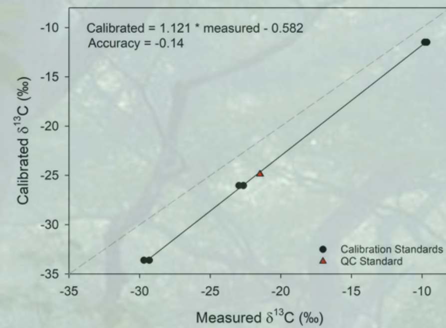
New Book: Stable Isotopes in Tree Rings: Inferring Physiological, Climatic and Environmental Responses

Introduction

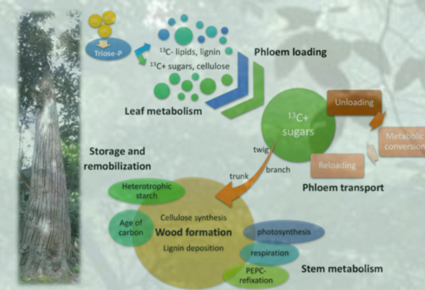
This will be the first book to comprehensively cover the field of tree ring stable isotopes.

This volume highlights in 24 Chapters how tree ring stable isotopes have been used to address a range of environmental issues from paleoclimatology to forest management, and anthropogenic impacts on forest growth.

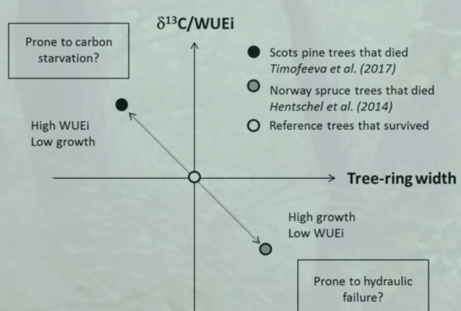
Methods



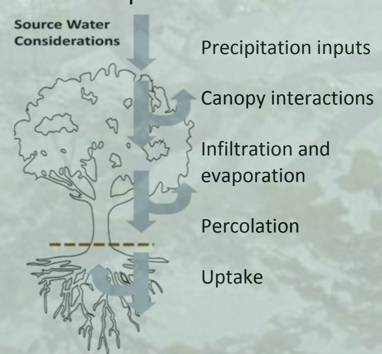
Isotopic fractionations from source to wood



Physiological interpretations



Environmental factors impacting isotopic fractionations



Synopsis and Outlook

OPEN ACCESS BOOK

Target Audience:

Researcher & educator interested in tree rings for

- reconstruction of paleoclimate
- contemporary functional processes
- anthropogenic influences on native ecosystems.

The use of stable isotopes in biogeochemical studies has expanded greatly in recent years, making this volume a valuable resource to a growing and vibrant community of researchers.

Rolf Siegwolf, J. Renée Brooks, John Roden, Matthias Saurer

Institute for Forest, Snow and Landscape Research (WSL), Pacific Ecological Systems Division, US EPA, Southern Oregon University.

EGU General Asssembly 2020—06 May 2020, Vienna, Austria

INTRODUCTION

This new book in the Springer Tree Physiology Series is due out in 2020.

This book will be the first to comprehensively cover the field of tree ring stable isotopes.

This volume highlights how tree ring stable isotopes have been used to address a range of environmental issues from paleoclimatology to forest management, and anthropogenic impacts on forest growth.

This book focuses on physiological mechanisms that influence isotopic signals and reflect environmental impacts. Each of the 24 chapters has been authored by leading experts providing the most recent developments in the area.

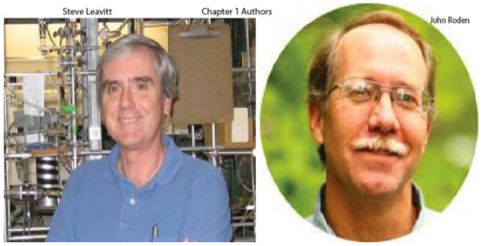
Introductory Chapters:

- **Chapter 1: Historical Aspects** *by Steve Leavitt and John Roden*
- **Chapter 2: Dendrochronology: Fundamentals and Innovations** *by David Frank, Keyan Fang, and Patrick Fonti*
- **Chapter 3: Anatomical, developmental and physiological basis of tree-ring formation in relation with environmental factors** *by Cyrille B.K. Rathgeber, Gonzalo Pérez-de-Lis, Laura Fernández-de-Uña, Patrick Fonti, Sergio Rossi, Kerstin Treydte, Arthur Gessler, Annie Deslauriers, Marina V. Fonti, Stéphane Ponton.*

Introduction

Chapter 1: Historical Aspects

Authors: Steven W. Leavitt and John Roden



Abstract: Although the fields of dendrochronology and light stable-isotope mass spectrometry emerged at different times in the first half of the 20th Century, their convergence with the earliest measurements of isotope composition of tree rings is now ca. 70 years old. Much of the early stable isotope analysis (including on wood) explored natural variation of isotopes in the environment, but those making the measurements were already contemplating the role of the isotope composition of the source substrates (water and CO_2), biochemical fractionation, and environment as contributors to final tree-ring isotope values. Growing interest in tree-ring isotopes was heavily motivated by paleoclimate or paleoatmosphere reconstruction, but this new field rapidly developed to generate greatly improved mechanistic understanding along with expanded applications to physiology, ecology, pollution, and more. This chapter primarily charts the historical progression in tree-ring C-H-O isotope studies over those seven decades, but it also identifies potential productive future directions.

Introduction

Chapter 2: Dendrochronology: Fundamentals and Innovations

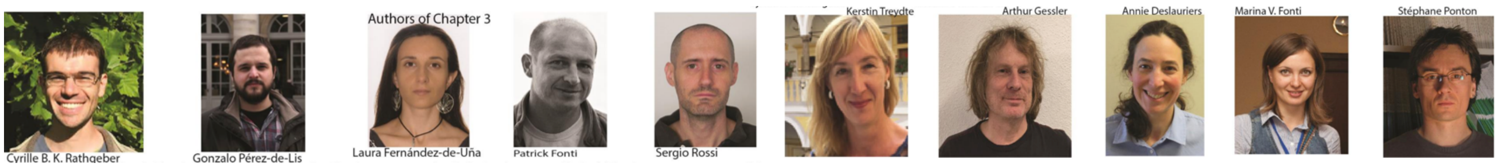
Authors: David Frank, Keyan Fang, and Patrick Fonti

This chapter overviews long-standing foundations, methods, and concepts of dendrochronology, yet also pays attention to a few related paradigm shifts driven by isotope measurements in tree-rings. The basics of annual ring formation are first described, followed by structural descriptions of tree-ring at the macroscopic-to-microscopic scale including early-wood and latewood in conifers (gymnosperms) and hardwoods (angiosperms). Xylogenesis – the process of wood formation – is superficially described including the kinetics (timing and duration) of cell enlargement and wall thickening of wood cells, as well as the molecular constituents "sequestered" into the annual rings during tree growth. We review definitions and methods related to field sampling, the process and necessity for crossdating, and the development of tree-ring chronologies. Quality control statistics used to assess the common signal and quality of tree-ring data-sets are introduced, along with the limitations in these classical statistics in addressing low-frequency (e.g., secular trends) signals (& noise) in tree-ring data. We describe low-frequency trends in tree-ring data such as those related to tree-age/size, and reviews methods such as detrending and standardization to mitigate such tree-age/size related noise common to many applications such as dendroclimatic reconstruction. An overview of some of the drivers of long-term trends in tree-ring isotope data such as the Suess effect, the increase in the atmospheric concentration of CO2, age/size/height trends, and some related debates/ uncertainties evident in literature are discussed in order to establish priorities for future investigations.

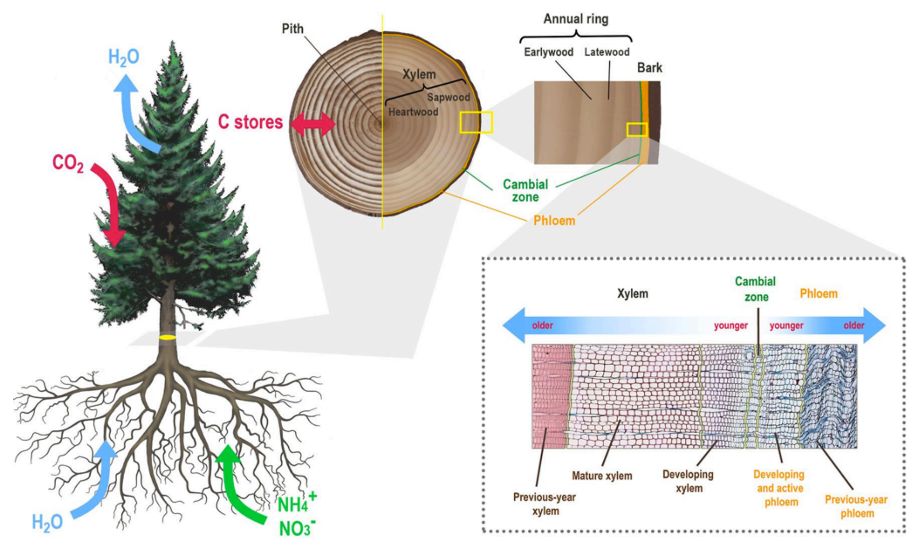
Introduction

Chapter 3: Anatomical, developmental and physiological basis of tree-ring formation in relation with environmental factors

Authors: Cyrille B.K. Rathgeber, Gonzalo Pérez-de-Lis, Laura Fernández-de-Uña, Patrick Fonti, Sergio Rossi, Kerstin Treydte, Arthur Gessler, Annie Deslauriers, Marina V. Fonti, Stéphane Ponton.

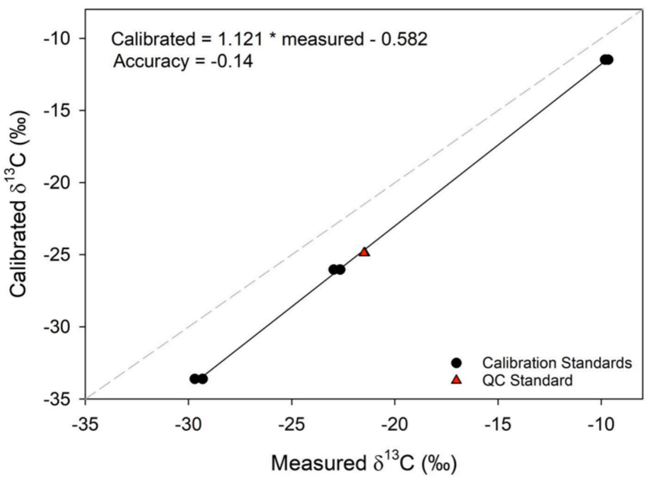


Understanding the process of wood formation and its dynamics over the growing season is fundamental to correctly interpret the isotopic signature of tree rings. Indeed, the isotopic signal recorded in tree rings does not only depends on the conditions influencing carbon, water, and nitrogen uptake and assimilation, but also on how these elements are translocated to the growing stem and incorporated into the forming xylem. Depending on environmental conditions, but also on species life-strategy, tree developmental stage and physiological status, wood formation dynamics can vary greatly and produce tree-ring structures carrying specific isotopic signatures. In this chapter, we present the fundamental processes involved in wood formation, along with their relationships with anatomical, developmental, physiological and environmental factors, in order to understand when and how substrates with peculiar isotopic composition are progressively incorporated into the forming xylem creating the final isotopic signature of the tree rings. First, we provide fundamental information on wood element composition, structure and functions. Second, we review the current knowledge on wood formation, and in particular, how and when new xylem cells produced by the cambium undergo profound transformations through successive differentiation phases. Third, we describe how these processes change over the seasons, with tree phenology and environmental factors. Finally, we explain the kinetics of xylem cell differentiation and show why the knowledge recently acquired in this field is paramount for understanding the creation of tree-ring isotopic signals.



METHODS

Figure 6.1: Typical calibration for adjusting measured sample values to the correct d scale illustrating the two types of systematic error affecting $\delta^{13}C$. The intercept represents the offset correction error, and the slope the scale factor error. The gray dashed line is a 1:1 line between measured and calibrated isotopic values.



- **Chapter 4: Sample Collection and Preparation for Annual and Intra-annual Tree-ring Isotope Chronologies** *by Soumaya Belmecheri, William E. Wright, and Paul Szejner*
- **Chapter 5: Chemical pre-treatment of wood for C, O, H stable isotope analysis** *by Gerhard Helle, Maren Pauly, Ingo Heinrich and Karina Schollän*
- **Chapter 6: Tree Ring Stable Isotope Measurements: The Role of Quality Assurance and Quality Control to Ensure High Quality Data** *by J. Renée Brooks, Roland A. Werner, and William Rugh*
- **Chapter 7: Newer Developments in Tree Ring Stable Isotope Methods** *by Katja Rinne-Garmston, Gerd Helle, M.M. Lehmann, E. Sahlstedt, J. Schleucher, J. and J. S. Waterhouse.*

Methods

Chapter 4: Sample collection and preparation for annual and intra-annual tree-ring isotope chronologies.

Authors: Soumaya Belmecheri, William E. Wright, Paul Szejner

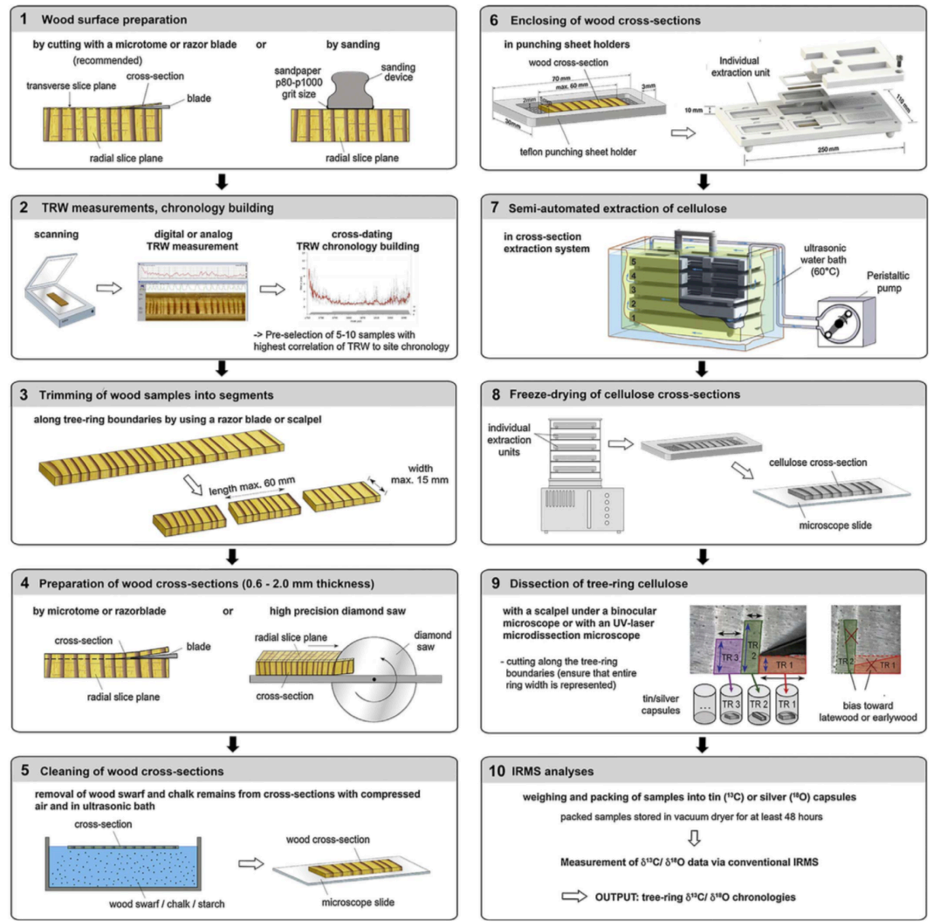
This Chapter highlights the different theoretical perspectives and practical steps to conduct sample collection and laboratory processing for the measurement of stable isotopes in tree rings. The chapter provides an overview of common protocols and consideration when using stable isotopes as tools to infer past and present variability of climate and ecophysiology. In particular, the theoretical perspective addresses new avenues towards a high seasonal resolution (inter and intra) to understand the isotopic signal recorded in tree rings; and to characterize the tree response to environmental stressors. Using case studies, this chapter demonstrates how a multi-disciplinary approach combining highly resolved stable isotope measurements, xylogenesis (tree ring formation processes) and process-based models, offers exciting opportunities to address a range of issues from paleoclimatology, ecophysiology, forest management, to anthropogenic impacts on forest growth.

Methods

Chapter 5: Chemical pre-treatment of wood for C, O, H stable isotope analysis

Authors: Gerhard Helle, Maren Pauly, Ingo Heinrich and Karina Schollän

This chapter covers the latest concepts around treating wood for C, O, and H isotopic analysis. We address the question on when and how much chemical extraction is necessary for particular isotopic applications. We give procedures for cellulose extraction, and cover extraction chemistry, and QA procedures. We expect this chapter will be useful for those beginning research into tree ring stable isotopes, as well as experienced researchers.



Schollaen et al., Dendrochronologia 44 (2017) 133–145

Methods

Chapter 6: Tree Ring Stable Isotope Measurements: The Role of Quality Assurance and Quality Control to Ensure High Quality Data

Authors: J. Renée Brooks, Roland Werner, and William Rugh

Quality assurance and quality control (QA/QC) are important components of every study. In this chapter, we give an overview of QA/QC specific for tree-ring stable-isotope analysis from the perspective of the entire research project, rather than from the operation of Isotope Ratio Mass Spectrometers (IRMS). We address how users of stable isotope tree ring data can quantify the quality of their data for reporting in publications by calculating accuracy and precision. We cover some of the potential sources of error that can occur during sample processing and isotopic measurements, basic principles of calibration to the appropriate isotopic scales, and how researchers can detect error and calculate uncertainty using duplicates and quality control standards.

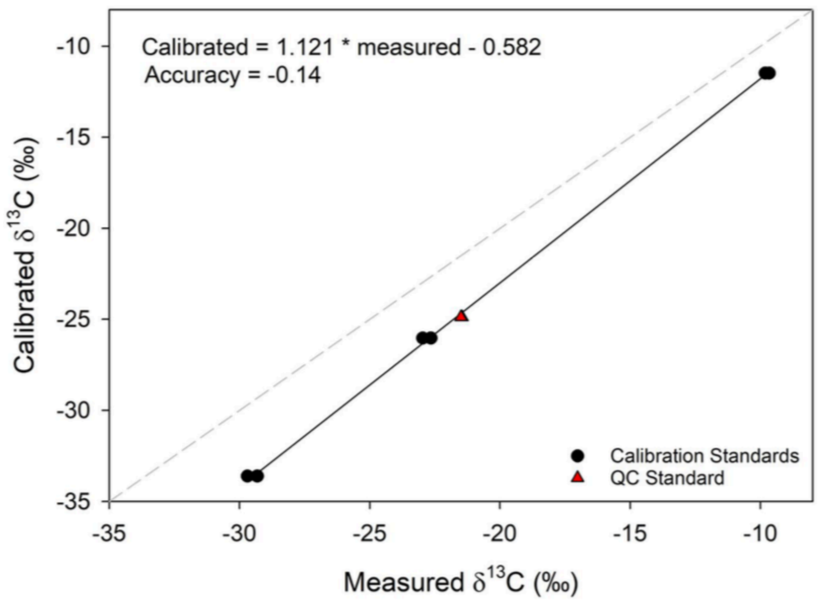


Figure 6.1: Typical calibration for adjusting measured sample values to the correct d scale illustrating the two types of systematic error affecting δ13C. The intercept represents the offset correction error, and the slope the scale factor error. The gray dashed line is a 1:1 line between measured and calibrated isotopic values.

Methods

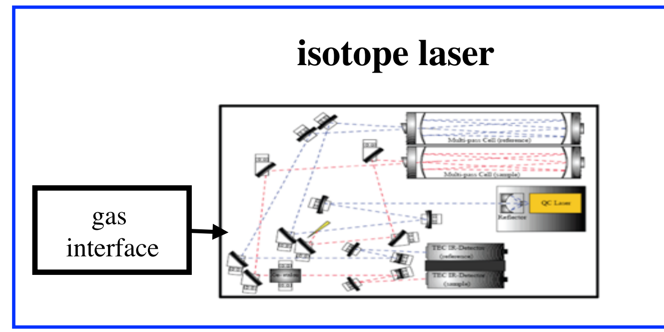
Chapter 7: Newer Developments in Tree Ring Stable Isotope Methods

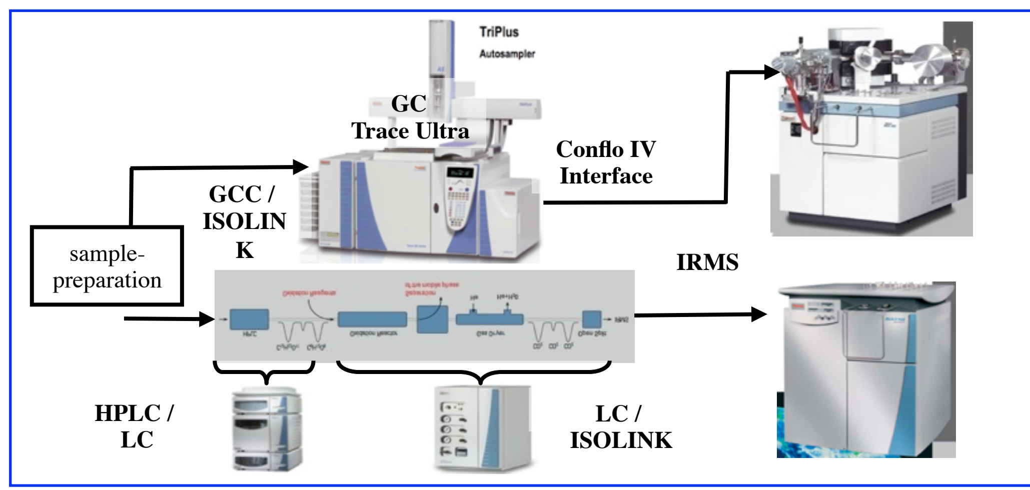
Authors: Katja Rinne-Garmston, Gerd Helle, M.M. Lehmann, E. Sahlstedt, J. Schleucher, J. and J. S. Waterhouse

Katja Rinne

Marco Lehmann

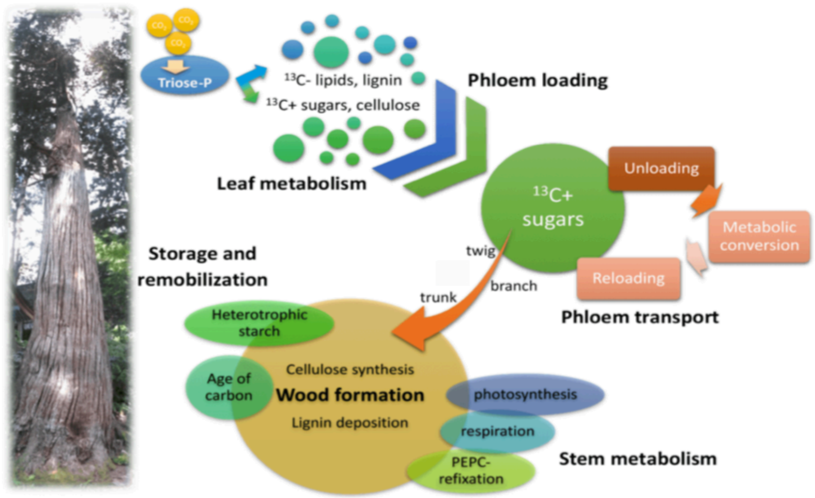
There are still significant gaps in our understanding about how a given isotopic composition of a tree ring is formed. This mainly concerns the metabolic processes and isotopic fractionations that occur post-photosynthetically in the leaf and phloem and also during tree ring formation (see Chapter 13). To achieve a profound level of knowledge of these processes that impact the environmental signal extractable from tree ring $\delta^{2}H$, $\delta^{13}C$ and $\delta^{18}O$ values, it is necessary to go beyond the conventional analytical methods in isotope analysis, which utilize “bulk” matter (e.g. leaves or sugar extract) and to focus on studies at inter-annual level and at intra-molecular level. New methodological developments have been made in the recent past that have shown high potential in this respect. They enable us to study isotopic fractionation processes and environmental signal in $\delta^{13}C$, $\delta^{18}O$ and to some extent also in $\delta^{2}H$ values at molecular (compound-specific isotope analysis, “CSIA”) and even at intra-molecular (position-specific isotope analysis) level. Combined with methodological advancements in intra-annual tree rings analysis (application of UV-laser), these new applications will improve our understanding of the relationships between climatic and isotope variability in tree rings. This chapter describes the new methodological developments of stable isotope analysis established for non-structural carbohydrates and tree rings.





ISOTOPIC FRACTIONATIONS FROM SOURCE TO WOOD

Figure 13.1. Conceptual scheme summarizing the main processes in the way from primary assimilates (triose-P) to the wood that may cause fractionation at time scales relevant to tree-ring archives.



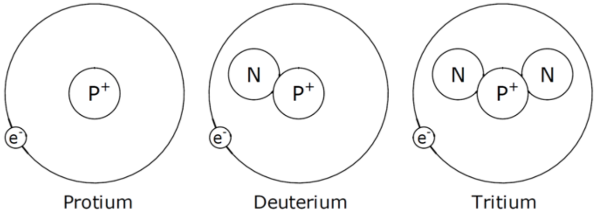
- **Chapter 8: Isotopes – Basic Terminology, Definitions and Properties** *by Roland Werner and Marc-Andre Cormier*
- **Chapter 9: Carbon isotope effects during assimilation of atmospheric CO2: implications for δ13C of tree-ring cellulose** *by Lucas A. Cernusak and Nerea Ubierna*
- **Chapter 10: Environmental, Physiological and Biochemical Processes Determining the Oxygen Isotope Ratio of Tree-ring Cellulose** *by Xin Song, Andrew Lorrey, Margaret M. Barbour*
- **Chapter 11: The Hydrogen Isotopic Signature: From Source Water to Tree Rings** *by Marco M. Lehmann, Philipp Schuler, Marc- André Cormier, Markus Leuenberger, Steve Voelker*
- **Chapter 12: Nitrogen Isotopes in Tree Rings: Challenges and Prospect** *by Martine M. Savard & Rolf T. W. Siegwolf*
- **Chapter 13: Postphotosynthetic Fractionation in Leaves, Phloem and Stem** *by Arthur Gessler and Juan Pedro Ferrio*

Isotopic fractionations from
source to wood

Chapter 8: Isotopes – Basic Terminology, Definitions and Properties

Authors: Roland Werner and Marc-Andre Cormier

The intention of this chapter is to give insight into the properties and peculiarities of the stable isotopes of the bioelements. Following an overview about the terminology and “technological jargon” used in stable isotope sciences, methods to calculate and express isotope abundances are presented. A short description of the physico-chemical basis of isotope effects is followed by a discussion on the concept of kinetic and/or thermodynamic isotope effects in (biochemical) reactions and the subsequent effects and consequences. Measures for calculation of isotope fractionation are introduced and the corresponding properties are discussed.

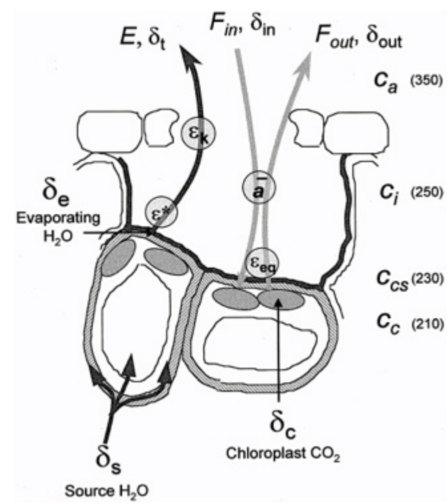


Isotopic fractionations from source to wood

Chapter 9: Carbon isotope effects during assimilation of atmospheric CO_2: implications for $\delta^{13}C$ of tree-ring cellulose

Authors: Lucas A. Cernusak and Nerea Ubierna

The carbon atoms deposited in the cellulose of tree rings originate in the pool of atmospheric CO_2 to which a tree's canopy is exposed. Thus, the first control on the stable carbon-isotope composition of tree-ring cellulose is in the atmosphere. Atmospheric CO_2 is, for the most part well mixed, but the sub-canopy air space can become depleted in ^{13}C in situations where turbulent exchange with the troposphere is hindered by high leaf are indices. Furthermore, there has been a monotonic decrease in the $\delta^{13}C$ of atmospheric CO_2 over the past two centuries as CO_2 has been added to the atmosphere through combustion of fossil fuels and land- use change. Discrimination against ^{13}C occurs upon assimilation of atmospheric CO_2 through the process of photosynthesis, with C3 trees, which comprise the overwhelming majority of all trees, showing the largest discrimination among photosynthetic pathways. The primary control on the extent of discrimination during C3 photosynthesis is the drawdown in CO_2 concentration from the air outside the leaf to the site of carboxylation in the chloroplast. Part of this drawdown is captured by the ci/ca ratio, that is, the ratio of intercellular to ambient CO_2 concentrations. The utility of this is that ci/ca can be related to intrinsic water-use efficiency, the amount of CO_2 taken up by photosynthesis for a given amount of water loss to the atmosphere, assuming a given evaporative demand. In this chapter, we review models that explain variation in carbon-isotope discrimination during C3 photosynthesis, and the opportunities that they present for extracting physiological information from $\delta^{13}C$ of tree ring cellulose. This information has proven invaluable in revealing how woody vegetation has responded to human-induced global change.

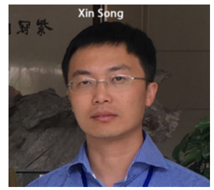


Gillon & Yakir, Plant Physiol. 123, 201-213; 2000

Isotopic fractionations from source to wood

Chapter 10: Environmental, Physiological and Biochemical Processes Determining the Oxygen Isotope Ratio of Tree-ring Cellulose

Authors: Xin Song, Andrew Lorrey, Margaret M. Barbour



Analysis of oxygen isotope ratio of tree-ring cellulose ($\delta^{18}O_{cell}$) is a promising tool for reconstructing past climatic variations and their influences on terrestrial ecosystems, but control mechanisms of $\delta^{18}O_{cell}$ complicated, involving multiple fractionation steps along the oxygen transfer pathway from precipitation water to the site of cellulose formation. The goal of the current chapter is to provide an overview of the current knowledge concerning fractionation mechanisms related to $\delta^{18}O_{cell}$. The review is organized by using the currently widely-used $\delta^{18}O_{cell}$ model as a reference context, and is focused on three main determinants of $\delta^{18}O_{cell}$: source water isotope ratio ($\delta^{18}O_{sw}$), leaf water isotope enrichment ($\Delta^{18}O_{lw}$), and biochemical fractionations downstream of $\Delta^{18}O_{lw}$. For each component, we summarize environmental, physiological, and/or biochemical processes underlying $\delta^{18}O$ fractionations, and provide explanations of how these processes are critically relevant for linking $\delta^{18}O_{cell}$ to climatic factors in real-world scenarios. We identify knowledge gaps in mechanistic controls of $\delta^{18}O_{cell}$, and highlight opportunities for more research to improve upon the existing model.

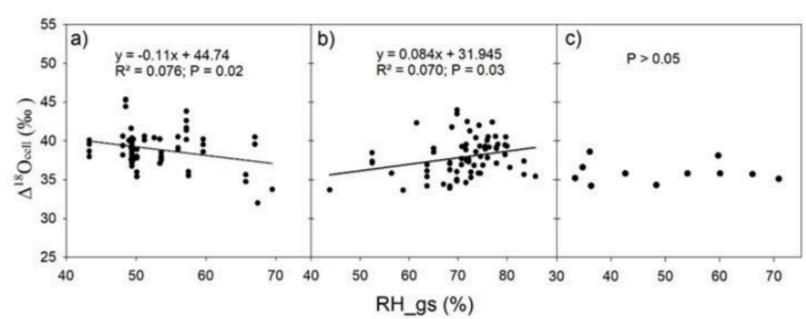


Figure 10.3 The relationships between $\Delta^{18}O_{cell}$ and relative humidity (RH) across geographic scales. Data presented in a) and b) were obtained from Helliker & Richter (2008) and Song et al. (2011) respectively. c) was adapted from Figure 3 of Cheeseman & Cernusak (2017).

Isotopic fractionations from source to wood

Chapter 11: The Hydrogen Isotopic Signature: From Source Water to Tree Rings

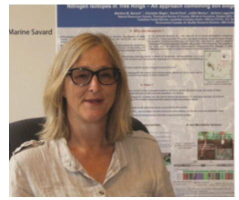
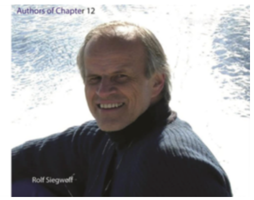
Authors: Marco M. Lehmann, Philipp Schuler, Marc-André Cormier, Markus Leuenberger, Steve Voelker

The hydrogen isotopic signature (δ^2H) of water in trees contains information on plant functional responses to hydrological and climatic changes. This is also true for non-exchangeable hydrogen isotopic signature (δ^2_{HNE}) of tree organic material, which holds, however, additional physiological and biochemical information that can be dated well if extracted from annual rings. Nevertheless, due to methodological difficulties and complications to interpret the signal, the δ^2_{HNE} analysis of tree-ring cellulose is still not widely applied compared to other isotope signals. In this chapter, we briefly explain the hydrogen isotope fractionation that occurs between source water and leaf water, however, mainly focusing on the mechanisms and drivers of δ^2_{HNE} variations in tree-ring material, methods and calculation to determine δ^2_{HNE}, and recent δ^2_{HNE} applications. Newest research show that the δ^2_{HNE} variations depend on the photosynthetic activity and the use of carbon storage and thus δ^2_{HNE} of tree-ring cellulose may therefore help to reconstruct such physio-biochemical instead of hydro-climatic processes. Nitration is still the most applied method to determine δ^2_{HNE} of cellulose, however, we recognized an increasing development to equilibrate cellulose with a water vapor of known isotopic source before δ^2_{HNE} analysis. The latter allows to correct for the fraction of exchangeable hydrogen isotopes, which is explained in more detail in this chapter. Moreover, we reviewed the most important findings related to δ^2_{HNE} variation in tree-ring cellulose from paleo to modern hydro-climatic research and studies of (sub-)annual variations across temporal and spatial scales. Finally, we give an outlook how δ^2_{HNE} can be used in future tree-ring studies. We conclude that δ^2_{HNE} has a very high potential to better understand tree-ring formation and thus further studies improving our understanding of δ^2_{HNE} variations in tree rings in concert with environmental condition proxies are suggested.

Isotopic fractionations from source to wood

Chapter 12: Nitrogen Isotopes in Tree Rings: Challenges and Prospect

Authors: Martine M. Savard & Rolf T. W. Siegwolf

Nutritive, but detrimental if at high levels, several nitrogen (N) forms involved in air and soil biogeochemical reactions constitute the N load trees assimilate. Although a large body of literature describes series of tree-ring N isotopes ($\delta^{15}N$) as archival systems for environmental changes, several questions relative to the isotopic integrity and reproducibility of trends still linger in the dendroisotopist community. This chapter reviews the fundamentals of forest N cycling and examines trees as N receptors in their very position, at the interface between the atmosphere and pedosphere. The related scrutiny of intrinsic and extrinsic mechanisms regulating isotopic changes also underlines flaws and forces of tree-ring $\delta^{15}N$ series as environmental indicators.

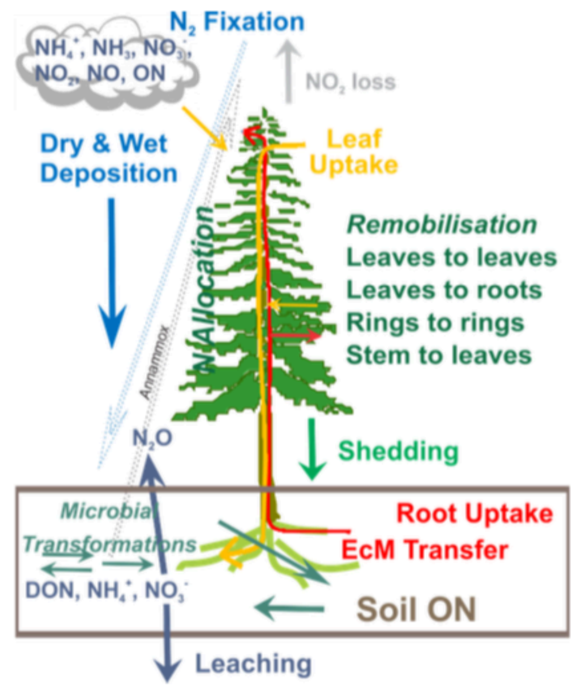


Figure 12.1 Representation of the forest nitrogen cycle. Processes influencing the bioavailability of N forms taken up by boreal and temperate trees are included; NO_2 loss is significant mostly in wetlands and tropical settings. EcM stand for ectomycorrhiza

Isotopic fractionations from source to wood

Chapter 13: Postphotosynthetic Fractionation in Leaves, Phloem and Stem

Authors: Arthur Gessler and Juan Pedro Ferrio

While the understanding of stable isotope fractionation during photosynthesis and the environmental factors affecting it is well developed (Cernusak et al., 2013), there is a larger gap of knowledge about the processes leading to alteration of $\delta^{13}C$ in downstream metabolic processes in the leaves and in heterotrophic tissues as well as during transport. Such processes lead to the generally observed pattern that non-photosynthetic tissues are enriched in ^{13}C compared to leaves in C3 plants (Badeck et al., 2005; Cernusak et al., 2009). In this chapter we will thus mainly focus on the path of carbon and its carbon isotopic composition from leaf photosynthate production to wood formation, as summarised in Figure 13.1. We will discuss here the different post-assimilation processes that might be able to alter $\delta^{13}C$ and thus cause a (partial) decoupling between the original leaf isotopic signals and the archived signals in tree rings and aim to provide an update of a recent review also tackling this topic (Gessler et al., 2014). Tree-ring carbon isotopes are determined on a broad range of temporal scales from very fine scale interannual variations up to millennial time scales (Barbour & Song, 2014). Knowledge of the potential alteration of the isotope signal on its way to the tree ring at various time scales allows for a better estimation of the uncertainties when reconstructing the coupling between tree processes and climatic drivers.

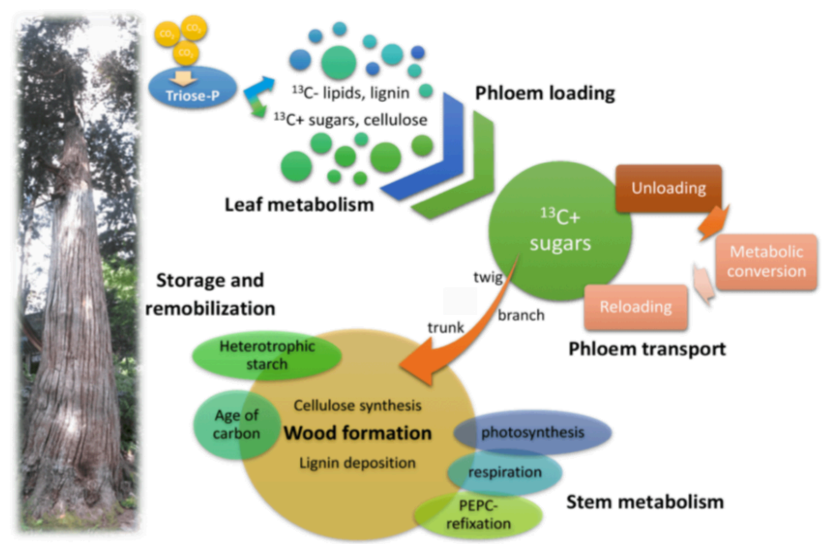
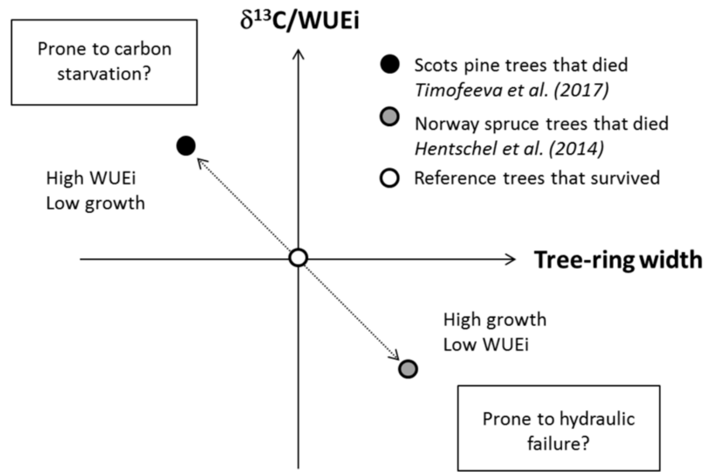


Figure 13.1. Conceptual scheme summarizing the main processes in the way from primary assimilates (triose-P) to the wood that may cause fractionation at time scales relevant to tree-ring archives.

PHYSIOLOGICAL INTERPRETATIONS

Figure 17.2: Conceptual diagram for explaining death or survival of trees from the same stand based on their earlier physiology and growth patterns.



- **Chapter 14: Fingerprint of environmental factors recorded in tree-ring stable isotopes** *by Laia Andreu-Hayles, Mathieu Levesque, Rossella Guerrieri, Rolf Siegwolf and Christian Körner*
- **Chapter 15: Intra-annual stable isotopic variation in tree rings** *by Akira Kagawa, Russell K. Monson, Giovanna Battipaglia*
- **Chapter 16: Probing tree physiology using the dual isotope approach** *by John Roden, Matthias Saurer, and Rolf Siegwolf*
- **Chapter 17: Intrinsic water-use efficiency derived from stable carbon isotopes of tree-rings** *by Matthias Saurer and Steve Voelker*

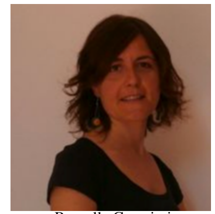
Physiological Interpretations

Chapter 14: Fingerprint of environmental factors recorded in tree-ring stable isotopes

Authors: Laia Andreu-Hayles, Mathieu Levesque, Rossella Guerrieri, Rolf Siegwolf and Christian Körner


Laia Andreu-Hayles


Mathieu Levesque


Rossella Guerrieri


Rolf Siegwolf


Christian Körner

This chapter aims to summarize strengths and caveats on the suitability of stable isotopes in tree rings for recording the fingerprint of environmental factors. First, environmental constraints limiting tree growth and shaping tree species distribution worldwide are discussed. Second, examples on optimal environmental range where tree-ring isotopes perform at best for recording environmental signals are provided, but also cases where physiological processes can mask climate signals. Third, connections between carbon assimilation at leaf level and investment for sugar production in the stem during the annual ring formation are described. Finally, the chapter highlights caveats in the interpretation of stable isotopes in tree rings, often due to lack of understanding on when and how tree canopy, stem and roots are physiologically interconnected. In some cases, carbon storage can be associated to a decoupling between photosynthesis and radial growth leading to complications in the interpretation of environmental signals recorded in tree- ring isotopes. As concluding remarks, the chapter provides possible solutions on how to improve the detection of climate signals by integrating scales and approaches

Physiological Interpretations

Chapter 15: Intra-annual stable isotopic variation in tree rings

Authors: Akira Kagawa, Russell K. Monson, Giovanna Battipaglia



In this chapter, we discuss the current state-of-understanding of intra-annual variation in the stable isotopes of carbon, oxygen and hydrogen in tree rings by combining research findings gained by using either natural-abundance or artificially-enriched isotopes. We focus on within-ring variation in carbon and oxygen isotope ratios, with an emphasis on aligning observed ratios in whole wood or extracted cellulose to seasonal dynamics in climate and phenology. We also present a discussion of isotopic fractionation that operates within the scope of observed variations across individual rings. Finally, we introduce a model that traces the seasonal partitioning of photosynthates into tree rings, which is based on experimental data gained by labeling photosynthates with artificially enriched $^{13}CO_2$ gas.

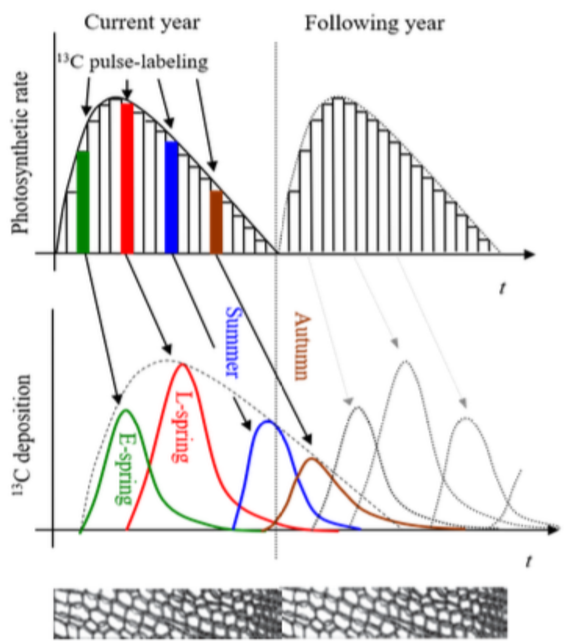


Figure 15.1: Conceptual model for carbon isotope signal transfer from leaves to tree rings.

Physiological Interpretations

Chapter 16: Probing tree physiology using the dual isotope approach

Authors: John Roden, Matthias Saurer, and Rolf Siegwolf

The environmental and physiological interpretation of stable isotope variation in organic matter is affected by many different and interacting factors. This is especially true when considering isotope variation in tree-rings, which are influenced not only by leaf-level photosynthetic processes but also by post-photosynthetic fractionation. It has been proposed that measuring multiple isotopes on the same sample may constrain such interpretations if one isotope provides independent information about important fractionation events that cause variation in another isotope. Here we describe one such "dual isotope approach" where oxygen isotope variation ($\delta^{18}O$) is used to probe the effects of stomatal conductance on carbon isotope ($\delta^{13}C$) variation for the same sample. This chapter describes the development of this conceptual model, constraints on model applicability, particularly with respect to tree-rings, and how it has been utilized to explore aspects of tree physiology.

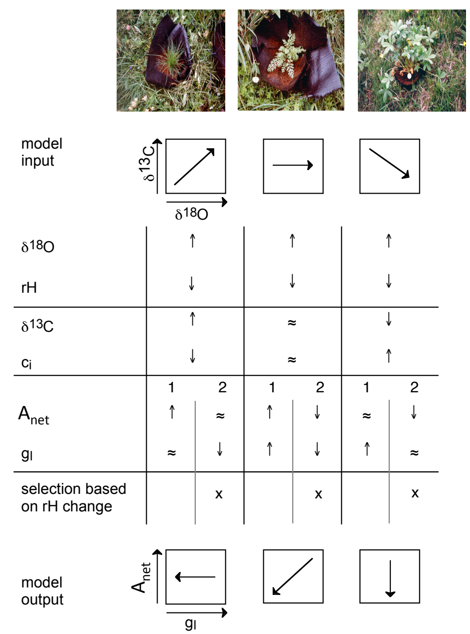


Figure 16.1. A subset of potential scenarios on how the dual-isotope conceptual model is used to interpret $\delta^{13}C$ variation. Adapted from Scheidegger et al., *Oecologia*, **125**, 350-357 (2000).

Physiological Interpretations

Chapter 17: Intrinsic water-use efficiency derived from stable carbon isotopes of tree-rings

Authors: Matthias Saurer and Steve Voelker

Stable carbon isotopes in tree-rings are not only useful to derive climatic information of the past. Based on the isotope fractionations during uptake and fixation of CO_2, physiological information can be retrieved, namely the ratio of assimilation to stomatal conductance, which is termed the intrinsic water-use efficiency (WUEi). This crucial plant physiological trait varies among species and environments and is characteristic of how much water is lost from leaves for a certain carbon gain. WUEi is of great importance at the scale of individual plants because it can determine plant performance and survival. WUEi also contributes how closely canopy- or ecosystem-scale carbon and water fluxes are coupled or divergent, which has implications for understanding biogeochemical cycling. Carbon isotopes in tree-rings can be used to estimate how WUEi of trees has changed in the past, e.g. due to increasing CO_2, nitrogen or other factors. Accordingly, many applications have explored this tool for various forest ecosystems across the globe, often reporting a strong increase in WUEi over the 20th century. Explicit comparisons of tree-ring WUEi to growth-data obtained from the same rings can help distinguish among strategies plants employ to take advantage of certain conditions (e.g., rising CO_2) or cope with various environmental stressors that often include increasing drought stress. In this chapter, we describe the theory of WUE-calculation, show some limitations of the method, give examples of the combined application of WUEi and tree-ring width, discuss photosynthetic limitations of WUEi and finally show how the method has been applied in large-scale tree-ring networks.

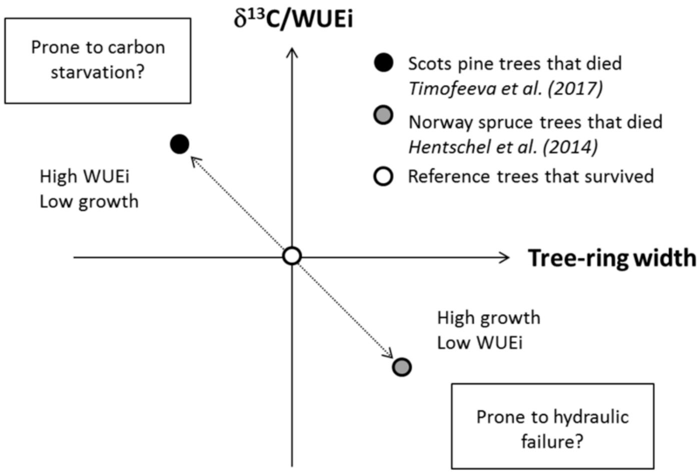


Figure 17.2: Conceptual diagram for explaining death or survival of trees from the same stand based on their earlier physiology and growth patterns. The location of the black circle indicates the position of dead trees from the Scots pine site in Switzerland (Timofeeva et al. 2017), while the grey circle refers to Norway spruce trees from southern Norway (Hentschel et al. 2016). Surviving trees indicated as open circle are considered as the reference in both studies.

ENVIRONMENTAL FACTORS IMPACTING ISOTOPIC FRACTIONATIONS

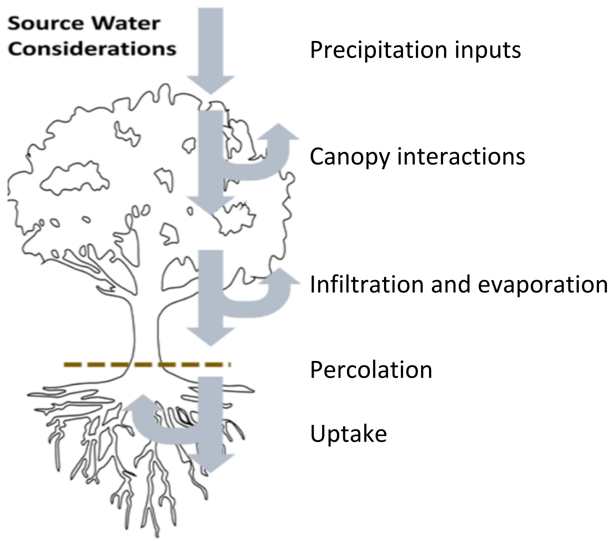


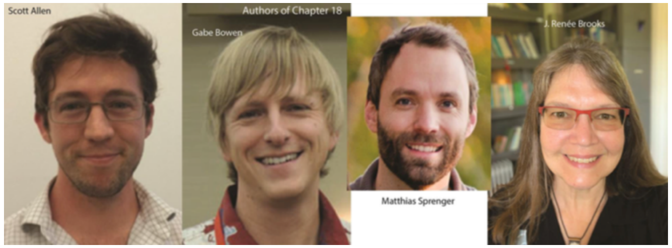
Figure 18.1 To estimate source waters to trees, we need to not only consider the average isotopic composition of precipitation, but also which precipitation reaches the soil layers from where roots take up water during the growing season and how that water is influenced by mixing and fractionation processes before reaching roots. While it will be rare that these questions can be considered to evaluate any insights drawn from tree-ring isotope ratios.

- **Chapter 18: Understanding temporal and spatial variations in source water: O and H isotope ratios from precipitation to xylem water** *by Scott T. Allen, Matthias Sprenger, Gabriel J. Bowen, J. Renée Brooks*
- **Chapter 19: Climate signals in stable isotope tree ring records** *by Mary Gagen, Josie Duffy, Giovanna Battipaglia, Valerie Daux, Isabel Dorado Linan, Laia Andreu Hayles, Elisabet Martínez-Sancho, Danny McCarroll, Tatiana A. Shestakova, Kerstin Treydte*
- **Chapter 20: Characteristics for different climate zones: Boreal, Mediterranean, and Tropical** *by Peter van der Sleen, Pieter A. Zuidema and*
  Thijs L. Pons (Tropical)
  Giovanna Battipaglia and Paolo Cherubini (Mediterranean)
  Olga V. Churakova (Sidorova), Trevor Porter, Alexander V. Kirdyanov, Vladimir S. Myglan, Marina V. Fonti and Eugene A. Vaganov (Boreal)
- **Chapter 21: Forest Management Effects on Tree-Ring Stable Isotopic Composition** *by John D. Marshall, J. Renée Brooks, Alan Talhelm*
- **Chapter 22: Impact of increasing CO_2, and air pollutants (NOx, SO_2, Ozone) on the C and O isotope ratio in tree rings** *by Rolf Siegwolf, Martine Savard, Thorsten Grams and Steve Voelker.*
- **Chapter 23: Insect and pathogen influences** *by Danielle E. M. Ulrich, Steve Voelker, J. Renée Brooks, Frederick C. Meinzer*
- **Chapter 24: Modelling tree ring isotope ratio, from leaves to whole trees** *by Liang Wei, J. Renée Brooks, John Marshall*

Environmental factors …

Chapter 18: Understanding temporal and spatial variations in source water: O and H isotope ratios from precipitation to xylem water

Authors: Scott T. Allen, Matthias Sprenger, Gabriel J. Bowen, J. Renée Brooks



Precipitation inputs
In what regions are the trees?
How do isotopes vary seasonally and inter-annually?
How much precipitation falls and when?
How does precipitation amount seasonality vary ?

Canopy interactions
Are fog and water taken up?
Are interception losses large?
From where is the ambient vapor sourced?

Infiltration and evaporation
Which precipitation infiltrates?
How much and when do soil waters evaporate?

Percolation
What is the turnover time?
How much do inputs bypass stored waters?

Uptake
Are roots accessing shallow or deep storages?
Are roots accessing recent or old water?
What is the growing season (when is water taken up?

Trees generally use water that originated as precipitation, but this does not mean that the isotope ratios of water used by trees and reflected in cellulose is an exact matches to that of precipitation. Precipitation isotope ratios are dynamic and only a (potentially biased) fraction of all precipitation reaches roots. In this chapter, we provide an overview of the terrestrial water cycle and the associated transport and fractionation processes that influence xylem-water isotope ratios. We highlight obstacles and opportunities to be considered, towards more accurately interpreting cellulose O and H isotope ratios.

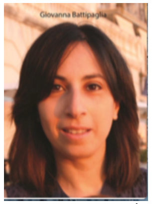
Figure 18.1 To estimate source waters to trees, we need to not only consider the average isotopic composition of precipitation, but also which precipitation reaches the soil layers from where roots take up water during the growing season and how that water is influenced by mixing and fractionation processes before reaching roots. While it will be rare that these questions can be quantitatively addressed to support modeling source waters, these questions can be considered to evaluate any insights drawn from tree-ring isotope ratios.

Environmental factors …

Chapter 19: Climate signals in stable isotope tree ring records

Authors: Mary Gagen, Josie Duffy, Giovanna Battipaglia, Valerie Daux, Isabel Dorado Linan, Laia Andreu Hayles, Elisabet Martínez-Sancho, Danny McCarroll, Tatiana A. Shestakova, Kerstin Treydte

Marx Gagen



Giovanna Battipaglia

Laia Andreu-Hayles

Kerstin Treydte

Our understanding of the climate variability of the last two thousand years has been significantly aided by large, network tree ring reconstructions, based on ring width and density data. However, the increase in data availability, for example of temperature reconstructions over the last two millennia has been accompanied by an understanding of the vital need for more information on past climates, from more places, including more variables than warm season temperature. Stable isotope measurements from tree- rings, both annual and non-annual, contain valuable climate, physiological and environmental information that can contribute to these research drives. Here we review the research frontier in stable isotope dendroclimatology and explore its contribution to palaeoclimate science. A cluster of studies carried out in the 1970's began the process of exploring what environmental information could be accessed by measuring isotopic variations in tree rings. However, without the quantitative knowledge of how plants fractionated isotopes as they moved through the metabolic pathways of photosynthesis, and physically around the plant, and how sensitive these fractionations were to temperature changes, the tantalizing evidence for a new climate proxy was effectively stalled until the underlying theoretical frameworks were in place. When this happened in the 1980s isotope dendroclimatology was born, with unequivocal evidence that stable isotope ratios measured from tree rings provided a usable environmental archive. The use of stable isotope dendroclimatology to explore past climates is dominated by evidence from stable carbon and stable oxygen isotope archives. The stable carbon isotope tree ring archives integrates 1) the stable isotope composition of atmospheric carbon dioxide, 2) various regulation rates within trees (photosynthetic and stomatal conductance rates), and 3) the environmental variables which influence those rates, such as temperature, sunlight, relative humidity and precipitation. Oxygen isotope records archives a balance of hydro climate variables (relative humidity, precipitation etc.) and the isotope signature of the meteoric source water. The research power of stable isotope dendroclimatology has increased tremendously in recent decades, thanks to better analytical systems that allow greater sample throughput and thus greater sample replication, greater understandings of the mechanistic controls over the isotope signal and increased geographical and species coverage of isotope studies. Whilst there are still questions to be answered around signal strength and age-related effects in different environments, and in different species, the proxy is now contributing to paleoclimatology in a far greater way than in the days of the first hints of 'isotope tree thermometers'.

Environmental factors …

Chapter 20: Characteristics for different climate zones: Boreal, Temperate Mediterranean, and Tropical

Authors:

***Tropical**: **Peter van der Sleen**, Pieter A. Zuidema and Thijs L. Pons.*



***Mediterranean**: Giovanna Battipaglia and Paolo Cherubini*


***Temperate:** see Chapter 19*

***Boreal**: Olga V. Churakova (Sidorova), Trevor Porter, Alexander V. Kirdyanov, Vladimir S. Myglan, Marina V. Fonti and Eugene A. Vaganov* .






Trees across latitudinal ranges are subjected to different environmental conditions and vary in their adaptations to cope with variability of the physical environment. Such differences affect tree physiology and stable isotope ratios in tree rings. In the following subchapters, we will discuss research on stable isotopes in tree rings from four climate zones: the boreal, (temperate see Chapter 19), Mediterranean, and tropical. Based on the available tree-ring stable isotope studies we focus on distinct climatological aspects that affect tree-ring stable isotope values for each climate zone separately, and highlight methodological as well as interpretational issues. In addition, we mention where, and how, stable isotope research could be expanded in the future. Notwithstanding a tremendous variability in the responses of trees to environmental conditions, and their change, we show that some generalization can be made for each climate region.

Environmental factors …

Chapter 20: Characteristics for different climate zones: Boreal, Temperate Mediterranean, and Tropical

Continued …

In ***Boreal*** forests, tree growth is inhibited by severe climate conditions – low temperature and low amount of precipitation -, and in some regions by the permafrost availability. Thaw of the latter affects $\delta^{18}O$ in melt water in such ways that it can lead to 'inverse' relationships between climate parameters and tree-ring isotopes. Stable isotope studies on trees from the boreal zone indicate that climate change, although lengthening the growing season, has increased drought stress in some regions.

Temperate forests are characterized by a distinct growing season with high precipitation and temperatures, resulting in often close to optimum growing conditions, but also high forest density and competition for light. While traditional tree-ring parameters are limited in recording strong climatic information in such complex growth conditions, tree-ring isotopes fill an important gap here by performing particularly well as proxies of climatic, and especially moisture related variations, but also of the tree physiological response to environmental changes.

In ***Mediterranean*** forests, tree growth is mainly controlled by low winter temperature and summer drought, often resulting in so-called "double stress" and the formation of Intra Annual Density Fluctuation (IADF) in tree rings. Stable isotope research in Mediterranean forests has helped to understand recent tree diebacks, as well as the consequences of (increased) forest fires.

In **Tropical** forests, tree growth is generally determined by seasonality of precipitation, and not temperature. Growth- and isotope anomalies are often associated with variability of the El Niño Southern Oscillation (ENSO), which can affect weather systems throughout the tropics and subtropics. Many tropical tree species lack visually distinct rings, or form highly regular growth bands, and intra-annual isotope sampling (in particular of $\delta^{18}O$) has been used to identify annual rings in such species. A consistent observation throughout these four climate zones is a general increase of iWUE during the last century (usually not associated with increased tree growth). Such trends are a direct consequence of the global increase of atmospheric CO_2 concentration, which in some regions is also reinforced by increased drought conditions.

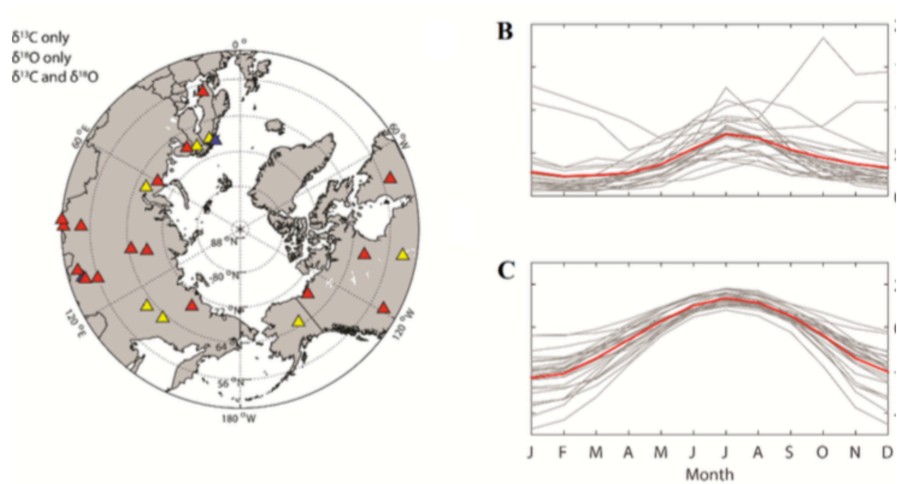


Figure 20.1 | Location of the Boreal study sites with $\delta^{13}C$ (yellow triangles), $\delta^{18}O$ (blue triangles) and both $\delta^{13}C$ and $\delta^{18}O$ (red triangles) isotope tree-ring cellulose chronologies (A). Precipitation (B) and temperature (C) distribution for the common period (1961-1990) for all published sites were calculated.

Environmental factors …

Chapter 21: Forest Management Effects on Tree-Ring Stable Isotopic Composition

Authors: John D. Marshall, J. Renée Brooks, Alan Talhelm

Forest management can sometimes have clear effects on stable isotope composition. These isotope effects often provide evidence of a particular mechanism at work in the response. We follow the growth of a forest stand from planting to harvest and discuss the measureable influences on isotopic composition along the way. In particular, we address 1) species and genotype differences resulting from planted seedlings, 2) thinning effects, 3) height growth and stand development, 4) competition and its control, and 5) fertilization effects. The chapter relies on meta-analyses where they are available and includes the results of a new meta-analysis of thinning and fertilization. We also elaborate on several studies of particular interest. We conclude that where the management effects are the question of interest, the isotopic data often helps to interpret their cause. In contrast, where the tree-ring data are being used for other purposes, these management events are sources of nuisance variation. Fortunately, they are predictable and therefore their influence can often be removed.

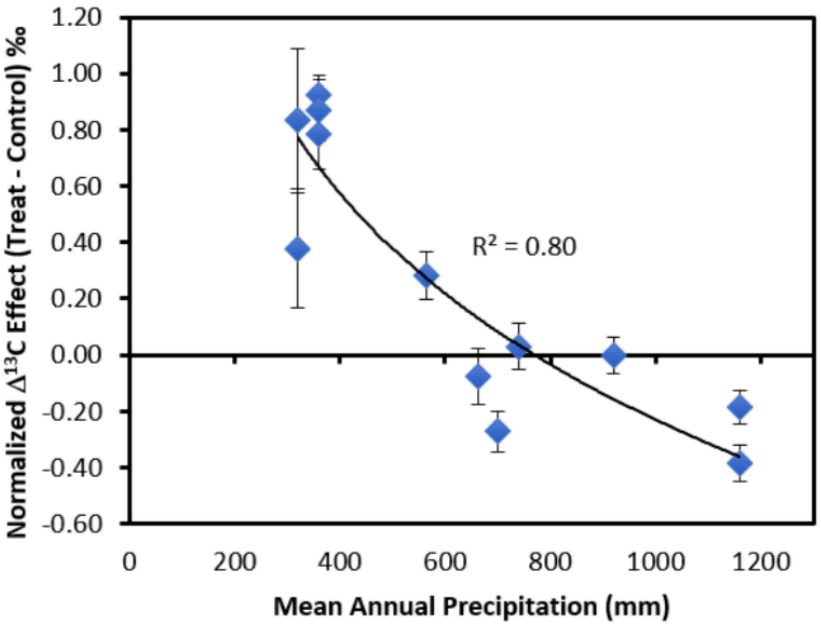


Figure 21.1 The effect of thinning on $\Delta^{13}C$ as a function of mean annual precipitation (MAP). $\Delta^{13}C$ increases with thinning when mean annual precipitation is low, and water is limiting, but decreases when water is abundant and changes in light drive the thinning response.

Environmental factors …

Chapter 22: Impact of increasing CO_2, and air pollutants (NOx, SO_2, Ozone) on the C and O isotope ratio in tree rings

Authors: Rolf Siegwolf, Martine Savard, Thorsten Grams and Steve Voelker.

Anthropogenic activities such as industrialization, land use change and intensification of agriculture strongly contributed to changes of the atmospheric trace gas concentration. Particularly CO_2, NOx, SO_2 and O_3 have a significant impact on plant physiology. CO_2as an essential component for plant growth is still strongly in the focus of interest as the effect of its increasing concentration is ambiguously discussed. Is its increase beneficial for plants or do plant respond “indifferently”? Oxidized N2- compounds (NOx), a product of combustion and lightning can either have a fertilizing or a toxic effect depending on its concentration. This is also the case for reduced forms of Nitrogen (NHy) mostly emitted from agricultural and industrial activities. Sulfur dioxide (SO_2) and Ozone (O_3) are mostly phytotoxic, depending on their concentrations and the tree health condition. Both substances are a product of industry and car traffic (combustion processes), besides natural backgrounds. All of the above mentioned compounds affect plant metabolism in their specific ways and to different degrees, leaving their fingerprints in the C and O isotope ratios of organic matter. In this chapter we will show how the impact of air pollutants and increasing CO_2 are reflected in the isotopic ratio of tree rings.

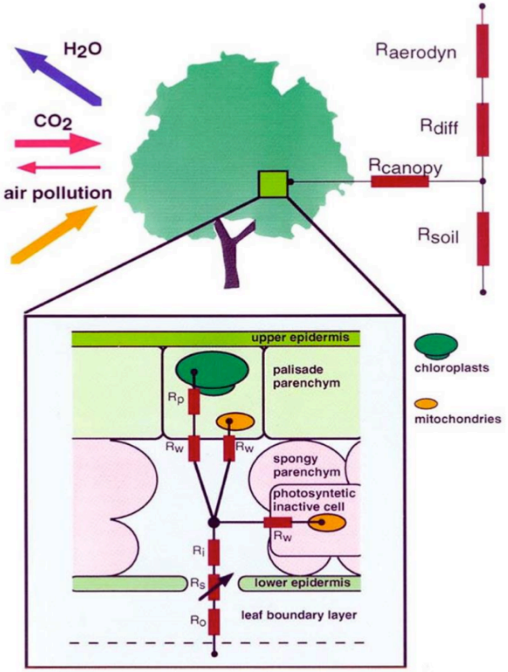


Fig 22.1 Pathways for the gaseous exchange between atmosphere and plant canopies and leaves and the various diffusive resistances for the traversing molecules (Nater, after Larcher, 2003).

Environmental factors …

Chapter 23: Insect and pathogen influences

Authors: Danielle E. M. Ulrich, Steve Voelker, J. Renée Brooks, Frederick C. Meinzer

Understanding long-term insect and pathogen effects on host tree physiology can help forest managers respond to insect and pathogen outbreaks, and understand when insect and pathogen physiological effects will be exacerbated by climate change. Leaf-level physiological processes are recorded in the carbon (C) and oxygen (O) stable isotopes of tree-rings (see Chapters 9, 10, 16 and 17). Therefore, tree-ring stable isotopes are affected by both the tree's environment and the tree's physiological responses to the environment, including insects and pathogens. Tree-ring stable isotopes provide unique insights into the long-term effects of insects and pathogens on host tree physiology. However, insect and pathogen impacts on tree-ring stable isotopes are often overlooked, yet can substantially alter interpretations of tree-ring stable isotopes for reconstructions of climate and physiology. In this chapter, 1) we discuss the effects of insects and pathogens on host physiology as they relate to signals possibly recorded by C and O stable isotopes in tree-rings, 2) we discuss how tree-ring stable isotopes reveal insect and pathogen impacts and the interacting effects of pathogens and climate on host physiology, and 3) we conclude by discussing the importance of considering insect and pathogen impacts on tree-ring stable isotopes for interpreting tree-ring stable isotopes to reconstruct past climate or physiology.

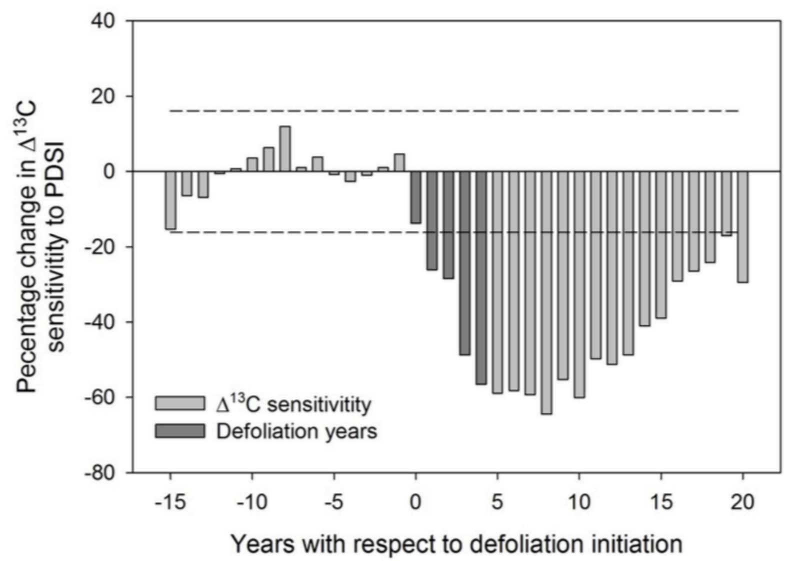


Fig. 23.1 Percentage change in ponderosa pine tree-ring $\Delta^{13}C$ sensitivity to PDSI before and after defoliation by pandora moth (C. pandora). Dashed lines indicate the percentage change in drought sensitivity that would be considered significantly different than 0 at $P < 0.01$ (±16.16%).

Isotope modeling

Chapter 24: Modelling tree ring isotope ratio, from leaves to whole trees

Authors: Liang Wei, J. Renée Brooks, John Marshall

As myriads physiological and physical processes from root to leaf are related to the variations of $\delta^{13}C$ and $\delta^{18}O$ in tree rings, an ideally perfect mechanistic model should represent all these processes. However, limited by our current knowledge and modeling power, we could only build models with known processes and parameterize them with reliable data. Tree ring stable isotopes could help process-based modeling by providing long-term data that can be used for parameterizing and validating models. In this chapter, we focus on reviewing what has been done in modeling tree ring stable isotopes, how physiological understandings have improved the modeling tools for the simulations of tree-ring stable isotopes, and how the modeling would help to improve our knowledge in studies of stable isotopes and tree physiology in return. We urge that stable isotope components should be included in any forest models with physical descriptions of photosynthesis and transpiration, especially when it is convenient to do so. Renee

BOOK-ABSTRACT

We are compiling a new book in the Springer Tree Physiology Series entitled, "Stable Isotopes in Tree Rings: Inferring Physiological, Climatic and Environmental Responses", due out in 2020. Because trees produce annual growth increments that can be precisely dated, annual and interannual variations in tree ring width and stable carbon, oxygen and hydrogen isotopes provide detailed records of past physiological responses to biotic and abiotic impacts over many decades and centuries. In contrast to non-living chronologies (ice cores, stalagmites etc.), trees modify base physical inputs in response to local microclimates through their physiological response to light, temperature, humidity, water availability, CO_2 and nutrients. Although this can make interpretation of isotopic variation in organic matter more complicated, it also means that these proxies can provide a wealth of additional information. Thus, an understanding of the combined physical and biological drivers of isotope fractionation in tree rings is crucial for paleoclimate interpretation. In addition, tree rings and the stable isotopes contained therein integrate dynamic environmental, phenological and developmental variations that can be used to study organism function in the present, recent anthropogenic influences, and can stand in as proxies for conditions in the distant past. The last few decades have seen tremendous progress in understanding the mechanisms by which tree physiology modifies stable isotope fractionation in organic matter.

This book will be the first to comprehensively cover the field of tree ring stable isotopes. It will highlight how tree ring stable isotopes have been used to address a range of environmental issues from paleoclimatology to forest management, and anthropogenic impacts on forest growth. It will also evaluate known strengths, as well as weaknesses, in the application of tree ring stable isotope analyses in inferring responses to complex environmental factors. Each of the 24 chapters has been authored by leading experts providing the most recent developments in the area.

Thank you for your interest and hopefully your feedback