# Cutting time slices of tree rings —How intra-annual dynamics of wood formation help to decipher space for time conversion in tree-ring sciences

Gonzalo Pérez-de-Lis, Cyrille B.K. Rathgeber, Stéphane Ponton
Université de Lorraine, AgroParisTech, INRAE, SILVA, 54000 Nancy, France

## Context

The retrospective analysis of the intra-annual information recorded in tree rings is challenged by the uncertain association between tracheid's position and the time at which environmental cues can be imprinted in their structure (cell diameter or wall thickness) and isotopic composition.

## Objectives & data collection

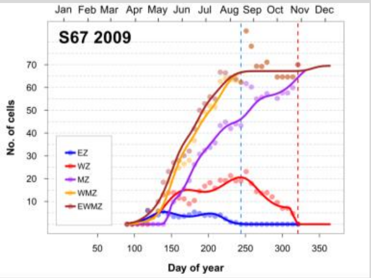
We investigated the association between space and time across regular tree-ring sectors, for which we compiled data on wood anatomy and xylogenesis for 15 *Abies alba* L. trees grown in North-East France (3 years).

Dates of tracheid formation obtained from an empirical model of wood formation dynamics (A) and tracheid dimensions measured on anatomical sections were used to compute duration of tracheid (B) and sector (C) formation.

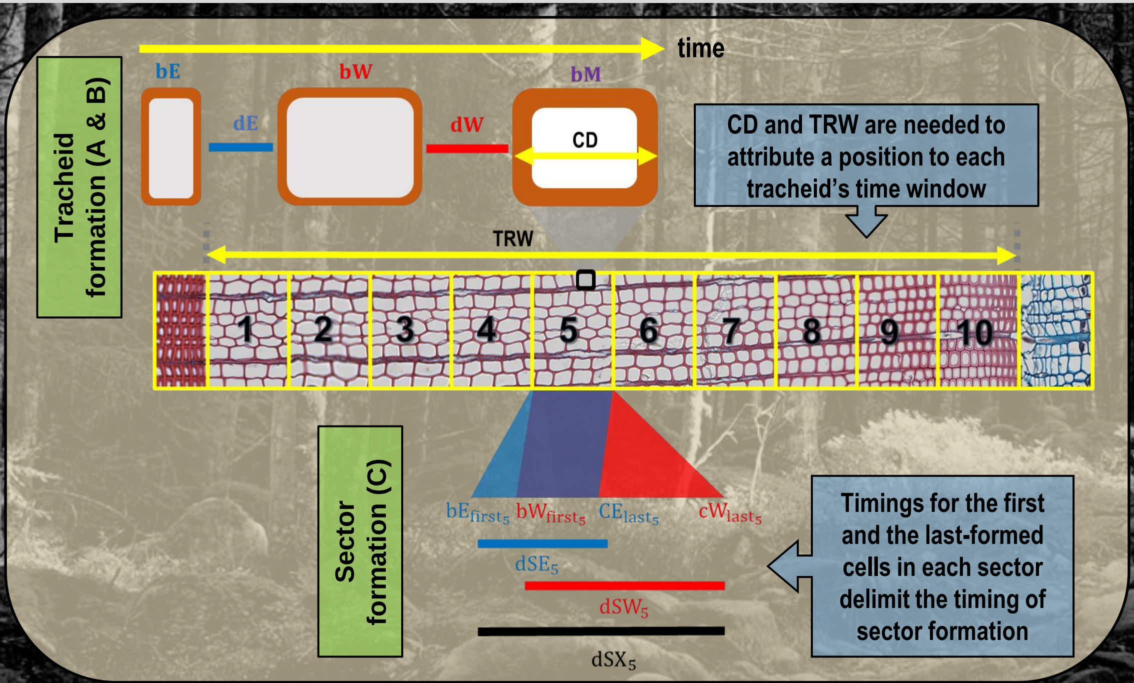
Kinetics of sector formation were used to assess changes in duration and overlapping across successive sectors and variability of growth across trees and between years.

## Methods A. Timing of tracheid formation

1. GAM models were fitted for each tree on weekly cell counts in the enlarging (EZ) and wall thickening (WZ) zones, while a monotone increasing SCAM model was used for the mature zone (MZ).
2. Cumulative sum of MZ and WZ zones (WMZ), and the total number of cells (EWMZ) was used to calculate cell entry dates in each zone.



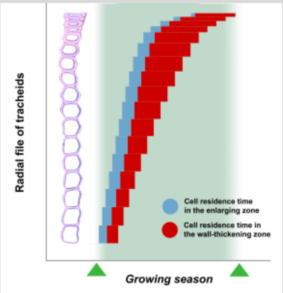

bE (Cell entry date in the enlarging zone)
bW (Cell entry date in the wall-thickening zone)
bM (Cell entry date in the mature zone)




## Methods B. Duration of tracheid formation

3. Cell residence times in the enlarging (dE) and wall-thickening (dW) zones were computed for each tracheid from cell entry dates in each zone.

$dE = bW - bE$
$dW = bM - bW$



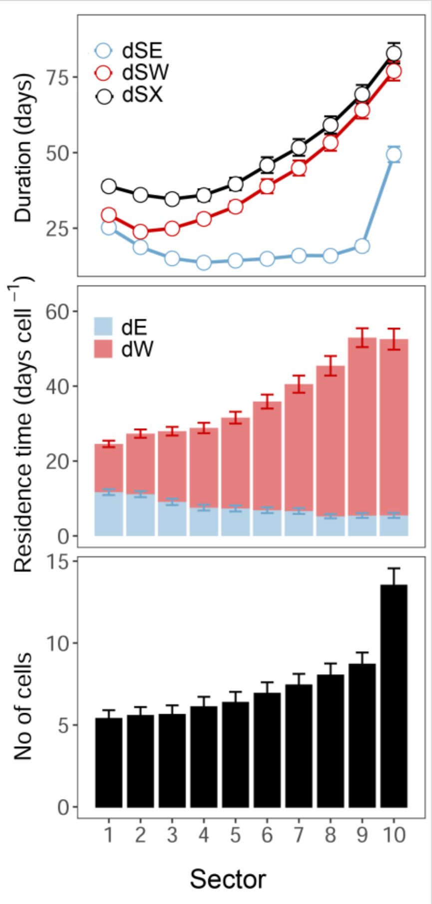

4. The proportion of the tree-ring width (TRW) occupied by each tracheid was assessed using cell diameter (CD) data from tracheidograms, which were previously normalized to allow comparisons between datasets.

## Methods C. Duration of sector formation

5. After dividing the ring in regular sectors, we computed the timing of sector formation using dated tracheidograms from point 4.
   - First cell of the sector
     $bE_{first}$ (Onset of sector enlargement)
     $bW_{first}$ (Onset of sector maturation)
   - Last cell of the sector
     $cE_{last}$ (Cessation of sector enlargement)
     $cW_{last}$ (Cessation of sector maturation)
6. Dates for first and last cells of the sectors served to assess the duration of sector formation

$dSE = cE_{last} - bE_{first}$
$dSW = cW_{last} - bW_{first}$
$dSX = cW_{last} - bE_{first}$

## Results I: Variable duration along the ring

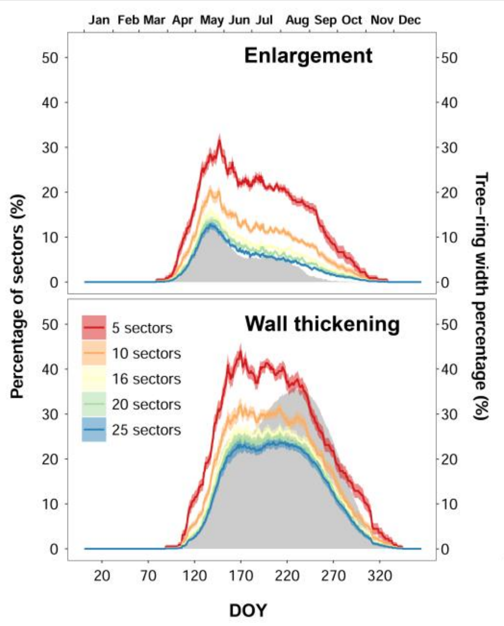



The time taken by each sector to be formed increased from 35 to 83 days as we moved from earlywood (wide thin-walled tracheids) to latewood (narrow thick-walled tracheids).

Sector maturation lasted longer than sector enlargement (except for the first two sectors) and reflected the increasing time spent by tracheids in the wall-thickening zone throughout the ring.

Sector enlargement was also related to cell residence times in the enlarging zone but also to the increasing number of tracheids per unit area from earlywood to latewood (sectors had the same width).

## Results II: Variable overlapping along the year



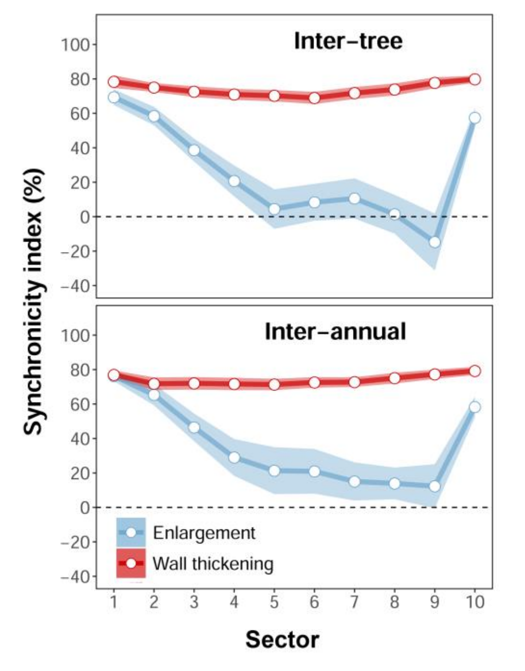

Despite successive tree-ring sectors were separated in space, their formation was overlapped in time, evidencing that they cannot be "sliced" in independent time intervals.

Sector overlapping culminated in early summer, reaching 40 % for 10 sectors, being higher for the wall-thickening phase.

Overlapping reflected the amount of contemporary tissue (grey shadow in the figure), which results from the balance between rates of cambial division and cell residence times in the enlarging and wall-thickening zones.

Although overlapping could be reduced to approx. 30 % by increasing the number of sectors (from 5 to 20, for example), it was not significantly reduced above 20 sectors.

## Results III: Synchronous and stable growth




Formation of equivalent sectors was noticeably synchronous across trees (upper panel), and highly stable along the three years of monitoring (bottom panel).

Synchronicity for the wall-thickening phase was approximately 80 % throughout the ring, likely due to the long duration of this phase.

However, sectors 5 to 9 showed a more distinct period of enlargement across trees and between years.

This result may explain the high common signal found in literature for chronologies of intra-annual series of tree-ring features.

## Conclusion

The amount of biologically meaningful information that we can potentially obtain from tree-ring records is not only limited by instrumental capacity but also by the maximum time resolution imposed by kinetics of cell division, enlargement and wall thickening.

Patterns of duration, overlapping and synchronicity may shift across tree-ring traits (e.g. wood anatomy, stable isotope ratios) according to their association with developmental phases (i.e. tracheid size is tied to the enlargement phase, but wood isotope signature would be largely registered during wall thickening).

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