quantification of forest growth, Global Change Biol., 20(9), 2867-2885, 2014.

Nock, C. A., Baker, P. J., Wanek, W., Leis, A., Grabner, M., Bunyavejchewin, S., & Hietz, P.: Long-term increases in intrinsic water-use efficiency do not lead to increased stem growth in a tropical monsoon forest in western Thailand, Global Change Biol., 17(2), 1049-1063, 2011.

Norby, R. J., DeLucia, E. H., Gielen, B., Calfapietra, C., Giardina, C. P., King, J. S., ... & De Angelis, P.: Forest response to elevated CO2 is conserved across a broad range of productivity, Proc. Nat. Acad. Sci., 102(50), 18052-18056, 2005.

Peñuelas, J., Canadell, J. G., & Ogaya, R.: Increased water-use efficiency during the 20th century did not translate into enhanced tree growth, Glob. Ecol. Biogeograph., 20(4), 597-608, 2011.

Peters, R. L., Groenendijk, P., Vlam, M., & Zuidema, P. A.: Detecting long-term growth-trends using tree-rings: a critical evaluation of methods, Global Change Biol., 21(5), 2040-2054, 2015.

Phipps, R. L.: Comments on the interpretation of climatic information from tree rinds, eastern North America, Tree-Ring Bulletin, 42,11-22, 1982.

Silva, L. C., & Anand, M.: Probing for the influence of atmospheric CO2 and climate change on forest ecosystems across biomes, Glob. Ecol. Biogeograph., 22(1), 83-92, 2013.

Silva, L. C., Anand, M., & Leithead, M. D: Recent widespread tree growth decline despite increasing atmospheric CO2, PloS one, 5(7), e11543, 2010.

Stayton, C. L., & Hoffman, M.: Estimating sugar maple bark thickness and volume (USDA Forest Service Research Paper NC-38), St. Paul, Minnesota: U.S., 1970.

Sullivan, P. F., Pattison, R. R., Brownlee, A. H., Cahoon, S. M., & Hollingsworth, T. N.: Effect of tree-ring detrending method on apparent growth-trends of black and white spruce in interior Alaska, Environ. Res. Lett., 11(11), 114007, 2016.

Villalba, R., Lara, A., Masiokas, M. H., Urrutia, R., Luckman, B. H., Marshall, G. J., ... & Allen, K.: Unusual Southern Hemisphere tree growth patterns induced by changes in the Southern Annular Mode, Nat. Geosci., 5(11), 793, 2012.

West, G. B., Brown, J. H., & Enquist, B. J.: A general model for ontogenetic growth, Nature, 413(6856), 628, 2001.

Wood, S. N.: Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models, J. R. Stat. Soc. Series B Stat. Methodol., 73(1), 3-36, 2011.

Zhao, S., Pederson, N., D'Orangeville, L., HilleRisLambers, J., Boose, E., Penone, C., ... & Manzanedo, R. D.: The International Tree-Ring Data Bank (ITRDB) revisited: Data availability and global ecological representativity, J. Biogeogr., 46(2), 355-368, 2019.