



## Unravelling the influence of environment and development on intra-annual dynamics of wood formation and resulting tree-ring structure and isotope ratios

*Principle investigator:* Cyrille Rathgeber

*Collaboration:* Stéphane Ponton & Gonzalo Pérez-de-Lis

**Context** — Tree rings play a major role in documenting past and ongoing climate change and its impacts on forest ecosystems. However, past climatic reconstructions and future growth projections are still hampered by a poor understanding of the influence of environmental and developmental factors on the physiological processes governing wood formation.

**Objectives** — The WoodIsotop project aims to advance our knowledge of the interactions between environmental factors, developmental constraints, and physiological processes involved in wood formation. Our investigations focus on a better understanding of the mechanisms by which seasonal climate variations and extreme events leave permanent imprints in the tree rings. We focus in particular on (i) identifying the environmental factors influencing the intra-annual dynamics of wood formation and the characteristics of the rings formed (i.e. micro-densitometric profile, anatomical characteristics of the wood, and intra-ring variations in isotopic composition); (ii) understanding the mechanisms involved; and (iii) their temporal coordination.

**Approach** — To carry out this project, we relied on a network of instrumented plots composed of 3 mixed stands of conifers, containing 3 species, monitored over 3-4 years, and installed along an altitudinal gradient in the Donon (Vosges Mountains). The dataset was completed to contain all the

information concerning the formation dynamics, quantitative anatomy and isotopic composition ( $\delta^{13}\text{C}$ ) of the rings. In addition, we have improved our model of wood formation dynamics to accurately relate cell differentiation kinetics, tracheid morphology, and wood isotopic composition to concomitant environmental conditions.

**Key results** — By connecting causes (environmental and developmental conditions) and consequences (tree-ring characteristics and wood isotope signature) through a mechanistic understanding of the physiological processes involved in wood formation, the WoodIsotop project will not only increase the reliability of the dendrochronological variables used for climate reconstructions, but will also reduce uncertainties in future assessments of the impact of climate change on tree growth, the functioning of forest ecosystems, and the quantification of flows exchanged between terrestrial biomass and the atmosphere.

The results obtained during this project concern:

- Assigning a temporal window to variations in wood density and isotopic composition in the ring;
- Highlighting the temporal "overlap" between sections of the rings (see illustration);
- Evidence of the probable "isolation" effect of the tracheids in formation, which would only be supplied with carbohydrates during their creation in the cambial zone, but not anymore during their differentiation in the developing xylem;
- The acquisition of evidences suggesting that cellulose deposition and lignin impregnation are concomitant processes.

**Main conclusions including key points of discussion** — Despite many methodological difficulties inherent in the technique of wood formation monitoring, we were able to improve our statistical model of xylogenesis dynamics sufficiently to assign each section of wood cut within the tree ring to a specific time window. This allowed us to show that despite the delineated wood sections are separated spatially, they cannot be attributed to isolated time periods, being temporally "overlapped" each other. These sections cannot therefore provide independent climate information, contrary to what is regularly proposed in scientific publications on the subject.

**Future perspectives** — During this project we were able to demonstrate that our approach was applicable and challenged the results previously achieved by less accurate approaches. At present, the results obtained for fir in the Vosges Mountains using intra-ring variations of  $^{13}\text{C}$  and micro-densitometric profiles are rather disappointing from a dendroecological point of view. We believe that this is due to the low variability observed between the study sites and the years of monitoring, as well as to the physiological behavior of the species, which is very stable during the growing season. Three new research tracks are being considered to extend this project: (1) further analyzing the coordination between cellulose deposition and lignin impregnation using confocal microscopy, and understanding the consequences on intra-ring patterns of C isotope signal in tree-rings; (2) comparing our results with the simulations of a growth model including carbon isotope discrimination in tree rings (MUSICA) to better interpret our results and to verify the consistency of the model; (3) using our methodology to look at variations of  $^{18}\text{O}$  in larch tree-rings along an altitudinal gradient in Switzerland (Lötschental) for which climatic constraints are much stronger.

**Valorization** —

### **Publications**

SADERI S, RATHGEBER CBK, ROZENBERG P, FOURNIER M. 2019. Phenology of wood formation in larch (*Larix decidua* Mill.) trees growing along a 1000-m elevation gradient in the French Southern Alps. *Annals of Forest Science*: 76–89.

ANDRIANANTENAINA AN, RATHGEBER CBK, PÉREZ-DE-LIS G, CUNY H, RUELLE J. 2019. Quantifying intra-annual dynamics of carbon sequestration in the forming wood: a novel histologic approach. *Annals*

of *Forest Science*: 1–12.

DE MICCO V, CARRER M, RATHGEBER CBK, CAMARERO JJ, VOLTAS J, CHERUBINI P, BATTIPAGLIA G. 2019. From xylogenesis to tree rings: wood traits to investigate tree response to environmental changes. *IAWA JOURNAL*: 155–182.

DELPYERRE N, LIREUX S, HARTIG F, CAMARERO JJ, CHEAIB A, ČUFAR K, CUNY H, DESLAURIERS A, FONTI P, GRIÇAR J, HUANG J-G, KRAUSE C, LIU G, DE LUIS M, MÄKINEN H, MARTINEZ DEL CASTILLO E, MORIN H, NÖJD P, OBERHUBER W, PRISLAN P, ROSSI S, SADERI SM, TREML V, VAVRICK H, RATHGEBER CBK. 2019. Chilling and forcing temperatures interact to predict the onset of wood formation in Northern Hemisphere conifers. *Global Change Biology* 25: 1089–1105.

FRIEND AD, ECKES-SHEPHARD AH, FONTI P, RADEMACHER TT, RATHGEBER CBK, RICHARDSON AD, TURTON RH. 2019. On the need to consider wood formation processes in global vegetation models and a suggested approach. *Annals of Forest Science* 76.

CUNY H, FONTI P, RATHGEBER CBK, ARX VON G, PETERS RL, FRANK DC. 2018. Couplings in cell differentiation kinetics mitigate air temperature influence on conifer wood anatomy. *Plant, Cell & Environment* 11: 328–11.

RATHGEBER CBK, SANTENOISE P, CUNY H. 2018. CAVIAR: an R package for checking, displaying and processing wood-formation-monitoring data. *Tree physiology* 38: 1246–1260.

### **Presentations at conference**

PÉREZ-DE-LIS G, RATHGEBER, CBK, PONTON S. Can we chop a tree-ring into time-slices? What wood formation dynamics can bring to intra-annual tree-ring sciences. Eurodendro 2019, 9-13 September 2019, Brno (Czech Republic).

RATHGEBER CBK, SADERI S, ROZENBERG P. Wood formation phenology of larch trees growing along a 1,000 m elevation gradient in the French Southern Alps. *Topwood international conference*, 12-15 march 2019, Bariloche (Patagonia, Argentina).

RATHGEBER CBK, SADERI M, CUNY H. How cell differentiation kinetics drive tree-ring structure plasticity over changing climate and site conditions. *Plasticity in plant vascular systems: roles, limits and consequences*. Multiscale plant vascular biology, Gordon Research Conference, 17–22 June 2018, Mount Snow (Vermont, USA).

### **Posters**

Using intra-annual dynamics of wood formation to disentangle wood structure and C isotope signals in tree rings. Gonzalo Pérez-de-Lis, Cyrille B.K. Rathgeber & Stéphane Ponton. *Le Studium: Wood formation and tree adaptation to climate*, 23-25 Mai 2018, Orléans (France).

Kinetics of wood formation: Are they helpful to explain climate effects on wood density and carbon isotope signals? Gonzalo Pérez-de-Lis, Cyrille B.K. Rathgeber & Stéphane Ponton. *GRC: Plasticity in plant vascular systems: roles, limits and consequences*, 16-22 juin 2018, Mount Snow (Vermont, USA).

### **Articles in preparation**

PÉREZ-DE-LIS G, RATHGEBER, CBK, FERNÁNDEZ-DE-UÑA L, PONTON S. Cutting time slices of tree rings — How intra-annual dynamics of wood formation help to decipher space for time conversion in tree-ring sciences.

RATHGEBER CBK, PÉREZ-DE-LIS G, FERNÁNDEZ-DE-UÑA L, FONTI P, ROSSI S, TREYDTE K, GESSLER A, DESLAURIERS A, FONTI MV, PONTON S. Anatomical, developmental and physiological basis of tree-ring formation in relation with environmental factors. In SIEGWOLF R, BROOKS JR, RODEN J, SAURER M (Eds), *Stable Isotopes in Tree Rings: Inferring Physiological, Climatic and Environmental Responses*. *In preparation for Springer Series on Tree Physiology*.