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A THEORY-DRIVEN APPROACH TO TREE-RING STANDARDIZATION: DEFINING THE BIOLOGICAL TREND FROM EXPECTED BASAL AREA INCREMENT

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ABSTRACT

One of the main elements of dendrochronological standardization is removing the biological trend, *i.e.* the progressive decline of ring width along a cross-sectional radius that is caused by the corresponding increase in stem size and tree age over time. The “conservative” option for removing this biological trend is to fit a modified negative exponential curve (or a straight line with slope ≤ 0) to the ring-width measurements. This method is based on the assumption that, especially for open-grown and/or shade-intolerant species, annual growth rate of mature trees fluctuates around a specific level, expressed by a constant ring width. Because this method has numerical and conceptual drawbacks, we propose an alternative approach based on the assumption that constant growth is expressed by a constant basal area increment distributed over a growing surface. From this starting point, we derive a mathematical expression for the biological trend of ring width, which can be easily calculated and used for dendrochronological standardization.

The proposed C-method is compared to other standardization techniques, including Regional Curve Standardization (RCS), of tree-ring width from ponderosa pines (*Pinus ponderosa* Douglas ex P.Lawson & C.Lawson) located at the Gus Pearson Natural Area (GPNA) in northern Arizona, USA. Master ring-index chronologies built from ring area, RCS, and C-method reproduced stand-wide patterns of tree growth at the GPNA, whereas other standardization options, including the “conservative” one, failed to do so. In addition, the C-method has the advantage of calculating an expected growth curve for each tree, whereas RCS is based on applying the same growth curve to all trees. In conclusion, the C-method replaces the purely empirical “conservative” option with a theory-based approach, which is applicable to individual ring-width measurement series, does not require fitting a growth curve using nonlinear regression, and can be rigorously tested for improving tree-ring records of environmental changes.

Keywords: Tree growth, forest ecology, ring width, regional curve standardization, ponderosa pine, Gus Pearson Research Area.

INTRODUCTION

Through proper site and species selection, dendrochronologists have generated a wealth of annually resolved, multi-century long, well replicated tree-ring chronologies (Grissino-Mayer and Fritts 1997) that have been used to analyze, and then reconstruct, patterns of environmental change at local, regional, and hemispheric scales

(Bradley 1999; National Research Council 2006). Tree-ring records allow for a large degree of sample replication and internal data quality control, as ring-width series are crossdated by comparing and matching high- and low- frequency patterns from one specimen to another (Douglass 1941; Holmes 1983). Once crossdated, individual series are standardized and combined into a single tree-ring chronology to provide a synthetic representation of historical trends. The final tree-ring chronology is a discrete time series

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of standardized indices, which can be used to represent growth variability for a given forest species and geographical area (Cook and Kairiukstis 1990).

At the heart of tree-ring standardization is the fact that, as trees grow older and increase in size, annual ring width generally decreases along a cross-sectional radius, mostly because of the geometrical constraint to add new wood layers over an expanding surface (Douglass 1919; Fritts 1976; Cook 1987). In shade-intolerant, open-grown trees, this trend dominates the temporal sequence of annual wood formation throughout the life history of the tree (Husch *et al.* 2003; Helama *et al.* 2005). In shade-tolerant forest-interior trees, this period of ring-width decline normally occurs after the tree has become dominant, and is commonly preceded by one or more periods of growth suppression and release while the tree occupies lower canopy levels (Canham 1990; Fraver and White 2005; Piovesan *et al.* 2005). Regardless of their overall shape, such individual growth trends are associated with a change in the year-to-year ring-width variation, so that when ring widths are larger, their variability is larger as well (Cook and Peters 1997). A number of techniques have been proposed in the literature to remove growth variations in both mean and variance that are specific to an individual tree, *i.e.* to “standardize” ring-width series prior to combining them into a master chronology (Cook and Kairiukstis 1990; Warren and Leblanc 1990; Biondi 1993). Most of these techniques require the elimination of the biological trend by fitting a curve to the raw ring-width measurements. ‘Standardized indices’ are then computed as ratios between the measurement and the fitted curve value, although variance-stabilized residuals have also been used (Biondi 1992; Cook and Peters 1997; Helama *et al.* 2004). Other methods do not require the elimination of the biological trend, or even the numerical computation of a master tree-ring chronology, because they are based on the identification and interpretation of sudden changes in ring-width measurements (Schweingruber *et al.* 1990; Desplanque *et al.* 1999).

Recently, debate has focused on which standardization option should be used to retain

climatic variability at long timescales, *i.e.* “low-frequency” modes (Esper, Cook *et al.* 2003; Bunn *et al.* 2004; Esper *et al.* 2005; Helama *et al.* 2005; National Research Council 2006; Melvin *et al.* 2007). In fact, the length of individual ring-width series used to produce a master chronology (rather than the length of the chronology itself) can determine the maximum timescale of retrievable climatic fluctuations (Cook *et al.* 1995). A potential solution to this issue is to compute the expected value of the tree-ring parameter (width, density, *etc.*) as a function of biological age (that is, years since pith formation), then to use the resulting growth curve to standardize the individual tree-ring series. This method, now called Regional Curve Standardization (RCS), was first proposed in the 1930s (Grudd *et al.* 2002), later described by Fritts (1976), and finally made popular by Becker (1989) and Briffa *et al.* (1992). This technique is theoretically appealing, and widely employed in dendroclimatic reconstructions (Esper *et al.* 2002; Grudd *et al.* 2002; Gunnarson and Linderholm 2002; Helama *et al.* 2002; Naurzbaev *et al.* 2002; Esper, Shiyatov *et al.* 2003; Büntgen *et al.* 2005; D’Arrigo *et al.* 2005, 2006). On the other hand, because most core samples do not include the pith, the RCS curve is usually calculated assuming that the innermost ring of each segment has biological age equal to one (Briffa *et al.* 1992). Because this assumption can generate large errors, especially when sampling old trees with irregular stems, accurately computing the regional growth curve “requires large amounts of tree growth data representing a wide range of different tree ages, each distributed widely through time and all drawn from a single species in a relatively small region” (Briffa *et al.* 2001). Considering this RCS limitation, the method of fitting smooth curves to individual ring-width series can still be preferred for standardization purposes (Frank and Esper 2005); an alternate procedure called “age banding” has also been suggested (Briffa *et al.* 2001; Collins *et al.* 2002).

As a contribution to the debate on tree-ring standardization, we have focused on those methods that remove the biological trend by fitting a modified negative exponential function or a

straight line with slope ≤ 0 to individual ring-width series. This option is commonly implemented through the software program ARSTAN (Cook and Holmes 1986), and is widely adopted in dendrochronological investigations under the loose term of “conservative” detrending (Villalba *et al.* 1998; Salzer and Kipfmüller 2005; Woodhouse and Lukas 2006). Historically, this method was developed at the Laboratory of Tree-Ring Research in Tucson, Arizona, where a large portion of wood specimens being analyzed was from open-grown and/or shade-intolerant species (Webb 1983; Nash 1999). As explained by Cook (1985, p. 2–3), “After a common short-lived increase in radial growth following germination, the growth increment curve of such open-grown trees reaches a maximum and then declines monotonically with increasing age to a relatively constant growth rate”, so that “the age trend is composed of two fairly distinct periods: an early youthful period where growth rate declines linearly with age, and a later mature period of equilibrium with the environment where the level of growth is constant over time” (p. 14). In other words, the conservative detrending option assumes that annual growth rate of mature trees fluctuates around a specific level, which is expressed by a constant ring width. As shown in the Model Specification section, this assumption is encapsulated by the asymptote of the modified negative exponential curve, and even more so by the horizontal line through the mean, which are used to conservatively standardize ring-width series.

Decades of forest ecology research have shown that another measure of radial tree growth, *i.e.* annual basal area increment, or ring area (LeBlanc 1990), is well suited to represent individual and stand-level changes (LeBlanc and Foster 1992; Bigler and Bugmann 2003; Piovesan *et al.* 2008; Voelker *et al.* 2008; Weber *et al.* 2008). The computation of basal area increment (BAI) is based on assuming that ring circumference can be approximated by a circle. Despite this imperfect premise, a surface (*i.e.* two-dimensional measure, such as BAI or ring area, represents overall tree growth (*i.e.* a volume, or three-dimensional measure) better than a linear (*i.e.* one dimension-

al) measure, such as stem diameter increment or ring width (Valentine 1985; LeBlanc 1990; Bigler and Bugmann 2003; Husch *et al.* 2003). To see how this might be the case, one can also consider the direct outcome of a constant ring width model: this assumption implies a constant increase of basal area increment over time. Although this pattern is occasionally found in nature (Phipps 2005), it is at odds with modern knowledge of tree biology and forest ecology. A number of studies have shown that BAI of dominant trees can rise for varying periods of time during their life, but even in the best growing conditions, BAI of mature, healthy trees approaches a constant level, and then declines when trees become stressed (Pedersen 1998; Duchesne *et al.* 2002; Poage and Tappeiner II 2002; Duchesne *et al.* 2003; Elvir *et al.* 2003; Valentine and Mäkelä 2005).

In this article we propose to replace the conservative standardization option with a method mathematically derived from the explicit assumption of distributing a constant basal area increment over an expanding stem surface. By formally describing this process, a purely empirical approach to tree-ring standardization is replaced with a theoretical one. An illustration of the method, and a comparison with other standardization options, including the RCS technique, is provided using data from pine trees located at the Gus Pearson Natural Forest Area, in western North America.

MODEL SPECIFICATION

A mathematical representation of the modified negative exponential option for ring-width standardization is as follows (Fritts 1976, p. 263):

$$w_t = ae^{-bt} + k \quad (1)$$

where w_t is ring width at year t , a is ring-width at year zero (if k is negligible), b is the slope of the decrease in ring width (hence, the “concavity” of the curve), and k is the minimum ring width, which is asymptotically approximated for large values of t . When the estimated value of either a or b is negative, a linear regression is fit

to the data, usually with slope ≤ 0 (Fritts *et al.* 1969; Cook and Holmes 1986). Historically, the asymptote of the modified negative exponential equation was introduced to allow for the relatively constant ring width of very old conifers in the western USA (Fritts *et al.* 1969), especially those that are capable of attaining a ‘strip-bark’ growth form, characterized by a band of trunk that remains alive and continues to grow after the rest of the stem has died (Schulman 1954; Matthes *et al.* 2002). This modification of the negative exponential equation, however, makes it “open form” because fitting this model is equivalent to estimating a nonlinear regression equation, hence model parameters are computed iteratively (Press *et al.* 2002). This implies that the method is sensitive to several choices made for estimation purposes. For instance, depending on the tolerance assigned for the goodness-of-fit statistic, the starting values, the number of iterations allowed, and the resolution of the incremental changes made to the initial parameter values, different results can be obtained. In other words, instead of fitting a modified negative exponential, a straight line could be selected simply because of numerical instabilities. This can have important consequences, especially if the estimated curve parameters are then used for drawing climatic or ecological inferences (as was done by Helama *et al.* 2005).

Even more relevant for tree-ring standardization is the presence of an asymptote in equation 1, given its implications for basal area increment (BAI), as mentioned above. Because BAI at year t is equivalent to annual ring area (Tessier 1986; Phipps and Whiton 1988; LeBlanc 1993; Biondi 1999), one can write

$$BAI_t = \pi R_t^2 - \pi R_{t-1}^2 \quad (2)$$

where R_t is the stem radius at the end of the annual increment, and R_{t-1} is the stem radius at the beginning of the annual increment (Figure 1). Considering that annual ring width (w_t) is equivalent to the annual increment of tree radius ($w_t = R_t - R_{t-1}$), it follows that

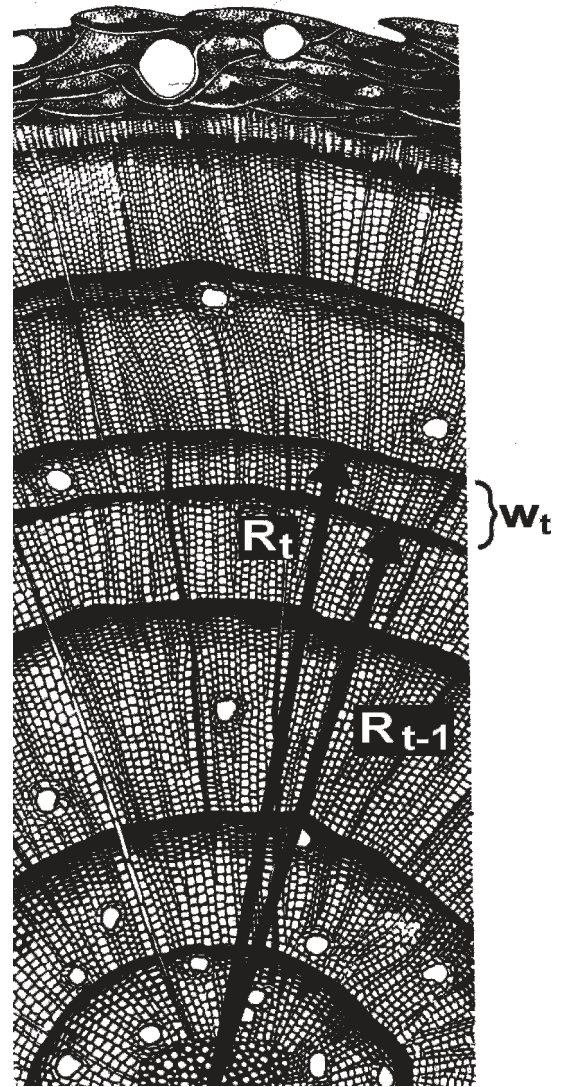


Figure 1. Schematic representation of a conifer cross section, modified from Figure 2.3 of Fritts (1976). At each year, annual ring width (w_t) is equal to the difference between the current tree radius (R_t , longer arrow) and the prior year radius (R_{t-1} , shorter arrow).

$$BAI_t = \pi (w_t^2 + 2 w_t R_{t-1}) \quad (3)$$

From equation 3 it is possible to see that BAI increases with ring width, and that when ring width is assumed to be constant, as in the horizontal line standardization option,

basal area increment becomes progressively larger over time, which is a biologically untenable result (as mentioned above).

Given the numerical and conceptual drawbacks of conservative standardization, we propose an alternative approach based on the assumption that constant radial growth is expressed by constant basal area increment, rather than constant diameter increment. The biological trend of ring width can then be estimated using this simple assumption, namely that a constant tree-ring area is distributed over a growing surface over time. From the definition of BAI_t given in equation 3, the assumption of constant BAI_t can be written as

$$w_t^2 + 2w_tR_{t-1} = c \tag{4}$$

with c being the constant BAI. It is easily shown that (4) is a quadratic equation in the variable w_t , and that the only logical solution (given that $w_t \geq 0$) is as follows:

$$w_t = -R_{t-1} + \sqrt{R_{t-1}^2 + c} \tag{5}$$

Considering that R_{t-1} is the sum of all ring widths from year 0 (the pith date) to year $t-1$, one can write

$$w_t = \sqrt{\left(\sum_{i=0}^{i=t-1} w_i\right)^2 + c} - \sum_{i=0}^{i=t-1} w_i \tag{6}$$

For $t = 0$ there is yet no ring width, hence an expression of the *tree potential for growth* can be derived from the previous equation, as follows:

$$w_0 = \sqrt{c} \tag{7}$$

At time 1, using equations 6 and 7, the expected ring-width is then given by

$$\begin{aligned} w_1 &= \sqrt{w_0^2 + c} - w_0 \\ &= \sqrt{c + c} - \sqrt{c} \\ &= \sqrt{2c} - \sqrt{c} \end{aligned} \tag{8}$$

At time 2, using equations 6 through 8, the expected ring-width becomes:

$$\begin{aligned} w_2 &= \sqrt{(w_0 + w_1)^2 + c} - (w_0 + w_1) \\ &= \sqrt{w_0^2 + w_1^2 + 2w_0w_1 + c} - (\sqrt{c} + \sqrt{2c} - \sqrt{c}) \\ &= \left[c + (\sqrt{2c} - \sqrt{c})^2 + 2\sqrt{c}(\sqrt{2c} - \sqrt{c}) + c \right]^{1/2} - \sqrt{2c} \\ &= \left[c + (2c + c - 2\sqrt{c}\sqrt{2c}) + 2c\sqrt{2} - 2c + c \right]^{1/2} - \sqrt{2c} \\ &= \sqrt{3c - 2c\sqrt{2} + 2c\sqrt{2} - \sqrt{2c}} \\ &= \sqrt{3c} - \sqrt{2c} \end{aligned} \tag{9}$$

By extending the procedure used in equations 6 through 9, it is straightforward to verify that, for any biological ring age t (=number of years since pith formation), the *expected ring width* (Ew_t) when *basal area increment remains constant* is given by

$$Ew_t = \sqrt{c(t+1)} - \sqrt{ct} \tag{10}$$

This relationship implies that the biological trend in ring-width of mature trees can be removed by knowing the value of c , which, in turn, can be mathematically derived from equation 10, with the following result:

$$c = \frac{(Ew_t)^2}{2t + 1 - 2t\sqrt{1 + \frac{1}{t}}} \tag{11}$$

Despite the relative simplicity of the initial assumption from which equations 10 and 11 have been derived, these mathematical findings represent an important theoretical result that has not been previously published in the peer-reviewed literature. It is also important to note that the proposed standardization method, although it does not require fitting a nonlinear model to the time series of ring-width measurements, still

generates the nonlinear, monotonically decreasing pattern eloquently described by Cook (1985). Although this could be considered intuitive, given the assumption of distributing the same amount of basal area increment over an ever expanding stem, it is worth repeating that the method is best suited for open-grown, shade-intolerant trees, whose growth is characterized by a rapid decrease of ring width during the early stages of tree growth, which is then followed by a progressively more and more gradual decline as the tree becomes older and larger.

For estimation purposes, it is necessary to calculate the value of c . This could be done in multiple ways, either using forest inventory data, or directly from the ring-width series themselves. In the latter case, one could use all available measurements, or only the part of the ring-width series that is not influenced by the juvenile increase. To maintain the possibility of standardizing individual samples, we propose estimating c separately for each ring-width measurement series. Obviously, no matter which estimation method is used, it is necessary to determine the biological age (= number of years since pith formation) of the innermost ring for each sample used in the calculations. If the pith is visible, and all ring-width measurements are used to estimate the value of c , the following equation could then be used:

$$\hat{c}_i = \underset{t=1, \dots, n}{\text{median}} \hat{c}_t$$

$$= \underset{t=1, \dots, n}{\text{median}} \left(\frac{w_t^2}{2t + 1 - 2t\sqrt{1 + \frac{1}{t}}} \right) \quad (12)$$

with \hat{c}_i = estimated constant basal area for tree i , \hat{c}_t = estimated constant basal area for biological age t , and n = number of years in the ring-width series. Equation 12 is based on the median, rather than the arithmetic mean, to minimize the influence of outliers. Also notice that, if the pith is not visible, the first biological age in the sequence $t = 1, \dots, n$ is not 1, but whatever biological age is assigned to the innermost ring. Given its notation, this approach is described as the “C-method” in the remainder of the article.

APPLICATION TO PONDEROSA PINE DATA

Tree-ring records from the Gus Pearson Natural Area, a long-term monitoring forest research area in northern Arizona (Biondi 1994), were used to illustrate the model (Table 1, Figure 2). The area is occupied by a ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) ecosystem, which has been thoroughly studied in relation to impacts on forest vegetation of land-use changes caused by Euro-American settlement (Biondi 1999; Covington *et al.* 2001; Moore *et al.* 2006). This dataset was selected because several increment cores either included the pith or came close to it, hence allowing for accurate ages to be assigned to each ring (Table 1). Furthermore, it was possible to make comparisons between younger trees, defined as having diameter at breast height (DBH) < 50 cm in 1990, and older ones, defined as having DBH > 50 cm in 1990 (Biondi 1996; Mast *et al.* 1999). Younger trees, whose xylem rings formed mostly during the 20th Century, when lack of fire and successful regeneration increased the density of the stand, are known locally as “blackjacks” because of the dark color of their bark, whereas the older trees, whose annual growth had occurred under widely different conditions prior to Euro-American settlement, are often called “yellow pines”, again based on the color of their outer bark (Pearson 1950). This dataset had already been used to compare the outcome of a few standardization methods, knowing what the overall growth trend in the forest had been over the 20th Century because of repeated timber inventories that were conducted at the study area (Biondi *et al.* 1994; Biondi 1999).

Ring-width series were visually crossdated, measured with a resolution of 0.01 mm, and checked for errors using computer-aided techniques (Holmes 1983; Grissino-Mayer 2001). Pines with 1990 DBH < 50 cm had fewer years between the innermost measured ring width and the stem pith (Table 1). Pith location was usually easier to identify in cores from these trees than in cores from pines with 1990 DBH > 50 cm (Biondi 1999). A tabulation of data on individual tree cores and all ring-width measurements is available in Supplementary Material. Time series plots of

Table 1. Summary of tree-ring samples collected from ponderosa pines at the Gus Pearson Natural Area (35.27°N, 111.74°W, 2,230–2,260 m a.s.l.), northern Arizona, USA (Blondi 1999), and used for illustrating the C-method of ring-width standardization.

Size Class *	Tree Information				Increment Core Summary				Ring-Width Statistics			
	DBH (cm)	Height (m)	Length (yrs)	Total No. of Rings	Years to pith	Period (yrs)	LAR	Mean (mm)	SD (mm)	Min (mm)	Max (mm)	A ₁
Small: DBH < 50 cm (“Blackjack”)	31.8 19.5–46.8	14.4 9.6–23.4	78 53–144	4,509	7 1–34	1847–1990	7 (0.16%)	1.45 0.92–2.23	0.78 0.30–1.48	0.34 0–0.94	3.75 1.96–7.21	0.78 0.26–0.95
Large: DBH > 50 cm (“Yellow pine”)	82.4 50.4–114.8	29.0 18.3–36.0	283 92–418	16,408	64 1–249	1570–1990	194 (1.18%)	1.08 0.48–2.05	0.61 0.23–1.24	0.08 0–0.65	3.17 1.20–5.50	0.73 0.38–0.92

* 58 cores from 29 trees were used for each of these two size classes.

DBH: diameter at breast height (the average as well as the min-max are shown)

Length: number of years included in the 58 wood cores (the average as well as the min-max are shown; the total is given in the next column)

Years to pith: estimated gap from the innermost ring of the core to the stem pith (the average as well as the min-max are shown)

Period: first and last year of the time interval covered by the combination of all measured rings

LAR = locally absent rings (ring width equal to zero; the percentage refers to the total number of rings)

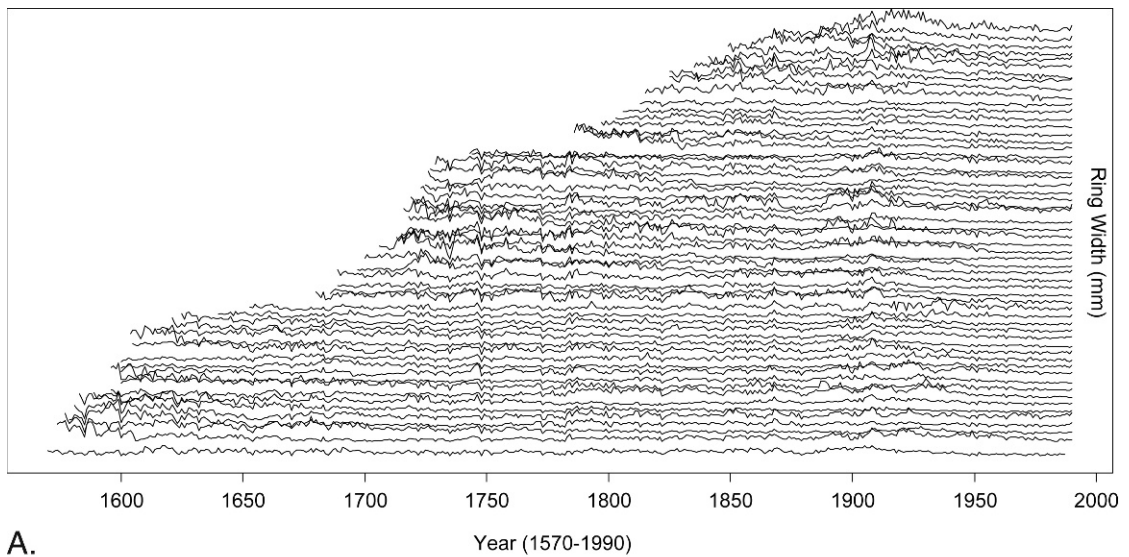
SD = standard deviation of the ring-width measurements (the average as well as the min-max are shown)

A₁ = first-order autocorrelation of the ring-width measurements (the average as well as the min-max are shown)

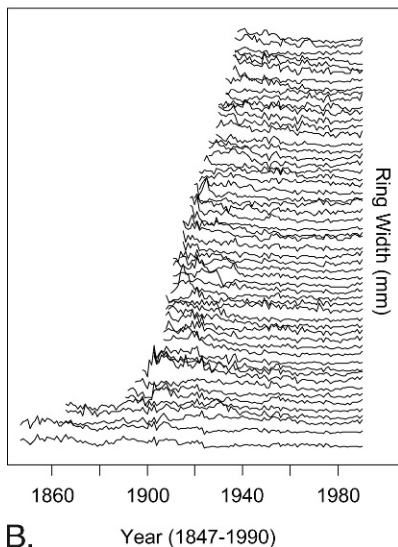
the original measurements (Figure 2) showed clearly the age difference between the two groups of trees, which was also reflected in the number of locally absent rings (Table 1). Older pines had more than seven times the percentage of locally absent rings found in younger ones.

Both the RCS and the C-method were used to standardize the ponderosa pine ring width series after aligning them according to biological age (*i.e.* years since pith formation). The C-method was applied to individual samples, hence generating a specific curve for each ring-width measurement series. On the other hand, the regional curve was computed separately for “yellow pines” and “blackjacks” by taking the average of ring-width measurements for a given biological age (Figure 3). A cubic smoothing spline (Cook and Peters 1981) with a 50% variance response to 10% of the RCS length (Esper, Cook *et al.* 2003; Bunn *et al.* 2004) was then fit to the average values. As commonly found in open-grown, shade-intolerant conifers, the RCS plot showed an initial increase (for about 20 years in pines with DBH < 50 cm, and for about 30 years in pines with DBH > 50 cm) followed by a progressive decline. For both the RCS and C-method, ring indices were obtained as ratios between the ring-width measurements and their expected values (*i.e.* either the smoothed regional curve or the individual C-method curves), then indices were realigned according to calendar years, and the master chronology computed as either the mean or the median of the indices by calendar year. Common patterns among index time series were quantified by pair-wise linear correlation coefficients (Wigley *et al.* 1984), by pair-wise Baillie-Pilcher’s *t*-values (Baillie and Pilcher 1973), and by the first principal component (Jolliffe 1986) for the 1938–1987 period common to all samples.

For the GPNA ponderosa pines, the final tree-ring chronology produced by the C-method was quite similar to that obtained using regional curve standardization (Figures 4 and 5). Statistics of ring indices were also comparable (Table 2), with a slight increase in common variability (as shown by the first principal component) when the C-method was used. There was little difference between computing chronologies either as the



A.



B.

Figure 2. Time-series plots of ring-width measurements, sorted by innermost year, from wood increment cores taken at the Gus Pearson Natural Area, Arizona, USA. The vertical scale (not shown) was the same for all segments. **A.** Ponderosa pines with DBH > 50 cm **B.** Ponderosa pines with DBH < 50 cm.

mean or the median of the indices for each year, hence only the latter results were plotted here (Figures 4 and 5). Linear correlation between the RCS and the C-method chronologies, when computed using the same samples, was ≥ 0.9 . For the “yellow pines” (DBH > 50 cm), the RCS indices were usually slightly less than those of the C-method, except at the beginning of the chronology, when less than 10 samples per year were

available (Figure 4A). For the “blackjacks” (DBH < 50 cm), indices computed using the two methods were more regularly distributed around a 1:1 line, although there was still a minor tendency for RCS indices to be slightly lower than those of the C-method (Figure 4B). Despite changes in sample depth from 1–2 samples per year in the early part of the chronologies to 58 samples per year in the most recent period, both

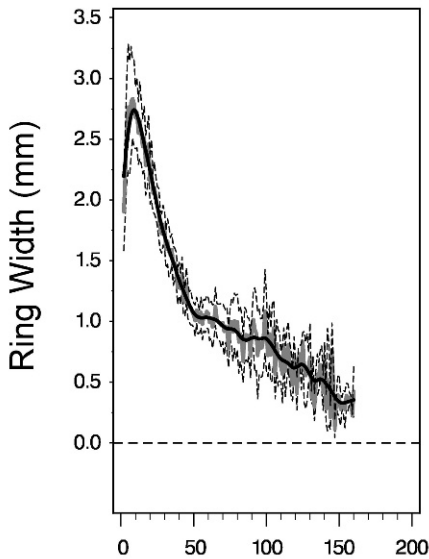
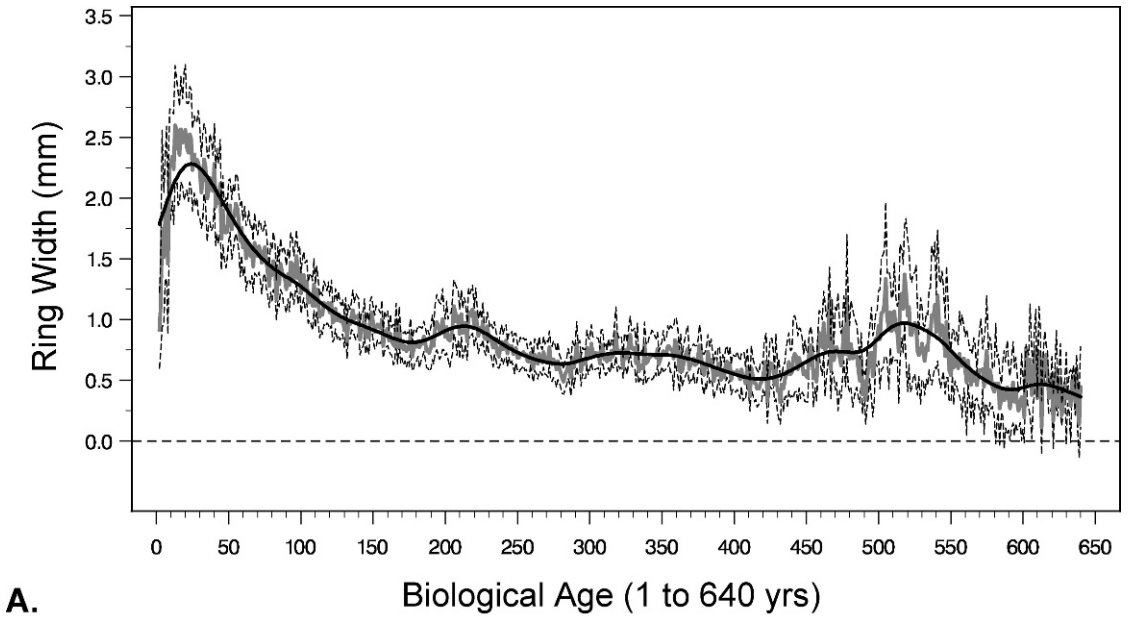
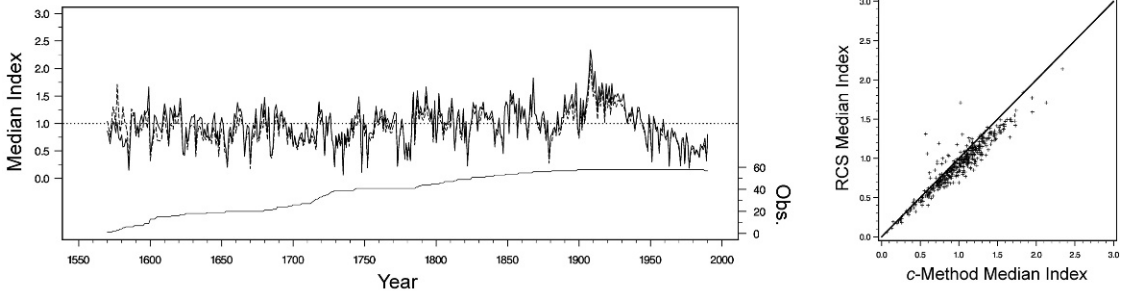


Figure 3. Regional Curve Standardization (RCS) plot of ring width by biological age (=number of years from the pith). Average values (gray solid line) and their two-standard error confidence intervals (black dashed lines) are shown together with a cubic smoothing spline (black solid line) fit to the mean RCS series using a 50% variance response at 10% of the RCS length. **A.** Ponderosa pines with DBH > 50 cm. **B.** Ponderosa pines with DBH < 50 cm.

A. Ponderosa Pines with DBH > 50 cm



B. Ponderosa Pines with DBH < 50 cm

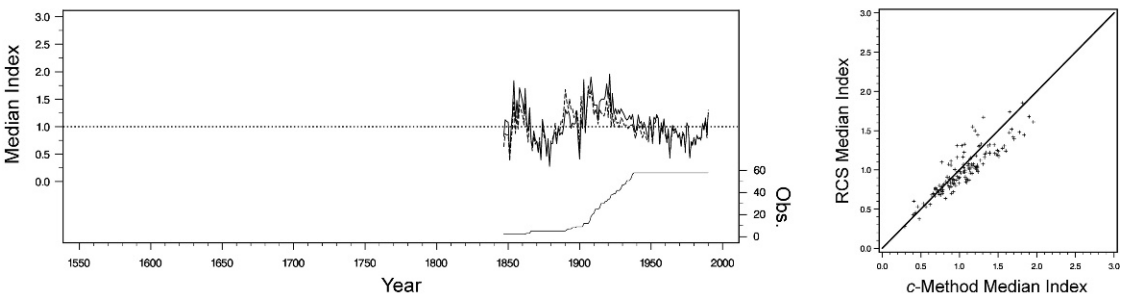


Figure 4. Comparison between tree-ring chronologies obtained using the RCS and C-method for ponderosa pines at the Gus Pearson Natural Area. In either **A** or **B**, the left panel shows time series plots of the Median Index (RCS: dashed line; C-method: solid line) for the entire period of record (AD 1570–1990) with respect to a 1.0 reference level (dotted line), together with the number of samples per year (Obs.: solid line). The right panels are scatterplots of the indices compared to a 1:1 relationship (solid line).

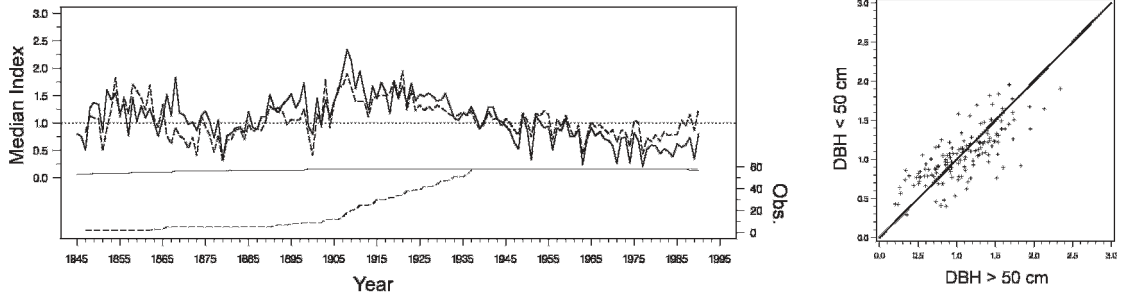
the RCS and the C-method generated master chronologies with relatively stable variance over time (Figures 4 and 5). The dispersion around each median index value was examined using the inter-quartile range for each calendar year, and it was found to be roughly equivalent between the two methods.

Both RCS and C-method chronologies shared the ability of ring-area chronologies (shown in Biondi 1999) to reproduce the stand-wide decline of tree growth during the 20th Century that had been identified in previous studies (Biondi 1994; Biondi *et al.* 1994). In addition, both methods captured the steeper decrease of annual wood increment found in large, pre-settlement pines compared to small, post-settlement pines (Biondi 1996), so that although older pines were growing faster than younger pines in the early 1900s, the opposite was true at the end of the 1900s (Figure 5). This reversal in the order of individual growth rates, which was uncovered by analyzing repeated forest inventories

conducted at the study area (Biondi 1994, 1996), was not accurately reproduced by any other standardization method employed in earlier investigations of the same dataset (see Figures 4 and 5 in Biondi 1999).

A greater amount of common variability was found in the older ponderosas than in the younger ones. This was shown by both the RCS and C-method, as they produced indices with higher crossdating statistics (pair-wise *r*-value, pair-wise Baillie-Pilcher's *t*-value, and % variance explained by the first principal component) when applied to pines with DBH > 50 cm (Table 2). Estimated constant basal area increment ($\hat{\epsilon}_i$, Table 2) was about twice as large for pines with DBH > 50 cm as for those with DBH < 50 cm. This was most likely related to the slower decline in ring size with biological age seen in the larger trees compared to the smaller ones (Figure 3). The increasing stand density during the 20th Century, which prompted drastic changes in individual growth rates (Biondi

A. Chronologies computed using the C-method



B. Chronologies computed using the RCS method

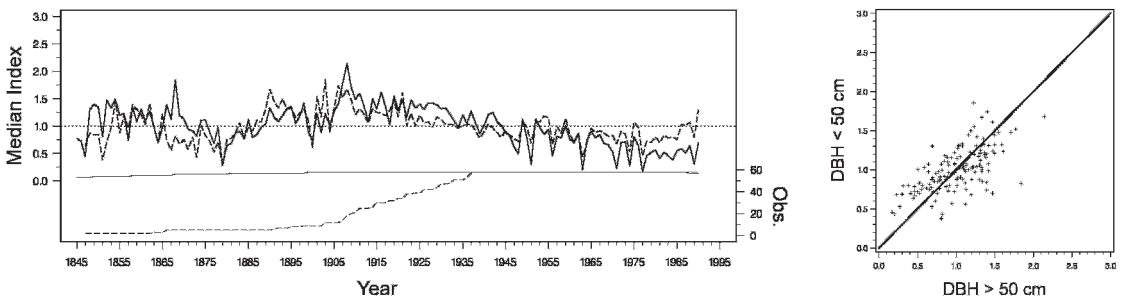


Figure 5. Comparison between tree-ring chronologies obtained using the RCS and C-method for ponderosa pines at the Gus Pearson Natural Area. In either A or B, the left panel shows time series plots of the Median Index (DBH < 50 cm: dashed line; DBH > 50 cm: solid line) for the common period (AD 1845–1990) with respect to a 1.0 reference level (dotted line), together with the number of samples per year (Obs.; DBH > 50 cm: solid line, DBH < 50 cm: dashed line). The right panels are scatterplots of the indices compared to a 1:1 relationship (solid line).

Table 2. Statistics of standardized ring-width indices; the arithmetic average and the minimum-to-maximum interval are shown for most parameters.

A. Indices obtained from the division between the original measurements and the smoothed RCS curve.									
DBH (cm)	Mean	SD	Min	Max	A ₁	Pairwise r-value	Pairwise t-value	1 st PC % Var.	
<50	0.98	0.34	0.29	1.93	0.51	0.30	4.8	37	
	0.61–1.54	0.19–0.74	0–0.73	1.14–3.57	0.01–0.86	–0.49 to 0.88	–0.1 to 28.0		
>50	1.02	0.49	0.09	2.74	0.66	0.43	9.9	59	
	0.67–1.56	0.30–0.92	0–0.60	1.61–4.49	0.42–0.84	–0.55 to 0.92	2.0–37.6		

B. Indices obtained from the division between the original measurements and the expected ring width from the c-method.									
DBH (cm)	Mean	SD	Min	Max	A ₁	Pairwise r-value	Pairwise t-value	1 st PC % Var.	\hat{c}_i (mm ² year ⁻¹)
<50	1.05	0.40	0.27	2.14	0.56	0.33	4.8	43	271
	0.96–1.29	0.22–0.86	0–0.57	1.35–3.94	0.09–0.87	–0.43 to 0.90	–0.1 to 28.3		75–713
>50	1.08	0.55	0.08	3.12	0.68	0.47	9.9	63	563
	0.98–1.32	0.29–1.08	0–0.45	1.91–5.34	0.43–0.87	–0.48 to 0.92	1.9–37.9		225–1,269

DBH, SD, A₁ = see definitions under Table 1

1st PC % Var. = percentage of overall variance during the common period 1938–1987 explained by the first principal component

\hat{c}_i = estimated constant basal area increment for each ring-width series

et al. 1994; Biondi 1996), also caused the RCS curve for small pines to reach the 1-mm level at about 50 years of age, whereas the large pines arrived at that point (starting from about the same high value of about 2.5 mm) when they were about 150 years old (Figure 3).

DISCUSSION

The C-method performance in the case study considered here provides support for its simple assumption, namely that the biological trend is mostly caused by the size and time-dependent constraint to distribute a fairly constant basal area increment over an expanding surface. Recently, debate on the role of senescence in trees has shifted towards emphasizing size-mediated reduction of vigor (Mencuccini *et al.* 2005; Peñuelas 2005). It should be emphasized that the conservative option, as well as all other standardization methods currently in existence, do not distinguish between a biological trend caused by increased stem size, and one caused by increased tree age. Although the C-method is equally unconcerned with trying to separate size from age effects, it allows for computing a rate of ring-width decrease that is specific to each tree, and can be considered a function of genetic potential for growth, bole geometry, ageing, site conditions and history (Fritts 1976).

Ring area usually outperforms ring width for measuring overall tree growth, as it has been repeatedly shown with regard to tree mortality (Bigler and Bugmann 2003, 2004a, 2004b; Bigler *et al.* 2004) and competition indices (Bazzaz 1996; Weber *et al.* 2008). In addition, the well-established pipe theory (Valentine 1985) suggests that sapwood cross-sectional area averaged over the length of the bole approximates the sapwood area at the base of the crown (Valentine and Mäkelä 2005). Considering that most ring-width series with climatic information come from mature, dominant trees (Fritts 1976), which have already reached their maximum height, the assumption of constant annual basal area increment translates directly into a constant rate of wood accumulation. It is interesting that, in the case study we analyzed, the younger pines (“blackjacks”, DBH

< 50 cm) had not all reached their maximum height (see Table 1 for a summary of height data on “blackjacks” and “yellow pines”), and yet the C-method still performed equally well on these smaller, younger, slower-growing trees.

The RCS and C-method require knowing the biological age of each growth ring, whereas the ring area method does not. On the other hand, computing ring area “from the inside out” requires the distance between the pith and the innermost measured ring width (Biondi 1999). If ring area is computed “from the outside in”, *i.e.* starting from diameter inside bark and progressively subtracting ring widths, then knowing the location of the pith is not required, but it is necessary to estimate bark thickness. An advantage of the ring area and C-method approaches is their numerical stability, because there is no need to fit a growth curve using nonlinear regression methods. Furthermore, both the C-method and the calculation of ring area can be applied to individual ring-width series, so they are better suited than RCS for relatively small sample sizes. In fact, the master chronology built with the RCS method is generated by dividing every ring-width measurement series by the same standardization curve, so that a relatively large number of specimens is needed to avoid biasing the final chronology (Briffa *et al.* 1992, 2001).

In any tree-ring standardization method based on biological ring age or on pith location, it is risky to assume that the innermost ring width has a biological age equal to one, especially when dealing with very old trees or irregular stems. For example, strip-bark samples could be adequately fit by the C-method as long as the innermost ring was given a biological age of a few centuries, which could be expected given that strip-bark growth forms are typical of extremely old trees (Schulman 1954; LaMarche Jr. 1969). As detrending methods based on biological age of growth rings and/or on ring area become more commonly used, specific metadata on the biological (or cambial) ring age, as well as other measurements (*e.g.* distance to pith, DBH, bark thickness) will have to be included in archived and publicly available datasets.

The C-method performed as well as the Regional Curve Standardization for producing

master tree-ring chronologies that replicated forest growth patterns. From a comparison with other detrending options applied to the same dataset (Biondi 1999), it was already known that applying 'conservative' standardization methods generated chronologies with trends that did not match those of repeated forest inventories. In addition, both RCS and C-method chronologies were better than ring-area chronologies at reproducing stand-wide patterns. In general, however, computing indices as ratios between the measurements series and the RCS curve has the potential to generate large outliers, given that some trees may widely diverge from the overall expected growth patterns computed for the whole dataset. At the same time, the C-method implies a very rapid reduction in expected ring width during the early years, when instead there is often a slight increase ("juvenile growth") in ring width, so that computing indices as ratios may also generate outliers when using the C-method.

Benchmarking dendrochronological standardization methods against forest growth data is ecologically sound. Additional research should be aimed at comparing the C-method with other ways of removing the biological trend in terms of their ability to properly reconstruct climatic signals for a variety of biogeographic regions, ecosystems, and tree conditions (species, age, *etc.*). For example, it is possible that when dealing with ring-width series from extremely old trees with irregular growth forms, from forest interior environments, from shade-tolerant species, and from relict or subfossil wood, the best standardization method would simply be a smoothing algorithm with a known frequency response, such as the cubic spline option in the ARSTAN package (Cook and Peters 1981; Cook and Holmes 1986). It should also be emphasized that a closer fit between the standardization curve and the measurements can sometime be obtained by means of additional data processing steps (*e.g.* a power transformation) or by fitting a more flexible curve (*e.g.* loess smoothing). Still, the C-method is proposed here not because it necessarily provides the best possible fit to the data, but because it is mathematically derived from a clearly specified assumption, hence it already

provides a superior alternative in all those cases where fitting a modified negative exponential curve (or a straight line with slope ≤ 0) is used for removing the biological growth trend from ring-width series.

CONCLUSIONS

The field of dendrochronology, or tree-ring science, is rapidly evolving, fueled in part by a number of applications in the larger discipline of environmental change research. Theoretical and process-based approaches are likely to improve reliability and robustness of analytical results, because they allow for more rigorous testing, easier quantification of uncertainty, and greater predictive power than purely empirical, regression-based approaches, even though the latter may perform better on training datasets. Computing an expected value of ring width for a clearly specified biological trend is one such theory-based approach. Among standardization methods that are based on the biological (or cambial) age of tree rings, the C-method has the advantage of calculating an expected growth curve for each measurement series, whereas RCS is based on applying the same growth curve to all samples. To summarize, the C-method is theoretically derived, it is applicable to individual ring-width measurement series, and it does not require fitting a growth curve using nonlinear regression.

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REFERENCES CITED

- Baillie, M. G. L., and J. R. Pilcher, 1973. A simple cross-dating program for tree-ring research. *Tree-Ring Bulletin* 33:7–14.
- Bazzaz, F. A., 1996. *Plants in Changing Environments: Linking Physiological, Population and Community Ecology*. Cambridge University Press, Cambridge, U.K.
- Becker, M., 1989. The role of climate on present and past vitality of silver fir forests in the Vosges mountains of northeastern France. *Canadian Journal of Forest Research* 19:1110–1117.
- Bigler, C., and H. K. M. Bugmann, 2003. Growth-dependent tree mortality models based on tree rings. *Canadian Journal of Forest Research* 33:210–221.
- Bigler, C., and H. K. M. Bugmann, 2004a. Assessing the performance of theoretical and empirical tree mortality models using tree-ring series of Norway spruce. *Ecological Modelling* 174:225–239.
- Bigler, C., and H. K. M. Bugmann, 2004b. Predicting the time of tree death using dendrochronological data. *Ecological Applications* 14:902–914.
- Bigler, C., J. Gričar, H. K. M. Bugmann, and K. Čufar, 2004. Growth patterns as indicators of impending tree death in silver fir. *Forest Ecology and Management* 199:183–190.
- Biondi, F., 1992. Development of a tree-ring network for the Italian Peninsula. *Tree-Ring Bulletin* 52:15–29.
- Biondi, F., 1993. Climatic signals in tree-rings of *Fagus sylvatica* L. from the central Apennines, Italy. *Acta Oecologica* 14: 57–71.
- Biondi, F., 1994. *Spatial and Temporal Reconstruction of Twentieth-Century Growth Trends in a Naturally-Seeded Pine Forest*. Ph.D. dissertation, University of Arizona, Tucson, 258 pp.
- Biondi, F., 1996. Decadal-scale dynamics at the Gus Pearson Natural Area: Evidence for inverse (a)symmetric competition? *Canadian Journal of Forest Research* 26:1397–1406.
- Biondi, F., 1999. Comparing tree-ring chronologies and repeated timber inventories as forest monitoring tools. *Ecological Applications* 9:216–227.
- Biondi, F., D. E. Myers, and C. C. Avery, 1994. Geostatistically modeling stem size and increment in an old-growth forest. *Canadian Journal of Forest Research* 24:1354–1368.
- Bradley, R. S., 1999. *Paleoclimatology*. Academic Press, San Diego, CA.
- Briffa, K. R., P. D. Jones, T. S. Bartholin, D. Eckstein, F. H. Schweingruber, W. Karlén, and P. Zetterberg, 1992. Fennoscandian summers from AD 500: temperature changes on short and long timescales. *Climate Dynamics* 7:111–119.
- Briffa, K. R., T. J. Osborn, F. H. Schweingruber, I. C. Harris, P. D. Jones, S. G. Shiyatov, and E. A. Vaganov, 2001. Low-frequency temperature variations from a northern tree ring density network. *Journal of Geophysical Research* 106:2929–2941.
- Bunn, A. G., T. J. Sharac, and L. J. Graumlich, 2004. Using a simulation model to compare methods of tree-ring detrending and to investigate the detectability of low-frequency signals. *Tree-Ring Research* 60:77–90.
- Büntgen, U., J. Esper, D. C. Frank, K. Nicolussi, and M. Schmidhalter, 2005. A 1052-year tree-ring proxy for Alpine summer temperatures. *Climate Dynamics* 25:141–153.
- Canham, C. D., 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bulletin of the Torrey Botanical Club* 117:1–7.
- Collins, M., T. J. Osborn, S. F. B. Tett, K. R. Briffa, and F. H. Schweingruber, 2002. A comparison of the variability of a climate model with paleotemperature estimates from a network of tree-ring densities. *Journal of Climate* 15:1497–1515.
- Cook, E. R., 1985. *A Time Series Analysis Approach to Tree Ring Standardization*, PhD dissertation, University of Arizona, Tucson; 183 pp.
- Cook, E. R., 1987. The decomposition of tree-ring series for environmental studies. *Tree-Ring Bulletin* 47:37–58.
- Cook, E. R., K. R. Briffa, D. M. Meko, D. A. Graybill, and G. Funkhouser, 1995. The ‘segment length curse’ in long tree-ring chronology development for palaeoclimatic studies. *The Holocene* 5:229–237.
- Cook, E. R., and R. L. Holmes, 1986. *Guide for computer program ARSTAN*. Laboratory of Tree-Ring Research, University of Arizona, Tucson; 65 pp.
- Cook, E. R., and L. A. Kairiukstis (Editors), 1990. *Methods of Dendrochronology*. Kluwer, Dordrecht, The Netherlands.
- Cook, E. R., and K. Peters, 1981. The smoothing spline: A new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin* 41:45–53.
- Cook, E. R., and K. Peters, 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. *The Holocene* 7:361–370.
- Covington, W. W., P. Z. Fulé, S. C. Hart, and R. P. Weaver, 2001. Modeling ecological restoration effects on ponderosa pine forest structure. *Restoration Ecology* 9:421–431.
- D’Arrigo, R. D., E. Mashig, D. C. Frank, R. J. S. Wilson, and G. C. Jacoby, 2005. Temperature variability over the past millennium inferred from Northwestern Alaska tree rings. *Climate Dynamics* 24:227–236.
- D’Arrigo, R. D., R. J. S. Wilson, and G. C. Jacoby, 2006. On the long-term context for late twentieth century warming. *Journal of Geophysical Research* 111:1–12, D03103, doi:10.1029/2005JD006352.
- Desplanque, C., C. Rolland, and F. H. Schweingruber, 1999. Influence of species and abiotic factors on extreme tree ring modulation: *Picea abies* and *Abies alba* in Tarentaise and Maurienne (French Alps). *Trees* 13:218–227.
- Dougllass, A. E., 1919. *Climatic Cycles and Tree-Growth*. Carnegie Institution, Washington.
- Dougllass, A. E., 1941. Crossdating in dendrochronology. *Journal of Forestry* 39:825–831.
- Duchesne, L., R. Ouimet, and D. Houle, 2002. Basal area growth of sugar maple in relation to acid deposition, stand health, and soil nutrients. *Journal of Environmental Quality* 31:1676–1683.
- Duchesne, L., R. Ouimet, and C. Morneau, 2003. Assessment of sugar maple health based on basal area growth pattern. *Canadian Journal of Forest Research* 33:2074–2080.
- Elvir, J. A., G. B. Wiersma, A. S. White, and I. J. Fernandez, 2003. Effects of chronic ammonium sulfate treatment on basal area increment in red spruce and sugar maple at the Bear Brook Watershed in Maine. *Canadian Journal of Forest Research* 33:862–869.

- Esper, J., E. R. Cook, P. J. Krusic, K. Peters, and F. H. Schweingruber, 2003. Tests of the RCS method for preserving low-frequency variability in long tree-ring chronologies. *Tree-Ring Research* 59:81–98.
- Esper, J., E. R. Cook, and F. H. Schweingruber, 2002. Low-frequency signals in long tree-ring chronologies for reconstructing past temperature variability. *Science* 295:2250–2253.
- Esper, J., S. G. Shiyatov, V. S. Mazepa, R. J. S. Wilson, D. A. Graybill, and G. S. Funkhouser, 2003. Temperature-sensitive Tien Shan tree ring chronologies show multi-centennial growth trends. *Climate Dynamics* 21:699–706.
- Esper, J., R. J. S. Wilson, D. C. Frank, A. Moberg, H. Wanner, and J. Luterbacher, 2005. Climate: Past ranges and future changes. *Quaternary Science Reviews* 24:2164–2166.
- Frank, D. C., and J. Esper, 2005. Temperature reconstructions and comparisons with instrumental data from a tree-ring network for the European Alps. *International Journal of Climatology* 25:1437–1454.
- Fraver, S., and A. S. White, 2005. Identifying growth releases in dendrochronological studies of forest disturbance. *Canadian Journal of Forest Research* 35:1648–1656.
- Fritts, H. C., 1976. *Tree Rings and Climate*. Academic Press, London.
- Fritts, H. C., J. E. Mosimann, and C. P. Bötterf, 1969. A revised computer program for standardizing tree-ring series. *Tree-Ring Bulletin* 29:15–20.
- Grissino-Mayer, H. D., 2001. Evaluating crossdating accuracy: A manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57:205–221.
- Grissino-Mayer, H. D., and H. C. Fritts, 1997. The International Tree-Ring Data Bank: An enhanced global database serving the global scientific community. *The Holocene* 7:235–238.
- Grudd, H., K. R. Briffa, W. Karlén, T. S. Bartholin, P. D. Jones, and B. Kromer, 2002. A 7400-year tree-ring chronology in northern Swedish Lapland: Natural climatic variability expressed on annual to millennial timescales. *The Holocene* 12:657–665.
- Gunnarson, B. E., and H. W. Linderholm, 2002. Low-frequency summer temperature variation in central Sweden since the tenth century inferred from tree rings. *The Holocene* 12: 667–671.
- Helama, S., M. Lindholm, M. Timonen, and M. Eronen, 2004. Detection of climate signal in dendrochronological data analysis: A comparison of tree-ring standardization methods. *Theoretical and Applied Climatology* 79:239–254.
- Helama, S., M. Lindholm, M. Timonen, J. Meriläinen, and M. Eronen, 2002. The supra-long Scots pine tree-ring record for Finnish Lapland: Part 2, interannual to centennial variability in summer temperatures for 7500 years. *The Holocene* 12: 681–687.
- Helama, S., M. Timonen, M. Lindholm, J. Meriläinen, and M. Eronen, 2005. Extracting long-period climate fluctuations from tree-ring chronologies over timescales of centuries to millennia. *International Journal of Climatology* 25:1767–1779.
- Holmes, R. L., 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin* 43:69–78.
- Husch, B., T. W. Beers, and J. A. Kershaw, Jr., 2003. *Forest Mensuration*. John Wiley & Sons, Hoboken, New Jersey.
- Jolliffe, I. T., 1986. *Principal Component Analysis*. Springer-Verlag, New York.
- LaMarche, Jr., V. C., 1969. Environment in relation to age of bristlecone pines. *Ecology* 50:54–59.
- LeBlanc, D. C., 1990. Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface Mountain, New York. *Canadian Journal of Forest Research* 20:1399–1407.
- LeBlanc, D. C., 1993. Temporal and spatial variation of oak growth–climate relationships along a pollution gradient in the midwestern United States. *Canadian Journal of Forest Research* 23:772–782.
- LeBlanc, D. C., and J. R. Foster, 1992. Predicting effects of global warming and mortality of upland oak species in the midwestern United States: A physiologically based dendroecological approach. *Canadian Journal of Forest Research* 22:1739–1752.
- Mast, J. N., P. Z. Fulé, M. M. Moore, W. W. Covington, and A. E. M. Waltz, 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. *Ecological Applications* 9:228–239.
- Matthes, U., P. E. Kelly, C. E. Ryan, and D. W. Larson, 2002. The formation and possible ecological function of stem-strips in *Thuja occidentalis*. *International Journal of Plant Sciences* 163:949–958.
- Melvin, T. M. M., K. R. Briffa, K. Nicolussi, and M. Grabner, 2007. Time-varying-response smoothing. *Dendrochronologia* 25:65–69.
- Mencuccini, M., J. Martínez-Vilalta, D. Vanderklein, H. A. Hamid, E. Korakaki, S. Lee, and B. Michiels, 2005. Size-mediated ageing reduces vigour in trees. *Ecology Letters* 8: 1183–1190.
- Moore, M. M., C. A. Casey, J. D. Bakker, J. D. Springer, P. Z. Fulé, W. W. Covington, and D. C. Laughlin, 2006. Herbaceous vegetation responses (1992–2004) to restoration treatments in a ponderosa pine forest. *Rangeland Ecology and Management* 59:135–144.
- Nash, S. E., 1999. *Time, Trees, and Prehistory: Tree-Ring Dating and the Development of North American Archaeology, 1914–1950*. The University of Utah Press, Salt Lake City, UT.
- National Research Council, 2006. *Surface Temperature Reconstructions for the Last 2,000 Years*. The National Academies Press, Committee on Surface Temperature Reconstructions for the Last 2,000 Years, Washington, D.C.; 196 pp.
- Naurzbaev, M. M., E. A. Vaganov, O. V. Sidorova, and F. H. Schweingruber, 2002. Summer temperatures in eastern Taimyr inferred from a 2427-year late-Holocene tree-ring chronology and earlier floating series. *The Holocene* 12:727–736.
- Pearson, G. A., 1950. *Management of Ponderosa Pine in the Southwest*. USDA For. Serv., Agric. Monogr. No. 6.
- Pedersen, B. F., 1998. The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. *Ecology* 79:79–93.
- Peñuelas, J., 2005. A big issue for trees. *Nature* 437:965–966.
- Phipps, R. L., 2005. Some geometrical constraints on ring-width trend. *Tree-Ring Research* 61:73–76.
- Phipps, R. L., and J. C. Whitton, 1988. Decline in long-term growth of white oak. *Canadian Journal of Forest Research* 18:24–32.

- Piovesan, G., F. Biondi, A. Di Filippo, A. Alessandrini, and M. Maugeri, 2008. Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology* 14:1265–1281.
- Piovesan, G., A. Di Filippo, A. Alessandrini, F. Biondi, and B. Schirone, 2005. Structure, dynamics, and dendroecology of an old-growth *Fagus* forest in the Apennines. *Journal of Vegetation Science* 16:13–28.
- Poage, N. J., and J. C. Tappeiner, II, 2002. Long-term patterns of diameter and basal area growth of old-growth Douglas-fir trees in western Oregon. *Canadian Journal of Forest Research* 31:1232–1243.
- Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery, 2002. *Numerical Recipes in C++: The Art of Scientific Computing*. Cambridge University Press, Cambridge, U.K.
- Salzer, M. W., and K. F. Kipfmüller, 2005. Reconstructed temperature and precipitation on a millennial timescale from tree-rings in the southern Colorado Plateau, U.S.A. *Climatic Change* 70:465–487.
- Schulman, E., 1954. Longevity under adversity in conifers. *Science* 119:396–399.
- Schweingruber, F. H., D. Eckstein, F. Serre-Bachet, and O. U. Bräker, 1990. Identification, presentation and interpretation of event years and pointer years in dendrochronology. *Dendrochronologia* 8:9–38.
- Tessier, L., 1986. Chronologie de mélèzes des Alpes et petit âge glaciaire. *Dendrochronologia* 4:97–113.
- Valentine, H. T., 1985. Tree-growth models: Derivations employing the pipe-model theory. *Journal of Theoretical Biology* 117:579–585.
- Valentine, H. T., and A. Mäkelä, 2005. Bridging process-based and empirical approaches to modeling tree growth. *Tree Physiology* 25:769–779.
- Villalba, R., H. R. Grau, J. A. Boninsegna, G. C. Jacoby, and A. Ripalta, 1998. Tree-ring evidence for long-term precipitation changes in subtropical South America. *International Journal of Climatology* 18:1463–1478.
- Voelker, S. L., R.-M. Muzika, and R. P. Guyette, 2008. Individual tree and stand level influences on the growth, vigor, and decline of red oaks in the Ozarks. *Forest Science* 54:8–20.
- Warren, W. G., and D. C. Leblanc, 1990. Dynamic standardization of tree-ring series. *Canadian Journal of Forest Research* 20:1422–1431.
- Webb, G. E., 1983. *Tree Rings and Telescopes: The Scientific Career of A.E. Douglass*. The University of Arizona Press, Tucson, Arizona.
- Weber, P., H. K. M. Bugmann, P. Fonti, and A. Rigling, 2008. Using a retrospective dynamic competition index to reconstruct forest succession. *Forest Ecology and Management* 254: 96–106.
- Wigley, T. M. L., K. R. Briffa, and P. D. Jones, 1984. On the average value of correlated time series, with applications in dendroclimatology and ydrometeorology. *Journal of Climate and Applied Meteorology* 23:201–213.
- Woodhouse, C. A., and J. J. Lukas, 2006. Multi-century tree-ring reconstructions of Colorado streamflow for water resource planning. *Climatic Change* 78:293–315.

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