Microstructure Alignment of Wood Density Profiles –
An Approach to Equalize Radial Differences in Growth Rate

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Abstract

We studied intra-annual wood density profiles of Douglas-fir tree rings (*Pseudotsuga menziesii* [Mirb.] Franco) in southwestern Germany. Growth rate varies differently over time throughout the circumference of trees. This leads to differences in wood formation, which can be observed in the shape of the density profiles of the same tree ring measured in different radial directions. Due to this spatial variation in density profiles, we need a reliable method to determine an average profile, which preserves the common characteristics of the data. To this end, we developed a multiple interval-based curve alignment (MICA) procedure. It identifies characteristic points within the profiles such as minima, maxima and inflection points. These reference points are shifted gradually against each other within a proportionally defined base line interval. Using our progressive alignment approach, we are able to calculate an average profile that represents very well the characteristics of all measured curves of a specific tree ring. We applied the procedure to get year-specific average profiles using various trees. This results in representative mean density profiles that preserves the density variations common to all aligned profiles. Individual noise is reduced thereby enabling the analysis of the impact of weather variations on wood density.

Keywords dendroecology, wood density, climate signal, wood anatomy, alignment

Introduction

Wood density as a function of cell dimensions is very responsive to environmental fluctuations, especially to water deficit (Kozlowski 1971, Rozenberg et al. 2002). In particular, conifers, growing in high latitudes or altitudes, showed significant correlations between density and summer temperatures (Fritts 1976, Schweingruber 1988, Briffa et al. 2001, Vaganov et al. 2006). Vaganov et al. (2006) found that conifers tend to produce false rings when intra-seasonal droughts occur. This phenomenon can also be observed by pronounced fluctuations in the density profile of annual tree rings (Figure 1). Therefore we deduce that variations in radial wood density profiles represent: i) a general annual trend controlled by genetic information, ii) average site conditions, and iii) a climatic signal driven by the hydraulic status of the tree and its ability to respond. In this article we define climatic signal as the fraction of growth variation which is externally induced and common for several trees in a collection. As noise, in contrast, we consider all other fluctuations. In the following, for simplicity, weather and climatic signals are used synonymous.

When measuring wood density in different radial directions, variations which are related to the same climatic event are often slightly shifted in their relative position within the ring (Figure 2a). Therefore we assume that growth rate varies disproportionally over time along different radial directions. This finding is consistent with heterogeneous auxine patterns around the stem, which trigger cambial activity (Kozlowski 1971). The disproportionality is obviously even stronger when different trees are compared.

Radial wood density measurements integrate over the characteristics of a certain portion of wood, which is usually wider than the width of one tracheid row. Nevertheless, wood density directly depends on the structures of the cells forming the analyzed tissue. Cells with wide lumen and thin walls are of low density whereas narrow lumen and thick walls form dense tissues. Wood density studies as well as cell structure analyses encounter the problem of calculating means from several measurements within the same ring. For a proper calculation of the mean, the normalized tracheidogram, described by Vaganov (2006), is widely used. The tracheid rows are standardized to a distinct number of cells before a mean of all measured rows of one annual ring is calculated. Assuming that neighboring tracheid files are selected, the proportional spatial discrepancies of temporal signals should be negligible. However, in order to fully detect the climatic signal, density measurements in different radial directions and measurements of several trees may be necessary. Therefore the disproportionality of growth rate may lead to a loss in signal strength if average profiles are calculated by using a simple mean of the normalized raw data (Figure 2a). To avoid such a signal loss, we need a method to eliminate spatial disproportions within the measured data. This would enhance the representation of climate induced characteristics within the averaged profiles.

Given these findings we analyzed spatial variations of wood density to identify profile characteristics common to all trees of the sample in a specific year. Because of the variation we observed in density profiles, even among different directions within one tree, we needed a procedure for determining a common profile for a single tree as well as for a whole stand. Hence, we developed a method to align the extreme values and inflection points of profiles, which we called Multiple Interval-based Curve Alignment (MICA). Using objective criteria this algorithm iteratively adjusts wood density profiles in order to reach a time synchronous arrangement of the measured values. The MICA procedure and the resulting consensus profiles may be used to study relations between wood density profiles and the plasticity and drought tolerance of trees. Furthermore it could improve retrospective analyses of intra annual growth processes, our understanding of growth-environment relations and climate reconstructions based on tree rings.

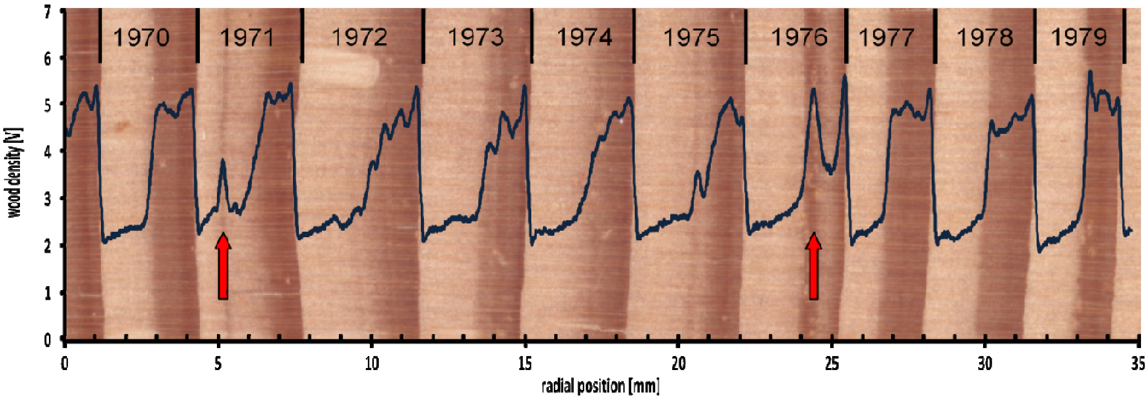

Figure 1: Density pattern of a sequence of 10 successive annual rings. The shape of the annual profiles shows considerable variations. The arrows are indicating false rings.

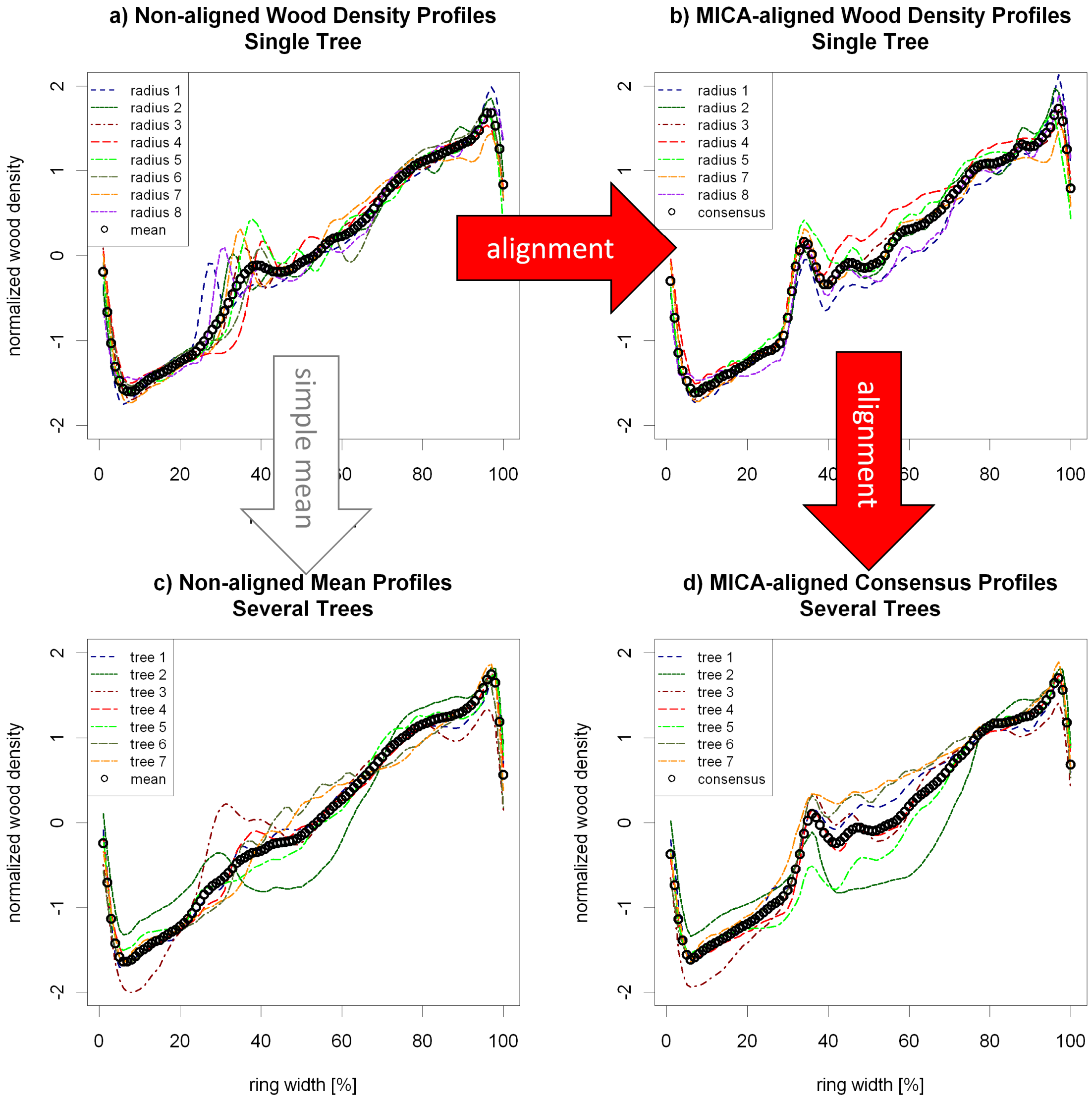

Figure 2: Normalized wood density profiles of the annual rings of 1971. Density is evaluated in eight radial directions within a single tree (a+b). Simple mean profile of seven trees (c). MICA-aligned consensus profile of seven trees (d). The black dotted line indicates the average profile of the non-aligned (a,c) and the aligned profiles (b,d) respectively. The arrows indicate the alignment pathway to year specific profiles of a sample of trees.

Materials and Methods

Sampling and Data Collection

We used stem disks taken from a stem height of 1.3 m of seven 78-year-old dominant Douglas-fir trees sampled in July 2009. The stand was established in 1933. It is located on the western slope of the middle Black Forest in southwestern Germany at an altitude of about 600 m a.s.l. The mean annual precipitation is about 1,200 mm with 650 mm occurring from May till October. The stand had been used as permanent research plot for yield studies since 1953. However, it was abandoned after a severe windthrow in 1999. After this event crown competition among the remaining trees was virtually absent. Tree rings formed after 1999 were not used to develop the alignment procedure.

Stem discs were air dried for six weeks in a room with circulating air. After six weeks, eight radii along eight directions of the discs were cut into bars containing the complete section from pith to bark. The surface was prepared with a diamond fly cutter (Spiecker et al. 2000). This technique prevents residues from sanding procedures from penetrating into cell lumina, which otherwise would distort the density measurements. Furthermore, it creates very smooth horizontal surfaces, which guarantees proper contact of the density probe. All bars were stored under the same ambient conditions before the measurement.

Wood density was determined along the eight radii of each stem disk using High Frequency Densitometry (Schinker et al. 2003). This technique utilizes the dielectric properties of wood, which are closely correlated to its density (Torgovnikov 1990). It is assessed by a micro-electrode system, which transmits electromagnetic waves at high-frequency through the wood sample. It uses a probe that has a superficial resolution of 0.078 mm^2 for each measuring point with a horizontal spacing between each point of 5 µm.

The borders of the annual rings within the profiles of a whole radius were set semi-automatically. For this step in the analysis we used WOODSCAN, version 5.9.2, which is an interactive software tool developed by the Institute for Forest Growth, University of Freiburg. It uses the variation in wood density as the indicator for ring borders. Ring border locations were checked visually to verify the results from WOODSCAN. Using these derived positions, ring width series were determined and cross dated with a regional reference. Pointer years and significant profile structures were analyzed visually. In most cases we dated the pith of the discs to 1935. The density profiles of the first 15 years (1935-1949) showed a significant diverging annual trend that we supposed were related to juvenile wood properties. In fact, according to Domec and Gartner (2002), the first 10-30 rings of conifers contain juvenile wood. Thus we have discarded the first 25 years for further analyses.

Data normalization

We used the statistical software package R, version 2.9.2 (Ihaka and Gentlemen 1996) for our statistical analysis and method implementation. Because mean and variance of the density profiles differ among trees, we normalized the amplitude (Y-axis) of the profiles. To this end, we subtracted the mean value from each measured profile and divided it by its standard deviation. In the next step, the Y-axis normalized density profiles are converted from an absolute diameter scale into a relative percentage scale (X-axis normalization of the profile). We derived a relative density profile $d = d_1, ..., d_{100}$ with a data point d_i for each relative position i from 1 to 100 using a linear interpolation of the data. In the following, we use the term (density) profile or (raw) curve to refer to the normalized relative profiles, d .

Consensus Calculation

Curve alignments, or curve registrations, are a key method for functional data analysis (FDA) when facing sets of similar but deformed functions. Among such problems are object silhouette recognition (Sebastian et al. 2003), micro-array data analyses (Coffey et al. 2011), handwriting recognition (Wirtz 1997), or the classic human growth curve alignment problem (Ramsay and Li 1998; Sangalli et al. 2010). Here, we follow and extend the landmark registration approach introduced by Bookstein (1978) and Kneip and coworkers (Kneip and Gasser 1992, Kneip and Ramsay 2008). Therein, a monotonic transformation of curve intervals is applied to align locations of important shape features. In the following, these locations, which mark the interval boundaries, are called reference points.

To generate a multiple alignment of profiles, we combine the pairwise landmark registration method for two curves with a progressive alignment scheme well studied in bioinformatics (Feng and Doolittle 1987, Higgins et al. 1994, Otto et al. 2008). The latter enables the efficient generation of multiple alignments based on pairwise alignments and is a central approach to compute sequence or sequence-structure alignments of DNA, RNA, or proteins.

The entire procedure is called the Multiple Interval-based Curve Alignment, MICA, which can be summarized in three steps:

1. Computation of all-versus-all pairwise curve alignments using landmark registration, while minimizing a distance function *dist.*
2. Derivation of a guide tree representing the pairwise distances of the curves.
3. Progressive alignment of the input curves following the guide tree from step 2 and the pairwise guide alignments from step 1.

1. Computation of all-versus-all pairwise curve alignments

In order to align profiles using landmark registration, we have to identify reference points to be matched between profiles (Kneip and Ramsay 2008). Those reference points should cover the characteristics of the individual gradient. To this end, local extrema, i.e. maxima and minima, as well as inflection points are considered as potential reference points and successively filtered according to the following criteria. Given the relative density profile d of 100 data points, d_i, we derive all local extrema, E, as well as the global minimal and maximal value $E_{\min}, E_{\max}$ within the profile. To differentiate between minor density variations and relevant density characteristics we use only extrema E, that show a large deflection compared to neighboring extrema in the opposite direction. Low amplitude changes of high frequency are mainly caused by the cell structures themselves (Schinker et al. under review) and do not directly represent the targeted climatic signal. Based on our experiments, we defined variation below 5 % of the whole spectrum as noise. More precisely, the maximal relative density change of an extremum E to the neighboring extrema E_{prev}, E_{next} has to be at least 5 % of the measured density spectrum, i.e., $\max(|E - E_{prev}|, |E - E_{next}|) \geq 0.05 * (E_{\max} - E_{\min})$.

We calculated the slope profile $s = s_1, ..., s_{100}$, of the given profile to identify inflection points, i.e., for each of the density values d_i we calculated a slope estimate s_i for the density profile. Since we have a data set composed of discrete values, we estimate s_i using linear regression[1] of a sliding interval of two leading and following density values $(d_{i-1}, ..., d_i, ..., d_{i+2})$ for the current position, i. The slope of the regression serves as the slope estimate, s_i. Based on this analysis, we identify the inflection points, I, as the extrema of the slope profile. As was done for the extrema of the density profile, we further filter the inflection points for inflections in steep ascents/descents, i.e., we force $|I| \geq 1$.

The remaining extrema and inflection points are used in the following description as reference points in the alignment procedure. They define curve intervals $[i, j]$ that can be matched onto each other such that the interval boundaries, defined by the respective reference points, are aligned onto each other. In the following, we use the set R of relative reference indices for a profile d defined by $R = \{1, ..., r, ..., 100 | 1 < r < 100$, where the profile point d_r is valid E or $I\}$.

The whole alignment procedure is based on a distance function *dist* that gives a quantitative measure of how different the slope intervals of two density profiles d and d' are. Given two intervals $[i, j]$ and $[i', j']$ from the respective profiles d and d', the distance function *dist* calculates the squared deviation of the slope values s and s' of the given intervals. Since the interval boundaries have to be aligned, i.e. *i* onto *i′* and *j* onto *j′*, the lengths of the intervals are equalized to the mean length $l = ((j - i + 1) + (j' - i' + 1)) / 2$. Via linear interpolation we derive $l - 1$ internal data points to be matched within the warped intervals. To incorporate the warping intensity into the distance measure, we use the interval warping factors $w = (j - i + 1) / l$ and $w' = (j' - i' + 1) / l$ respectively. Accordingly, the slopes of the warped intervals $\check{s}$ and $\check{s}'$ together with the warping factors are used to compute the final distance function given by

$$dist([i, j], [i', j']) = (w\check{s}_i - w'\check{s}'_{i'})^2 + (\sum_{1 \leq k < l} (w\check{s}_{i+k} - w'\check{s}'_{i'+k})^2) + (w\check{s}_j - w'\check{s}'_{j'})^2.$$

Within the alignment process, possible interval borders $[i, j]$ are defined by the reference points and their associated indices, R, introduced above. The alignment follows a gradual procedure in order to identify interval decompositions based on reference points that enable smaller decomposed distances compared to undecomposed intervals. Given a pair of intervals $[i, j]$ and $[i', j']$ of d and d', we have to find two reference indices $r \in R$ and $r' \in R'$ within the intervals $(i < r < j, i' < r' < j')$ that provide the minimal decomposed distance $(dist([i, r], [i', r']) + dist([r, j], [r', j'])) < dist([i, j], [i', j'])$. We further presuppose that the mapped reference points defined by r and r' are of the same type, i.e. both are maximum, minimum, or inflection points. By that we enforce similar shapes of the mapped interval boundaries.

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[1] Using the **lm** function from the R *stats* package.

Furthermore, we restrict the distortion of the profile by allowing only for decompositions where the length ratio induced by $dist$ is below a given threshold. Specifically, we apply $\max\{\frac{r-i}{r'-i'}, \frac{j-r}{j'-r'}\} \leq 1.5$, i.e. the maximal length distortion is one and a half times the old length. Finally, only intervals of a minimal length $(j-i) \geq 10$ are considered for decomposition.

Starting with the interval $[0,100]$ for both profiles, an iterative decomposition of the intervals and their resulting subintervals is performed until no better decomposition according to the given constraints can be found. This results in an interval decomposition of both profiles d and d' described by a set of mapped interval pairs $M = \{\ldots,([i,j],[i',j']),\ldots\}$.

The final distance of the aligned density profiles, given the interval decomposition, M, is defined by the root mean square deviation $(RMSD)$ of the derived warped profiles:

$$RMSD(d,d',M) = \sqrt[2]{\frac{1}{100} \sum_{([i,j],[i',j'])\in M} dist([i,j],[i',j'])}.$$

Note: all interval boundaries have to be handled only once to enable the correct normalization and to prevent a bias.

2. Derivation of a guide tree representing the pairwise distances of the curves.

In order to compute a multiple alignment, we follow a progressive alignment scheme that is based on the already computed pairwise alignments. The idea is to join progressively profiles sorted from low to high distance to each other into growing multiple alignments based on the derived distance function. Using the RMSD values calculated by the pairwise mapping procedure to sort the profiles, all profiles are joined within one final alignment (Feng and Doolittle 1987). This strategy was successfully applied for multiple sequence alignment in bioinformatics (Higgins et al. 1994) and results in a fast and efficient procedure. The joining of profiles follows a “guide alignment” which has the lowest RMSD compared to all other profiles of the group. To this end, we apply a single-linkage (shortest distance) clustering where the distance D between two clusters C and C' (or subtrees) is defined by the minimal distance between every two elements of the clusters, i.e. leaves of the subtrees,

$$D(C,C') = \min_{d\in C, d'\in C'} RMSD(d,d',M).$$

This clustering results in a “guide tree” which defines the ranking of the profiles for the following progressive multiple alignment procedure.

3. Progressive alignment of the input curves

Following the RMSD-based guide tree, we progressively join and warp profiles using the according pairwise alignments with minimal distance. We use a profile based representation of multiple alignments, which ensures that the pairwise combination of two alignments is always based on the original X-axis information. This information is used to add a single profile to a pairwise/multiple alignment or to merge two multiple alignments. The interval length correction described for the pairwise alignment procedure has to be altered for multiple alignments. Here, in contrast, two clusters of already aligned profiles are to be merged. Thus, one has to incorporate the cluster sizes, i.e. the number of profiles covered by the sub alignments, into the interval length calculation. For two intervals $[i, j]$ and $[i', j']$ given by a pairwise alignment joining two different clusters C and C', the mean length of the joined interval is given by $l = ((j-i+1)*|C| + (j'-i'+1)*|C'|) / (|C| + |C'|)$. This avoids a disproportionate bias when joining clusters/alignments of different sizes.

When all clusters are merged into one (for instance all radial measurements of one ring within a specific tree), we compute the multiple alignment of the given profiles. To derive the MICA-alignment consensus, we compute the mean value for each aligned relative position of the aligned profiles (see Figure 2b for an example). These year and tree specific consensuses can be further aligned for several trees per year in order to get a site specific year consensus (Figure 2d). This *consensus profile* represents the general shape of all profiles included in the sample and thus year specific variations.

Method Evaluation

To evaluate our method, we investigated and compared the slopes of the consensus curves that are computed using our alignment method MICA, and curves that are generated by taking the simple mean of several curves. The slope represents those characteristics of a wood density profile, which we assume to be, at least partially, affected by climatic variations. As a measure of the impact of the method, we calculated the sampling error of the mean (SEM) of the slopes for the eight MICA-aligned curves for each tree and year using s' in comparison to the non-aligned measured profiles using s. The sampling error SEM evaluates the standard deviation $\sigma_s(i)$ of the slopes at a specific relative curve position i and is given by

$$SEM = \tfrac{1}{100} \sum_{i=1}^{100} \tfrac{\sigma_s(i)}{\sqrt{8}}.$$

This measure evaluates the sample size corrected standard deviation of the eight profiles averaged over all positions.

Results

The method we have described produces aggregated wood density profiles based on a variable number of single measurements. In this study, we assembled eight radii per tree and year to develop an annual tree consensus using MICA. Dependent on the research question we additionally applied MICA to align the resulting annual tree consensuses of seven different trees to an annual stand consensus. The derived consensus profiles show significant variations compared to simple mean profiles calculated for the same samples without application of the developed MICA method (see Figure 3).

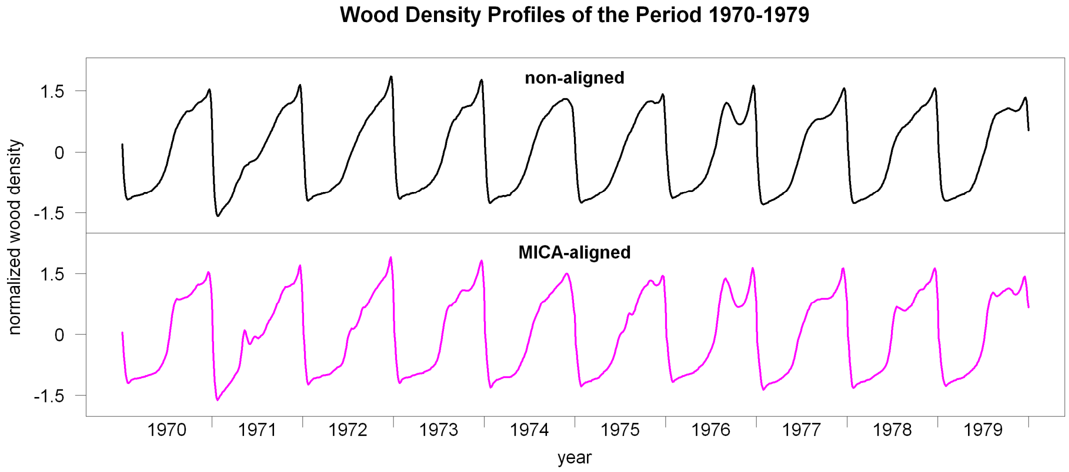

Figure 3: Comparison of a sequence of ten successive annual rings. Top) simple mean values of seven trees, bottom) MICA-aligned consensus profiles of seven trees following the procedure sketched in Figure 2.

Visual assessment of the sequences of the MICA-aligned profiles shows stronger short-term variations while the non-aligned sequences are much smoother. The peaks are clearer and turns are sharper. This observation is supported by the increase of the variance of the slopes from 0.89 to 0.94. The annual maximal density changed slightly using the MICA calculation but remained generally at the same level within the same range of variance. The same response could be observed for the annual minima. Variations within one year with corresponding peaks in the majority of samples are clearly recognizable in the MICA-aligned profiles (compare Figure 2 and Figure 3) while they are diminished when computed as a simple mean profile. The mean values for each data point of the consensus profiles are more stable with lower standard deviations compared to non-aligned average profiles. This finding is supported by the observed 26% decrease of the mean sampling error from 0.0142 to 0.0105. The density in most profiles increases tremendously within 50 % to 70 % of radial position (see Figure 1 and Figure 3). We define this increase as transition zone between earlywood and latewood. The majority of the raw profiles showed clear transition zones marked by the strongest inflection point. This clear border diminished when simple mean profiles were used. Since we align inflection points within the multiple alignments, the characteristics of the transition zone are maintained within MICA consensuses.

Our new technique aims to identify and quantify common intra annual variations contained within a set of measurements (i.e. different radii). We presume that the slopes of those common variations best represent the climatic impact on wood density. The sampling error of these slopes decreased when the MICA-alignment procedure was used (see Figure 4). A paired t-test showed this decrease to be highly significant ($p<0.001$). The mean ratio of the simple mean curves to the MICA-consensuses is 1.595, which demonstrates the higher sampling error for the mean profiles compared to the MICA-aligned consensuses.

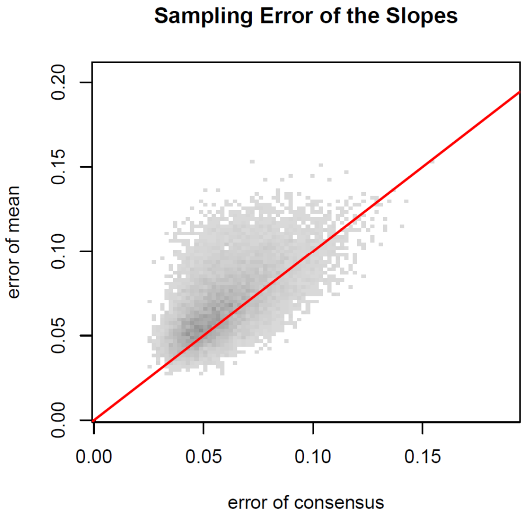

Figure 4: Scatterplot of the sampling error of the slopes of non-aligned (Y-axis) vs. MICA-aligned (X-axis) wood density profiles. The grey values indicate the data density at a certain point. White: none or outlier. Black: very high data density. The diagonal line indicates the balanced ratio of both errors, thus all values above the diagonal line show a higher error in the non-aligned mean profiles.

Discussion and Conclusion

In many cases density variations, which are present in a majority of repeated measurements in different radial directions, are slightly displaced to each other. This effect is even stronger when comparing different trees. Calculating mean curves without fitting the raw measurements against each other reduces variation that the curves have in common. The goal of the method presented here is to reduce this effect to preserve the common variations in the resulting mean profiles. This enables a multiple sampling of density variations with several repeated measurements of the same tree ring in different radial directions. This combined approach of multiple repeated measurements and the following MICA-alignment reduces noise while preserving common variations. The method we developed properly aligns density variations which are supposed to be built contemporaneously. This is especially evident in extreme years, e.g., in the year 1971. Here, a simple mean profile diminishes the year specific profile characteristic. Assuming that less intense drought events and slight variations of the water balance also affect the wood density, the method we have developed allows for the identification and quantification of less pronounced wood density variations. Since we found that the variance of the slopes increased by the application of the MICA, we assume that more density variation is maintained. To which extent slight density variations are caused by climatic variations should be the object for further study and analysis.

The beginning and the end of the density profiles represent the initiation and cessation of annual growth. In this study we assume that growth started and stopped synchronously around the circumference of individual trees as well as between and among trees. This simplistic assumption is due to the fact that there is a lack of models which are able to predict the beginning and end of radial growth retrospectively. This leads to limited warping within small intervals at the outer borders of the profiles. Here, further research is needed to estimate initiation and cessation of cambial growth in different parts of a tree as well as between different individuals.

In the majority of cases, sampling error of the slopes can be reduced by our proposed method. As mentioned above, the first deviation of the density curve is basically the characteristic which we assume to contain the strongest climatic information. The preservation, at least in parts, of this climatic signal is expressed in the reduction of the sampling error. Hence the negative effect of varying growth rate could be reduced effectively. Nevertheless there are cases where the sampling error of the slopes increased. At this point we see a potential for optimizing the proposed method. In summary, we assume that the presented MICA approach is an important tool to analyze multiple repeated intra-annual wood density profiles and to amplify year-specific characteristics.

Acknowledgements

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