

# Seasonal variations of stable carbon isotopes from tree-rings of *Quercus petraea*

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## Introduction

Climate change is frequently accompanied by changes in seasonality, seasonal hazards and increased inter- and intra-annual variations. The ability to identify the causes of these alterations especially in the context of past regional climatic changes will help in the detection of future environmental developments. In addition the identification of characteristic patterns or cycles will assist modelers in assessing their predictions.

Many high-resolution climate proxy data are derived from tree rings (ring density, ring width, and isotopic composition of wood). However, based on our current understanding of tree-ring formation we are unable to deduce annual or season specific climate variables in order to provide comprehensive climate data for reconstructions at regional scales (Jones *et al.* 2001). A better understanding of tree-ring response to seasonal changes and, thus, to climate forcing is important for understanding the causes on past tree growth. Therefore, more work is currently required to better interpret the gained proxies (Briffa *et al.* 1998; Briffa & Osborn 1999).

In this respect, high resolution intra-annual isotope studies can help to elucidate the seasonal signal transfer in trees. These studies should greatly help in the construction of novel plant/climate/isotope models.

Recent intra-annual studies have revealed significant seasonal changes in the carbon and oxygen isotope composition (Schleser *et al.* 1999, Helle & Schleser in prep.).

Environmentally influenced stomatal activity, in combination with changes of enzymatic turnover, provokes fractionation shifts that are currently assumed to show up similarly in the corresponding tree-rings.

Provided the above reasoning is correct, a high intra-annual resolution should screen the weather conditions along the season experienced by the corresponding tree. Highest  $\delta^{13}\text{C}$ -values of the year should appear in wood formed during summer, when high temperatures, low air humidity and a high ground-water deficit lead to narrow stomatal apertures of the leaves. Within each ring, the earlywood (EW) and the end of the latewood (LW) should be characterized by the lowest  $\delta^{13}\text{C}$ -values.

## Results and Discussion

Previously published data from investigations dealing with radial subsections of treerings in part reveal rather contradictory results (e.g. Wilson & Grinsted, 1977; Leavitt & Long, 1982, 1986, 1991; Kitagawa & Wada, 1993; Ogle & Mc Cormac, 1994; Loader *et al.* 1995).

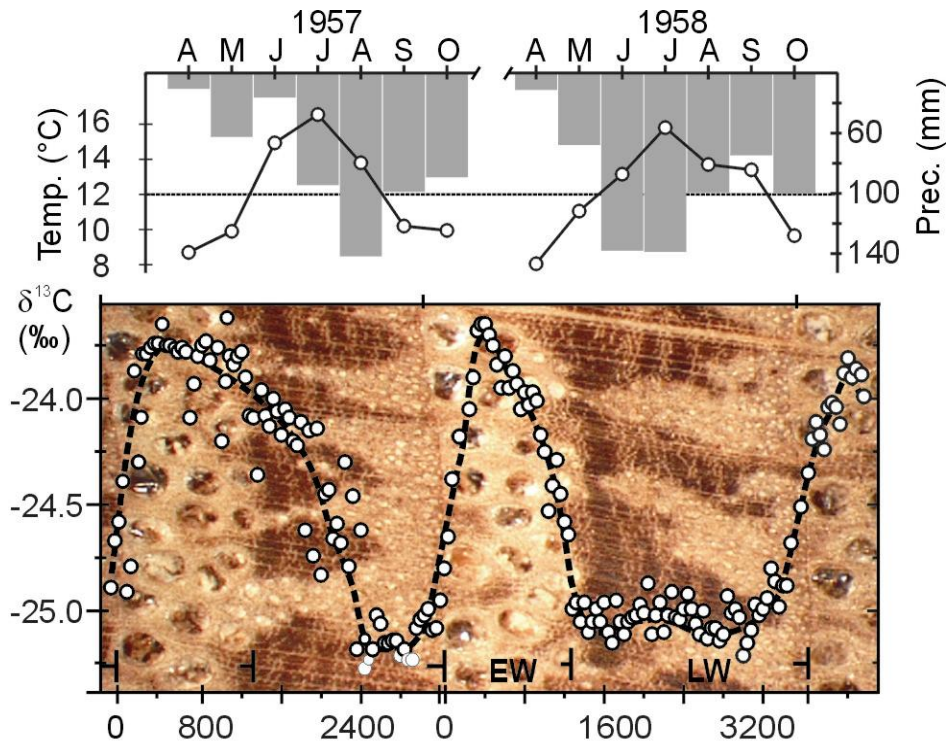


Fig. 1: Lower part: typical example of the seasonal tree-ring  $\delta^{13}\text{C}$  pattern in two tree rings of oak (*Quercus petraea*) from N-Ireland. The tree rings were divided into slices of  $40\mu\text{m}$ . Upper part: the corresponding monthly mean values of temperature (lines) and precipitation (bars).

However, many of these authors found systematic differences between EW and LW.

Detailed investigations of the intra-annual carbon isotope composition (Schleser *et al.* 1999, Helle & Schleser in prep.) revealed an overall pattern which is similar for all broad leaf species.

For this study, two tree rings of oak (*Quercus petraea* (Matt.) Liebl.) from Northern Ireland were subdivided into slices of  $40\mu\text{m}$  thickness. Oak belongs to the group of deciduous trees with ring porous wood. Their EW formation starts before bud burst. It is completed before the leaves have fully expanded, i.e. before they become net exporters of assimilates (e.g. Pilcher 1995). Consequently EW has to incorporate carbon from previous years, accumulated as starch during summer and stored during winter. In contrast, coniferous tree species like e.g. *Pinus resinosa* or *P. banksiana* are known to produce almost the entire EW from current photosynthates (Dickmann & Kozlowski 1970, Glerum 1980).

The results of our analysis, shown in Figure 1, constitute a typical example of the seasonal  $\delta^{13}\text{C}$  pattern in the growth rings of broad-leaved trees. During the development of EW,  $\delta^{13}\text{C}$  data rise to a maximum and subsequently fall to a minimum, which is reached in the LW section of a tree ring. At the end of LW formation  $\delta^{13}\text{C}$  values start rising again. In contrast to the model predictions of carbon isotope fractionation during  $\text{CO}_2$  fixation, highest  $\delta^{13}\text{C}$  values always show up in the EW section and lowest  $\delta^{13}\text{C}$  values are always found in the LW section.

The reasons for the observed  $\delta^{13}\text{C}$  pattern in oak tree rings are quite complex, not only because tree-ring material partly originates from the previous years. In addition carbohydrates undergo a number of post-photosynthetic chemical modifications, which involve isotope fractionations.

In general, shifts of the stable carbon isotopes can occur due to carbon partitioning at metabolic branching points. The extent to which the carbon isotope composition shifts, depends on pool size and flux rates into the different metabolic directions.

In this respect, it is important to note that previous years starch material is not necessarily isotopically labelled by the climate signal of its formation period. It rather exhibits a general enrichment of  $^{13}\text{C}$  as compared to far less polymerised sugars (Gleixner *et al.* 1993). Consequently, the incorporation of starch-derived  $^{13}\text{C}$ -enriched carbon can result in the observed isotopically heavier EW.

The rising  $^{13}\text{C}$  enrichment of EW in the period of fast growth at the beginning of the vegetation period might also be a consequence of the decreasing amount of available sugar reserves in conjunction with a  $^{13}\text{C}$  enrichment of these reserves. Isotopically “lighter” molecules are turned over faster and removed from the sugar pool by formation of EW and  $\text{CO}_2$  respiration, leading to an enrichment of the remaining sugars.

Bud burst and EW formation are accompanied by the highest respiration rates of the year in order to meet the energy requirements of the tree during this period of fast growth.

The intense carbon-isotope partitioning between anabolic and catabolic metabolism can lead to a further  $^{13}\text{C}$  enrichment of EW, since “heavier” sugar molecules are preferentially used for polymerization of cellulose, whereas “lighter” molecules are preferred in secondary metabolism, leading to  $^{13}\text{C}$ -depleted stem-respired  $\text{CO}_2$ , and secondary plant products (e.g. lignin) (Schmidt & Gleixner 1998).

The  $\delta^{13}\text{C}$  decline of late EW and early LW results from the increasing incorporation of currently produced assimilates. As soon as the leaves become net exporters of photosynthates, the sugar pool in the stem will be replenished. Simultaneously the sugar pool will be isotopically diluted by assimilates with  $\delta^{13}\text{C}$  signals from recent leaf-isotope fractionation processes, driven by the ambient environmental conditions.

Along with the increasing accumulation of starch during the summer months, changes in carbon-isotope partitioning take place between growth and storage. This probably leads to  $^{13}\text{C}$ -enriched starch and therefore  $^{13}\text{C}$ -depleted wood.

Effects from  $\text{CO}_2$  respiration might play a minor role, since much of the  $\text{CO}_2$  released is re-fixed by photosynthesis.

The increase in  $\delta^{13}\text{C}$  of late LW can be assigned to changes in the carbohydrate metabolism going along with leaf senescence in autumn.

Therefore, not only the isotope composition of EW but also that of LW is influenced by non-climatic, post-photosynthetic tree-internal processes, all of which have to be considered.

In addition, annual ring growth is a nonlinear process, which makes it difficult to assign intra-annual  $\delta^{13}\text{C}$  values to specific dates or weather events. The ability of a tree-ring to integrate environmental information depends on the longevity of its cells, which is, among other factors, species dependent.

Nevertheless, the  $\delta^{13}\text{C}$  pattern in tree rings of oak exhibits different peculiarities, which can be attributed to certain weather situations along the vegetation period. In Figure 1, the radial carbon-isotope distribution of the years 1957 and 1958 is compared to monthly means of temperature and the amount of precipitation.

The months of June and July of 1957 were particularly dry and warm. Following the model constraints for carbon-isotope fractionation during photosynthesis, the tree responded with narrow stomatal apertures and, therefore, the produced assimilates show a relatively high  $^{13}\text{C}$  content. This also caused a fairly slow decline of  $\delta^{13}\text{C}$  across the latewood. The  $\delta^{13}\text{C}$  values for 1958 fall immediately to a minimum at the beginning of latewood development, showing no significant  $^{13}\text{C}$  variations further on. Indeed, the weather conditions during the summer months of the year 1958 varied little, especially precipitation, obviously causing no isotopic variations. Presumably water supply and temperature conditions just varied within the optimum range of tree growth, inducing no stress to the tree.

## **Conclusions**

Carbon-isotope signals in tree rings are not direct proxies for changing meteorological variables encountered in the vicinity of trees. The present knowledge about carbohydrate partitioning during the transfer of photosynthates into tree rings is poor. In addition the fractionations involved in the seasonal interplay of major tree-physiological processes, such as accumulation and remobilization of storage material, varying stem respiration and build-up of tree-rings, are not known in detail. Therefore, their quantification is difficult to accomplish. The complexity of these processes presently prevents the establishment of a clear linkage of weather events to associated intra-annual isotope signals.

Only through a more complete knowledge of the factors controlling plant-physiological processes (e.g., respiration vs. photosynthesis, transitory storage, re-mobilization, length of dormancy), we may be able to better understand seasonal control and signal preservation.

The greater operating expenses of isotope work as compared to the costs of ring-width and ring-density investigations could well pay off in the future, because isotope studies bear the potential of improving the knowledge about tree-physiological processes. They could help to improve the understanding of growth in relation to climate. So far dendroclimatologists have treated the system as a “black box”, applying statistical methods that, although effective, mostly disregard direct plant-physiological processes. In future, a combination of plant-physiological and dendroclimatological methods could open up new opportunities for a more realistic approach. The tree-ring climate archive may then provide unique information on local to regional scales about the impacts of global change in regions that are sensitive to this change.

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