

Linking intra-seasonal variations in climate and tree-ring $\delta^{13}\text{C}$: A functional modelling approach

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ARTICLE INFO

Article history:

Received 26 May 2009

Received in revised form 8 April 2010

Accepted 17 April 2010

Available online 22 May 2010

Keywords:

Stable carbon isotope discrimination

Tree ring

Process-based model

Intra-seasonal variation

Quercus petraea

ABSTRACT

Stable carbon isotopic composition ($\delta^{13}\text{C}$) in tree rings is a widely recognized tool for climate reconstruction, and several works suggest that seasonal information can be extracted from intra-ring $\delta^{13}\text{C}$ variations. In this study, we explored the link between climate and intra-seasonal oak ring $\delta^{13}\text{C}$ using a process-based modelling approach. The ISOCASTANEA model was developed to compute the seasonal dynamics of tree-ring $\delta^{13}\text{C}$ for deciduous species from half-hourly climatic data by accounting for photosynthetic discrimination and carbon translocation and allocation at the tree scale and in tree rings.

The model was applied from March 2005 to December 2007 in a 150-year-old deciduous oak forest. Canopy photosynthesis and stomatal conductance were calibrated using H_2O and CO_2 fluxes measured by the eddy flux technique, and simulated $\delta^{13}\text{C}$ values were compared to seasonal patterns of total organic matter $\delta^{13}\text{C}$ measured in tree rings for 2006 and 2007 at the same site. With the inclusion of carbon translocation and with regard to ^{13}C enrichment of starch compared to soluble sugars, the model can reasonably simulate the intra-seasonal and inter-annual variability of tree-ring $\delta^{13}\text{C}$ using the same parameter values for 2006 and 2007. The amplitude of the seasonal carbon isotope pattern in tree rings was influenced by both photosynthetic and post-photosynthetic processes (starch enrichment and reserve use). The $\delta^{13}\text{C}$ variations in the early part of the ring, i.e., mainly in the earlywood, were related mostly to carbohydrate metabolism, although diluted information about environmental conditions during the previous year could also be found. The last part of the ring, consisting mainly of latewood, was found to be a good recorder of current-year environmental conditions, in particular relative humidity, at a fine temporal resolution when the growth rate was high. The sensitivity of the $\delta^{13}\text{C}$ in the early part of the ring to carbohydrate metabolism suggests that intra-ring $\delta^{13}\text{C}$ could be used to explore the relationship between tree decline or mortality and carbohydrate deficiency.

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1. Introduction

Stable carbon isotopic composition ($\delta^{13}\text{C}$) in tree rings is a widely recognized tool for climate reconstruction (Raffalli-Delerce et al., 2004). Carbon isotope composition is known to capture information both on environmental conditions (McCarroll and Loader, 2004) and on anthropogenic changes in the $\delta^{13}\text{C}$ content of atmospheric carbon dioxide (February and Stock, 1999).

The link between the climate and tree-ring $\delta^{13}\text{C}$ is usually analyzed using a model of photosynthetic discrimination at the leaf scale (Farquhar et al., 1982). This model mechanistically relates the $\delta^{13}\text{C}$ of photoassimilates to the ratio of intercellular and atmospheric CO_2 concentrations (C_i/C_a) and, therefore, to the ratio between CO_2 assimilation and stomatal conductance or intrinsic water use efficiency (WUE_i). In this way, the stable carbon isotopic

composition of tree rings provides a time-integrated estimate of WUE_i . Numerous studies have found correlations between tree-ring $\delta^{13}\text{C}$ and environmental factors known to influence WUE_i , such as soil water availability, rainfall, vapor pressure deficit, relative humidity, temperature, solar radiation, and nutrient availability (Farquhar et al., 1989; Leavitt, 1992; Dupouey et al., 1993; Saurer et al., 1997; Porté and Loustau, 2001; Barbour et al., 2002).

Growth rings are also known to exhibit radial (e.g., seasonal) variation in $\delta^{13}\text{C}$ (Leavitt and Long, 1986; Leavitt, 2002; Barbour et al., 2002; Helle and Schleser, 2004). Although some trends suggest that these variations are related to variations in temperature, soil water availability, radiation, atmospheric CO_2 concentration, or atmospheric $\delta^{13}\text{C}$ over the growing season (Leavitt, 2002; Barbour et al., 2002), other studies suggest that the seasonal variation in tree-ring $\delta^{13}\text{C}$ is not fully explained by this model of photosynthetic discrimination (Hemming et al., 2001; Ogée et al., 2009), particularly in deciduous species (Helle and Schleser, 2004). In fact, the relationship between climate and $\delta^{13}\text{C}$ in leaf assimi-

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lates could be altered before organic-matter deposition in tree rings by numerous physiological and biochemical processes, such as post-photosynthetic fractionation (Badeck et al., 2005) during the transport of assimilates (Damesin and Lelarge, 2003), during the biosynthesis of wood compounds (Panek and Waring, 1997) or during respiration (Duranceau et al., 1999; Tcherkez et al., 2003; Damesin and Lelarge, 2003), or by mixing with carbon reserves (Damesin and Lelarge, 2003; Kagawa et al., 2006; Keel et al., 2007; Ogée et al., 2009).

One of the main difficulties in correlating $\delta^{13}\text{C}$ in tree rings with environmental parameters arises from the translocation and storage of carbohydrates (Gessler et al., 2007). The use of carbon reserves for structural growth and the mixing of all sequentially-assimilated carbon within the mobile carbon pool dampens the link between climate and structural tissue $\delta^{13}\text{C}$ (Keel et al., 2007) and induces a temporal lag between photosynthesis uptake and the use of photosynthates for ring formation in the stem (Kagawa et al., 2006). In a modelling study, Hemming et al. (2001) stressed that the carbon source for growth may be extremely important in determining the $\delta^{13}\text{C}$ value of the resulting wood; in particular, it may affect the relative contributions of photosynthates and stored starch that is generally ^{13}C -enriched compared to soluble sugars (Brugnoli et al., 1988). Helle and Schleser (2004) described the $\delta^{13}\text{C}$ pattern in rings of broadleaf species as a recurrent triphase pattern that is largely independent of seasonal variations in photosynthetic fractionation and may be related to the relative use of ^{13}C -enriched stored carbon reserves (mainly starch) and of ^{13}C -depleted new photosynthates. According to this argument, earlywood is assumed to contain photoassimilates from previous years, while latewood is composed mainly of photoassimilates from the current growing season (Kagawa et al., 2006). This is particularly the case in oaks where trunks are known to begin radial growth before leaves are fully expanded (Breda and Granier, 1996).

The aim of this paper is to develop a model that links intra-seasonal $\delta^{13}\text{C}$ variations in deciduous oak tree rings and climatic conditions by doing the following:

- (1) Integrating a leaf gas exchange model of photosynthetic discrimination (Farquhar et al., 1989) and a quasi-topological model accounting for carbon translocation and distribution at the tree scale and in tree rings within CASTANEA, which is a physiological multilayer forest ecosystem model simulating energy, water, and carbon balances at the stand scale from half-hourly climatic data (Dufrêne et al., 2005);
- (2) Calibrating the model to obtain a best fit for carbon and water fluxes in the Barbeau forest from March 2005 to December 2007. The Barbeau forest site is equipped with a flux tower measuring half-hourly climatic data and exchanges of carbon and water between the atmosphere and the ecosystem;
- (3) Comparing simulated ring $\delta^{13}\text{C}$ outputs to high temporal resolution measurements of intra-seasonal ring $\delta^{13}\text{C}$ sampled in oaks at the study site and assessing the necessity of accounting for the main processes leading to post-photosynthetic discrimination, i.e., starch synthesis (Gleixner et al., 1993) and respiration (Tcherkez et al., 2003; Kodama et al., 2008).

Tree rings corresponding to the years 2006 and 2007 were sampled. The model was run from March 2005 to provide consistent initial $\delta^{13}\text{C}$ values for starch and soluble sugars at the beginning of 2006.

1.1. Model description

The main difficulty in the development of the model was the modelling of C translocation and partitioning within the tree (Fig. 1A). For example, the phloem pathway is explicitly described and organ compartmentalization for structural and mobile carbon

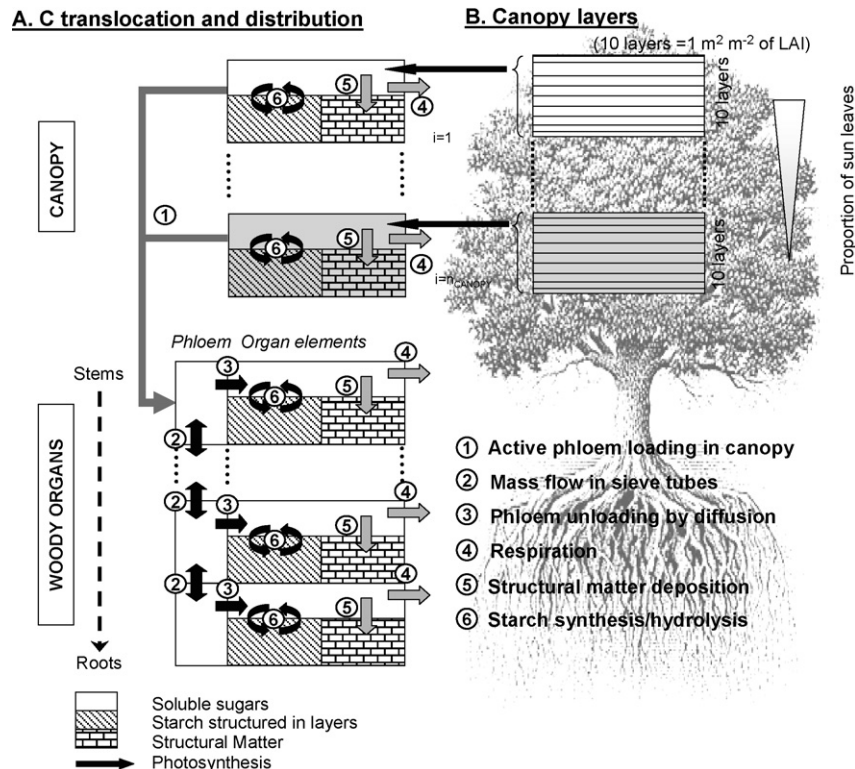


Fig. 1. Description of the C translocation and allocation model structure: (A) the C translocation module and (B) canopy layers in which photosynthesis occurs. The circled numbers associate physiological processes to the C fluxes in the C translocation model.

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