

Chapter 14

Limits and Strengths of Tree-Ring Stable Isotopes



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Abstract This chapter aims at summarizing strengths and caveats on the suitability of stable carbon and oxygen isotopes in tree rings as recorders for fingerprints of environmental influences. First, environmental constraints limiting tree growth and shaping tree species distribution worldwide are discussed. Second, examples are presented for environmental conditions under which tree-ring isotopes record environmental signals particularly well, but also cases where physiological processes can mask climate signals. Third, the link between leaf-level carbon assimilation and the investment of assimilates in the stem during the annual ring formation are discussed in light of the resulting deviations of the isotopic values between leaves and tree rings. Finally, difficulties and pitfalls in the interpretation of stable isotope signals in tree rings are reviewed. These problems often result from a poor understanding of when and how the tree canopy, stems and roots are physiologically interconnected. Current literature suggests that photosynthesis and radial growth are only loosely coupled, if at all, challenging the interpretation of environmental signals recorded in

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tree-ring isotopes. Harsh environmental conditions (e.g. low temperatures, drought) often result in a decoupling of carbon assimilation and growth. The chapter closes by providing possible solutions on how to improve the detection of environmental information from stable isotope signals by integrating scales and different methodological approaches.

14.1 Introduction

Climate exerts a major control of tree growth and has shaped the current phyto-geographical distribution of tree species and populations within tree species worldwide. Understanding the interactions between environmental factors and physiological responses at leaf and tree level and for tree growth is key for understanding tree species distributions, ecosystem functioning and the role of forests in the carbon and hydrological cycles (Pallardy 2008). Tree rings represent a proxy for radial growth that result from cambial activity (Chap. 3) integrating metabolic processes over time and space. Climate variations influence carbon sink processes such as radial growth (Körner 2003) and can be inferred using tree-ring width records (Fritts 1976), but they also modulate photosynthesis, transpiration and other physiological processes that are recorded in the stable isotopic composition of plant tissues (Dawson and Siegwolf 2007). The use of stable isotopes as an indicator of physiological responses to climate relies on a mechanistic understanding of the isotopic fractionation during metabolic and transport processes (see Chaps. 9 and 10). These isotopic “finger-prints” recorded in the tree’s tissue (such as leaf, wood and roots) represent the tree-environment interactions over a lifetime (McCarroll and Loader 2004; Cernusak et al. 2013). Environmental information reflected in isotopic signatures is fundamental for the reconstruction of past environmental changes and periods of extreme conditions such as flooding, drought, temperature extremes (Chaps. 19–22) or exposition to pollutants (Chap. 24).

Traditional tree-ring studies solely based on temporal variations in tree-ring width have been mostly conducted on trees from locations with limiting or extreme climatic growth conditions (Fritts 1976). This approach provides information on the dominant climate factor limiting tree growth, which is reflected in tree-ring width. Fritts (1976) postulated that under non-limiting environmental conditions for growth, high growth rates and low inter-annual variability (“complacent” tree growth) are observed, while for trees located at the limit of their distribution range, reduced growth rates and high inter-annual variations (“sensitive” tree growth) are found. However, advances in tree-ring analyses have shown a higher complexity in this conceptual framework. For instance, under non-limiting growth conditions, extreme events and environmental stressors can occur in specific moments of the growing seasons leading to differential imprints in tree-ring anatomical features. Nevertheless, samples for dendroclimatic purposes are often taken from trees growing near their ecological distribution limits with inter-annual variations in tree-ring width, which are more likely related to a single limiting environmental factor, e.g. temperature or precipitation. In contrast,

stable isotopic ratios in tree-ring samples usually show a higher sensitivity under non-limiting growth conditions than tree-ring width. For example, numerous studies have reported a stronger sensitivity of stable carbon, C ($\delta^{13}\text{C}$) and oxygen, O ($\delta^{18}\text{O}$) isotopes than ring width to temperature and moisture under temperate moist climates (e.g. Treydte et al. 2007; Hartl-Meier et al. 2015; Young et al. 2015; Levesque et al. 2017), but also in humid tropical regions (e.g. Brienen et al. 2012; van der Sleen et al. 2017 and references therein, see Chap. 22).

14.2 Environmental Constraints Impacting Tree Growth and Tree Species Distribution

Numerous biophysical and biogeochemical factors and their interactions limit tree physiology and growth, and thus species distribution and terrestrial vegetation growth. Besides soil nutrient availability (Du et al. 2020), the most important factors influencing distribution, physiology and vegetation growth of plant species (Pallardy 2008), are temperature, water availability, air humidity, sunlight and atmospheric CO_2 concentrations (Nemani et al. 2003; Running et al. 2004; Seddon et al. 2016). However, biogeochemical models often operate with a stringent hierarchy of the driving variables starting with water availability and temperature as the most important limiting factors for terrestrial net primary productivity, followed by sunlight limitation (Fig. 14.1a), while neglecting the importance of nutrient availability (Churkina and Running 1998). These models are often inaccurate because they frequently ignore the variability of the local site properties together with the available resources and environmental conditions as driving factors. The requirements and strategies in using resources, i.e. moisture, nutrients, and responsiveness to light, temperature and air humidity is species specific and impact their phytogeographical distribution across the globe in a mechanistic way. Stochastic events such as environmental extremes (e.g. frost, drought, fires events) or forest dynamics (e.g. mortality, regeneration, species competition) may also shape tree species distribution.

At high latitude and high elevation sites, temperature exerts the strongest control on plant physiology and growth, while in arid and semi-arid temperate and tropical regions soil moisture and air humidity are the most limiting factors. In regions with high frequency of cloud occurrence and/or cloud immersion light scattering via cloud / fog droplets improves the light distribution within the crown enhancing the irradiation for the shaded leaves in the lower tree crown sections. This often leads to a higher total crown C-acquisition (Berry and Goldsmith 2020), which impacts the isotope ratio in leaves and potentially growth. While water, irradiance and temperature are co-limiting photosynthesis and transpiration (Pallardy 2008) impacting the isotopic composition of plant tissues directly, nutrient availability is key for tree growth, with nitrogen (N) being most limiting in temperate and boreal forests and phosphorus (P) in tropical forests (Reich and Oleksyn 2004; Pallardy 2008). Recent estimates (Fig. 14.1) indicate that for natural terrestrial ecosystems about 18% are limited by

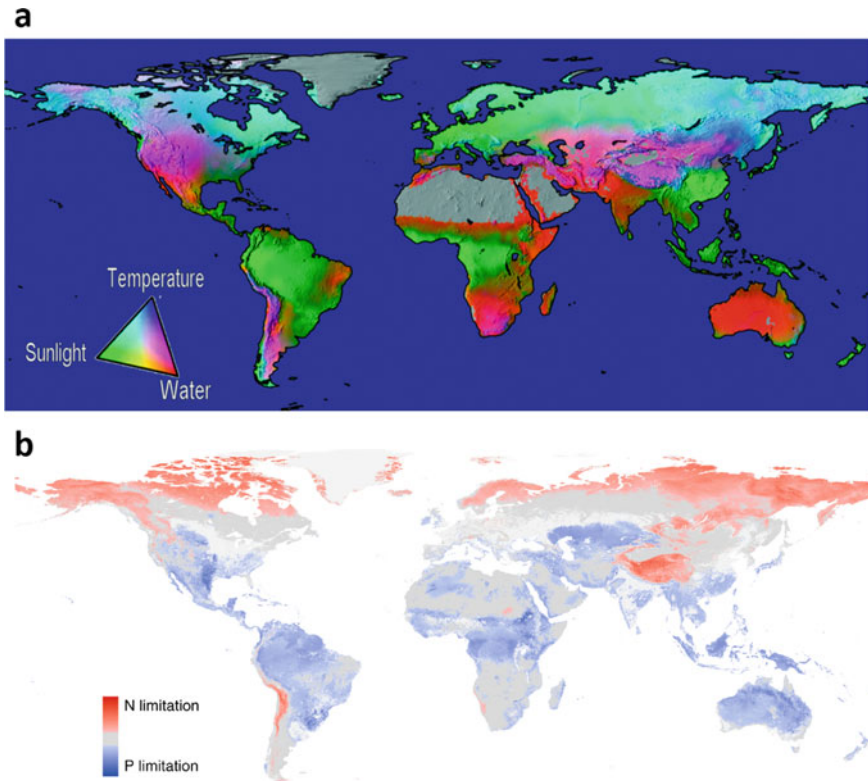


Fig. 14.1 Relative importance of temperature, water availability and sunlight on global terrestrial vegetation productivity (a), and soil nutrients (b). Figure (a) is reproduced from Churkina and Running 1998; Nemani et al. 2003; Running et al. 2004, and (b) from Du et al. (2020). Figure 14.1b reprinted by permission from Springer Nature: Nature Geoscience, Global patterns of terrestrial nitrogen and phosphorus limitation by Du et al. (2020), license number 4964260783580

N and 43% are limited by P (Du et al. 2020a). Although N deposition could partially alleviate N limitation in certain environments, excessive N or P deposition can have a detrimental effect on tree growth (e.g. Etzold et al. 2020). Therefore, tree growth can also be reduced when N (Norby et al. 2010) or P (Fleischer et al. 2019) availability are not limiting and other nutrients (Mg, Mn, Mo, K etc.) come into play. N-deposition can actually drive ecosystems into P-limitation as occurs in central Europe (Braun et al. 2010). In all these cases, growth rates are not regulated through C supply. Depending on seasonal, annual and decadal changes of these environmental factors and their interactions, tree physiology and growth vary in time and can leave their imprints in tree-ring isotopes.

14.3 Climatic Factors Recorded in Tree-Ring Isotopes

The interaction between environmental factors and isotopic fractionations at the leaf level are generally well understood (Chaps. 9 and 10). However, the processes responsible for the isotopic variation in tree rings still need a thorough examination for a correct interpretation of climatic and ecological information represented by tree-ring isotopes. Environmental signals recorded in tree-ring isotope ratios depend essentially on (a) temporal changes in environmental factors, including the intensity and duration of the environmental stressors (see also Chaps. 19–22) and their interactions; (b) their effect on the coupling between leaf gas exchanges (CO_2 and H_2O) and secondary growth, and their associated isotope fractionation processes (McCarroll and Loader 2004; Cernusak et al. 2013; Gessler et al. 2014; see also Chaps. 13, 19 and 23). Finally, the isotopic signals in leaves and even more so in tree rings integrate the variation of isotopic fractionation during the entire growth period represented by the sample (i.e. an annual ring). This integrated signal more strongly reflects periods when CO_2 uptake was greatest by the tree and contributed most strongly to the sampled biomass.

Along with the climate variability during the growing season, the isotopic ratios and growth are fluctuating as well. Therefore, the isotope signals are not uniformly distributed within a given tree ring. Tree-ring formation is a rather complex process where fluctuations in temperature and moisture, as well as in stored carbohydrates, influence the variations in the isotopic signal. The isotopic ratios of whole tree rings predominantly reflect the environmental conditions during which the photoassimilates were produced and allocated to woody tissue. This explains why tree-ring isotope studies, based on samples from trees growing under harsh environmental conditions may not reflect the actual severity of the conditions because no tissue was produced during such periods. In fact, such extremes may not show up in isotopic chronologies, while more moderate stress situations (with slowly ongoing growth and assimilation) do, and thus, produce tree rings with a strong isotope signal (Fig. 14.2) (Rodríguez-Caton et al. 2022). Under most severe drought conditions that prevent tissue production, no $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signals representing that event will be present in the ring produced during that current growing season (Körner et al. 2005; Cernusak and English 2015). On the other hand, if tree roots are exposed to too much moisture (submerged) an anaerobic condition develops and they gradually lose their functionality, impairing water uptake. Here we observe the paradox, that trees experience an “above ground drought”, while the roots are submerged in water, but non functional due to an anaerobic situation. Some trees are adapted to cope with flooded roots.

In contrast, other tree-ring parameters such as tree-ring width are most sensitive when trees grow in growth-limiting environments (very cold/hot or moist/dry) (Fig. 14.2). Tree-ring maximum latewood density and blue reflectance or intensity, a proxy for wood density (Campbell et al. 2007; Björklund et al. 2019), are also known to be very sensitive proxies in temperature-limited regions such as high-latitudes in North America (Wilson et al. 2017, 2019) or Europe (Björklund et al. 2013, 2019).

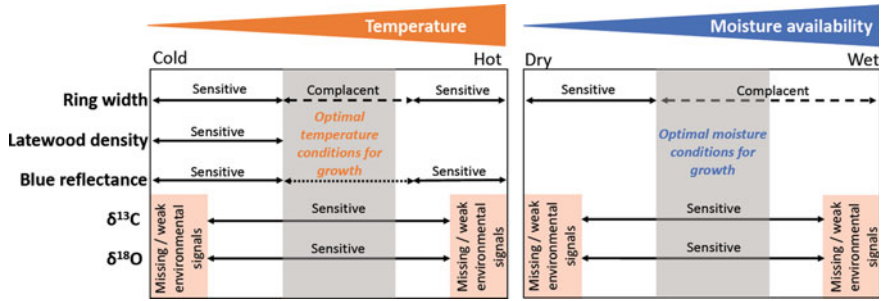


Fig. 14.2 Schematic representation of the variability and sensitivity of tree-ring variables (ring width, latewood density, blue reflectance and isotopes) to record environmental and climatic signals across a range of temperature and moisture conditions. No arrows indicate that not enough information is available. The orange rectangles indicate extreme climate conditions, where missing or weak environmental signals are recorded by $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in tree-ring cellulose. Modified from Fritts (1976, p. 301) and Cernusak and English (2015)

Recent studies report that blue intensity measured in earlywood in tropical conifers in Vietnam was sensitive to maximum temperature variations during the monsoon season (Buckley et al. 2018). Therefore, the combination of these other proxies beside stable isotopes can help to disentangle the relative influence of each factor (Levesque et al. 2017).

14.4 Climatic Controls of Plant Physiology as Reflected in Isotopic Signals

As the isotopic patterns and signal amplitudes between tree rings and leaves often differ, particularly under harsh climatic conditions, we focus on the influence of extremes such as low/high temperatures and mesic/xeric conditions. Which are the mechanisms responsible for the respective differences and which are the resulting interpretations? While the fractionation principles for C and O isotopes are presented in Chaps. 9, 10, and 13, here we focus our discussion on the processes that are relevant for the tree-ring signals detected under different climatic situations.

14.4.1 Meteorological, Microclimatic and Biogeochemical Impacts on the Isotopic Fractionations

Dominant climatic factors that exert control on carbon isotopic discrimination are those that control stomatal conductance and the rate of photosynthesis at the leaf level (Farquhar et al. 1982, 1989; McCarroll and Loader 2004), and thus modify the leaf

$\delta^{13}\text{C}$ values. Vapor pressure deficit (VPD) and soil moisture have the predominant control on stomatal conductance, whereas irradiance, CO_2 and air/leaf temperature control photosynthetic rates (Von Caemmerer and Farquhar 1981; Larcher 2003; see also Chap. 9). Variation of stomatal conductance at wide stomatal apertures exerts proportional changes in transpiration (at a given VPD), but hardly affects photosynthesis, simply because mesophyll resistance is almost 5 times larger than minimum leaf (stomatal) diffusive resistance, both operating in series (Körner et al. 1979), an insight that also relates to the ‘operating point’ as coined by Farquhar and Sharkey (1982).

Overall, the well-understood fractionation processes during photosynthesis are commonly the basis for interpreting $\delta^{13}\text{C}$ in tree rings, which per se is correct. This facilitates the decoding for climate reconstruction and tree physiological responses to various environmental impacts. Yet, during transport of fresh assimilates, post photosynthetic processes such as conversion of photoassimilates to structural biomass or storage reserves and remobilization of sugars, etc., modify the original isotope signals formed in leaves, which can result in considerable deviations between leaves and wood for both C and O isotope values. Here we refer to Chap. 13 where this topic is discussed in detail.

Besides post-photosynthetic fractionation and climate, other processes impact the isotopic composition in wood. The fractionation for $\delta^{18}\text{O}$ occurs at two different scales. At the first (meteorological) scale, fractionations occur before water is incorporated in the plants (Chap. 18), and at the second (microclimatic) scale, fractionations take place in the leaf and the whole plant (Chap. 10). In the first case, air temperature and evaporation are the main controlling factors. During condensation of water vapor the prevalent temperature determines the $^{18}\text{O}/^{16}\text{O}$ ratio in meteoric water (Dansgaard 1964), thus incoming precipitation varies seasonally. In the canopy and soil surface, some water may evaporate, causing enrichment in ^{18}O of the remaining water depending on the degree of evaporation. As water infiltrates into the soil, it mixes with residual water (Chap. 18, also Allen et al. 2019). This mixing between rainwater of different seasonal origins occurs mainly in temperate and boreal regions (Szejner et al. 2018), whereas in tropical regions the $^{18}\text{O}/^{16}\text{O}$ ratio in meteoric water have been related to the wet season (e.g. Brienen et al. 2012; Rodríguez-Catón et al. 2021, 2022). Irrespective of soil depth, plants absorb water where it is easiest accessible. No measurable fractionation occurs during water uptake. Deviations in $\delta^{18}\text{O}$ between xylem and soil water result from a mixture of water, absorbed along the rooting depth with varying $\delta^{18}\text{O}$ values of the soil moisture at different depths (Sprengr et al. 2016; Barbeta et al. 2020). Source water can change in time depending on the water availability and changes in the seasonal amount and precipitation type (Brinkmann et al. 2018; Allen et al. 2019), or shifts in rooting depth and water uptake from different soil water pools (Sarris et al. 2013; Barbeta and Penuelas 2017; Brinkmann et al. 2019).

At the second (microclimatic) scale, fractionations occurring in leaves (described in detail in Chap. 10) are essentially influenced by VPD and temperature (both controlling transpiration and stomatal conductance), as well as $\delta^{18}\text{O}$ of source water

and $\delta^{18}\text{O}$ of water vapor. The ^{18}O enrichment in leaf water is tightly linked to transpiration and stomatal conductance (g_s), with the lighter water molecule (H_2^{16}O) evaporating more easily than the heavier H_2^{18}O , leaving the remaining leaf water enriched in H_2^{18}O (Craig and Gordon 1965; Dongmann et al. 1974). The following three scenarios illustrate the significance on leaf water enrichment of VPD, g_s and soil water supply, as well as of the source water $\delta^{18}\text{O}$ and the ambient water vapor $\delta^{18}\text{O}$:

1. Low air humidity (high VPD) with sufficient soil water supply, high g_s and high net transpiration (E): large humidity gradient between the ambient air (e_a) and the leaf intercellular spaces (e_i) results in high evaporative losses and a moderate to low leaf H_2^{18}O enrichment. To maintain the plant water balance, water loss via E is continuously replenished with non ^{18}O enriched xylem (source) water. This results in a reduced leaf water ^{18}O enrichment, described by the Péclet effect (see Chap. 10; Farquhar and Lloyd 1993). The higher E, the less the leaf water enrichment due to less back-diffusion of ^{18}O enriched water at the evaporative site (in the leaf) with the non ^{18}O enriched xylem water that is continuously replenishing the leaf water pool. Under these conditions the variation in source water $\delta^{18}\text{O}$ is the basis for the $\delta^{18}\text{O}$ variation in the leaf water and organic matter. For example, this is found in temperate forests with abundant water supply.

2. High air humidity (low VPD) with sufficient soil water supply, high g_s and low E: small humidity gradient between e_i and e_a results in a low transpiration rate and minimal leaf H_2^{18}O enrichment. Under such conditions hardly any water flow occurs from the xylem into the leaf as VPD is low and the Péclet effect is minimal to ineffective. But the large exchange of ^{18}O depleted water molecules from the ambient air (i.e. vapor exchange) into the leaf via stomata results in a reduced to no leaf H_2^{18}O enrichment (Goldsmith et al. 2017; Lehmann et al. 2020). Under these circumstances the ambient water vapor $\delta^{18}\text{O}$ is reflected in the $\delta^{18}\text{O}$ of the leaf water and organic material. For example, this is the case in humid tropical forests or regions exposed to high occurrence of fog (e.g. Dawson 1998) or rain events.

3. Low to moderate air humidity (high VPD) with scarce soil water supply, thus low g_s and E: large humidity gradient between e_i and e_a with insufficient water supply results in closed stomata and low transpiration and high leaf H_2^{18}O enrichment. Since E is low the xylem flow into the leaf is low thus allowing back-diffusion of ^{18}O enriched water from the site of evaporation. Furthermore, the ambient water vapor pressure and g_s are lower too, resulting in a considerably reduced exchange with H_2^{18}O depleted, ambient vapor. Under these conditions the climate i.e., VPD and temperature are predominantly imprinted in the $\delta^{18}\text{O}$ of the leaf water and biomass, additionally to the $\delta^{18}\text{O}$ of the given source water. This is found under xeric, Mediterranean or drought conditions.

In reality there may be gradual transitions between the different scenarios. From scenario 1 to 3, stomatal conductance (g_s) is inversely related to leaf H_2^{18}O enrichment (Barbour et al. 2004). However, whether low leaf H_2^{18}O enrichment (i.e., similar values for leaf water $\delta^{18}\text{O}$ and xylem water $\delta^{18}\text{O}$) in very humid environment

with enough soil water supply is the result of high VPD (scenario 1) or low VPD (scenario 2) cannot be distinguished with tree-ring $\delta^{18}\text{O}$ alone. Other proxies, i.e., $\delta^{13}\text{C}$, tree-ring width or density could be useful to clarify the mechanism. In any case, a good knowledge of the site conditions is mandatory for a correct interpretation of the isotopic signals in tree rings. Although in scenarios 1 and 2 we find low, to no leaf H_2^{18}O enrichment with little variability, the causes can be different as shown above (i.e., very humid environment or abundant water supply allowing for high E). Scenario 3 is most frequent as the air humidity on average is more variable and generally lower in boreal, temperate and Mediterranean regions than in the tropics or at certain treelines/sites.

Numerous studies assume similar or even identical $\delta^{18}\text{O}$ values between source water and summer precipitation. Recent studies, however, indicated considerable deviations between $\delta^{18}\text{O}$ of precipitation and xylem (source) water. Depending on the soil structure (heavy, dense and clay rich versus light, predominantly organic soils), the infiltration of precipitation water can vary considerably, which is reflected in the infiltration time and $\delta^{18}\text{O}$ gradient from the soil surface to the roots. Brinkmann et al. (2018) and Allen et al. (2019) showed that trees rely only partly on the growing seasons precipitation and use considerable amounts of precipitation from winter and diverse seasonal origins. This can lead to a temporal shift in the seasonal course of the $\delta^{18}\text{O}$ values of source water. Therefore, Brinkmann et al. (2018) and Allen et al. (2019) refer to this temporal shift in source water $\delta^{18}\text{O}$ as seasonal origin. These shifts can potentially mask the physiological response signals of trees to variations in temperature and moisture, and thus they can dampen the prevalent climate signals in tree-ring $\delta^{18}\text{O}$ records (see Chap. 18). Such disparities between precipitation and source water have implications on tree-ring based climate reconstructions and deserve a cautious consideration in the data interpretation.

14.4.2 Tree-Ring Isotopic Signals Under Non-limiting Climate Conditions for Growth

In the absence of severe growth constraints, tree response to climate conditions for optimal growth can differ between species and is dependent on ecosystem properties (soil, water and nutrient availability, stand structure, species composition). In general, abundant precipitation, moderate temperatures, non-limiting light and adequate nutrient conditions are a precondition for detecting clear isotopic signals (Cernusak and English 2015; Hartl-Meier et al. 2015). The likelihood that a strong temperature and humidity signal is recorded in source water is given with high precipitation as indicated above and preferably on porous, organic soils where water infiltrates into the soil rapidly. For instance, the strongest precipitation signal recorded in tree-ring $\delta^{18}\text{O}$ observed in temperate regions is where soil water supply relies mostly on precipitation during the growing season (Treydte et al. 2014). Studies based on

tree-ring isotope networks agree with this theory and reported the strongest correlation between tree-ring $\delta^{18}\text{O}$ and precipitation in regions with abundant precipitation during summer in Europe and North America (Treydte et al. 2007; Hartl-Meier et al. 2015; Levesque et al. 2019), but also in the Southern Hemisphere in South America (Rodríguez-Catón et al. 2021, 2022).

For a clear interpretation of isotopic signals in tree rings, one needs to know when (season) and where (region) tree rings were produced. This requires a definition of conditions under which tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ signals are less influenced by confounding factors and under which conditions the strongest environmental and climatic signals can be obtained. As shown above, trees growing under quasi non-limiting growth conditions provide the most representative isotopic signal of environmental conditions.

In areas where a single limiting factor has the strongest effect on isotopic composition, the interpretation of the physiological and climatic signals is usually straightforward. For example, in regions where temperature is the most limiting factor for tree physiology during the growing season, tree-ring isotopes are expected to respond specifically to temperatures (e.g. Porter et al. 2009; for other examples see Chaps. 20 and 21). However, under natural conditions, it is rarely the case that a single limiting environmental factor is recorded in the isotopic composition of plant materials. Often several environmental variables impact physiological responses at the same time such as temperature and VPD (Grossiord et al. 2020). Such interactions complicate the interpretation of the environmental signals recorded in stable isotopes despite the relatively well understood physiological processes influencing isotopic fractionation at the tree level (Gessler et al. 2014).

14.4.3 Tree-Ring Isotopic Signals Resulting from Extreme Climate Conditions

The strength of the isotopic signal in tree rings in response to environmental changes may not be proportional to the strength of the environmental stressors. For instance, very low temperatures or severe water limitations during the growing season may halt growth, and thus, there is no woody tissue that the isotopic signal can be related to.

14.4.3.1 Cold Conditions

At high latitudes and in mountainous environments, low temperatures limit cambial activity, and thus, growth (Körner 2012). Although radial growth is very low when air temperature drops below 5–6 °C (Körner 2016), leaves are still producing photoassimilates (Körner 1991). So, the specific isotopic patterns in the freshly produced assimilates may represent a cold environment, while the amount of wood produced

during this cold phase is negligible. With temperature above 5–6 °C, wood production rate increases following a sigmoidal course. To the extent that temperature *per se* influences isotopic signals of the produced wood biomass in a warmer phase. Thus the isotope values representing higher temperatures is usually much larger than wood produced during the cold phase. This results in a disproportionate relationship between wood masses formed during cold versus warm phases for a given year. This means that the isotope signals from cold periods within the season may be underrepresented relative to the warmer phases due to less amount of wood mass. Therefore, isotopic signals specific to cold periods can be difficult to detect in tree rings. Still, climate signals from cold periods recorded by tree-ring isotopes have been used to reconstruct cold winter anomalies (Szejner et al. 2016, 2018; Voelker et al. 2019). Whatever the reason, such an analysis requires a careful splitting of tree-ring segments with either a microtome or ideally via laser ablation. Having very thin sections, which might consist of only a few cell layers, intra annual climatic variability can be uncovered even from periods with very small parts of the tree-ring material (Monson et al. 2018).

To summarize: During critically cold periods tree-ring increments are very small because cell division is very slow at low temperatures (Rossi et al. 2007; Körner 2015), but cell division increases with rising temperatures until a maximum growth rate is reached. Thus, the amount of wood that carries the isotopic signals for cold periods is very small relative to the whole tree ring. Consequently, the cold signal may be hardly detected in tree-ring isotopes.

14.4.3.2 Dry/Hot Conditions

With increasing temperature, the atmospheric evapo-transpirative demand (i.e. VPD) increases as well (Novick et al. 2016; Grossiord et al. 2020). However, as plants are generally more sensitive to VPD than to high temperature, VPD is predominantly limiting both assimilation and growth before temperature does. What is often indicated as temperature limitation could be in fact a limitation by VPD (Grossiord et al. 2020).

Drought and heat combined have a similar effect with regard to wood production as low temperature conditions (see above). These climatic signals (dry/hot) expressed in isotope ratios of individual tree rings may also be underrepresented. Beyond a species-specific maximum air temperature and VPD threshold, photosynthesis declines, and carbon allocation is shifted towards root expansion, rather than in radial growth (Pallardy 2008; Teskey et al. 2015). While these physiological responses to drought and heat alter the isotopic ratios at the leaf level, they can deviate strongly from the δ -values of tree rings. Such drought situations slow down or prevent xylogenesis and can result in a growth cessation leading to an isotopic uncoupling between leaves and tree rings (Pflug et al. 2015). In contrast, during situations with sufficient soil water and reduced VPD (spring/fall, e.g., in the Mediterranean), the wood production rate is much higher (Sarris et al. 2013). Again, this leads to a disproportionate relationship between wood masses formed during dry/hot versus wet/cool

phases. As the wood mass produced during cooler wetter phases is much more abundant, its isotopic signal is proportionally more expressed in the tree ring (similar to the cold but inverse situation, with regard to temperature, see Sect. 14.4.3.1).

To summarize: With increasing temperature, VPD increases as well, and this is often associated with a reduction in soil water availability. Both radial growth and physiological processes at leaf level, namely photosynthesis and stomatal conductance, can be affected. However, photosynthesis is restrained or even ceased, commonly long after cell and tissue growth had been halted. Thus, the isotopic signals in leaves could be decoupled from the isotopic signals in wood (Pflug et al. 2015). No new cell produced means no tree-ring isotopic signals are representing this specific climate situation.

14.5 Carbon Storage and Carry-Over Effects on Tree-Ring Isotope Signals

The approach to use stable isotopes in tree rings to reconstruct changes in leaf gas exchanges, over decades to centuries in response to anthropogenic (e.g. rising CO₂, Voelker et al. 2016, Chap. 24) and climate factors (Leonardi et al. 2012; Saurer et al. 2014; Frank et al. 2015; Levesque et al. 2017; Mathias and Thomas 2018; Guerrieri et al. 2019) is based on the assumption that carbon sources (tree canopies) and sinks (tree stem) are tightly coupled and synchronized in time. This implies that the isotopic signal in the annual rings, which is imprinted in foliage during photosynthesis and transpiration, would be closely related to the environmental impact. As discussed above, this is rarely the case, particularly when trees are not living at their most favorable environmental conditions (in terms of resource availability). Hence, they may allocate the recently assimilated carbon to sinks other than radical growth (C-storage see Sects. 14.5.3.1 and root biomass 14.5.3.2).

Translocation, storage and remobilization of old and new assimilates within a tree affect the isotopic composition of tree rings (see Chap. 13). Understanding how these processes influence $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in tree rings at the inter- and intra-annual time scale is a prerequisite for improving the use of isotope signals in tree rings to derive climate and environmental conditions retrospectively. This section will take a closer look at the dynamic of the annual ring formation, and at the fate of recently assimilated carbon and its isotopic signals when stored in tree rings.

14.5.1 Annual Ring Formation Through Xylogenesis (Tree Carbon Sink)

The production of new cells during the formation of annual tree rings—the xylogenesis occurs through a few steps, separated in space and time, but connected

among them: cell division, cell enlargement, deposition of secondary wall and finally maturation when thickening and lignification are completed. The production of new woody cells results in a tree carbon sink occurring during a given growing season (in temperate and boreal forests) and all year around (in humid tropical forests). Xylogenesis and the cambial activity, depends on the activity of meristem tissues and the rate at which new tissue becomes differentiated and matured (Rossi et al. 2012; see Chap. 3). All this relies on the developmental ‘preparedness’ to grow (hormones), the existence of active sinks (Körner 2015) and the coordination between phloem loading with sugars, the transport from autotrophic to heterotrophic tissues (Hölttä et al. 2014; Ainsworth and Lemonnier 2018), and the downloading capacity in developing xylem tissue. Xylogenesis is affected by developmental (genomic) and environmental factors (with particular reference to temperature, photoperiod and water). Assimilate availability is rarely limited in nature except for plants in deep shade. Temperature and photoperiod define the onset of cambial activity, particularly in temperate and boreal forest. Water availability and sugar concentrations plays a significant role in the cell growth by maintaining the turgor pressure needed for cellular expansion (e.g. Steppe et al. 2015 and references therein). Dynamics of cambial activity vary depending on tree age (Rossi et al. 2008) and environmental conditions. Xylogenesis lasts longer in young compared to mature trees, though this may be the result of tree size rather than simply an age-effect (Rossi et al. 2008; Zeng et al. 2018). Overall, previous findings in literature seem to indicate that xylogenesis is not limited by assimilate availability, but by developmental, thus hormonal and ultimately genetic factors (e.g. Grattapaglia et al. 2009) and direct environmental influences on the tissue forming processes (meristems, Körner 2015, and references therein).

In boreal and high-elevation forests at the treeline, growth occurs continuously following a unimodal curve during a short season when growth is determined by temperature thresholds (Fig. 14.3). In contrast, growth in Mediterranean ecosystems, can last longer, but is often discontinuous, as drought conditions may temporarily stop new cell production, and resume xylogenesis following precipitation. This leads to the formation of the so-called intra-annual density fluctuations (IADFs) (Battipaglia et al. 2016; De Micco et al. 2016). In some tropical trees, tree cambial activity is expected to be constant all year around and without periodicity, though alternation of dry and wet season may pause and resume xylogenesis, and reproductive cycles can induce growth cycles that materialize as growth rings (see Chaps. 3).

14.5.2 Tree Carbon Pools and Their Effect on the Isotopic Ratio in Tree Rings

Recently produced carbohydrates can move from the canopy down to the tree stem and roots within hours (Keel et al. 2006, 2007; Gessler et al. 2009a) and return back to the atmosphere through respiration from the soil within a few days (Steinmann et al. 2004; Höglberg et al. 2008; Mildner et al. 2014) or even become transferred

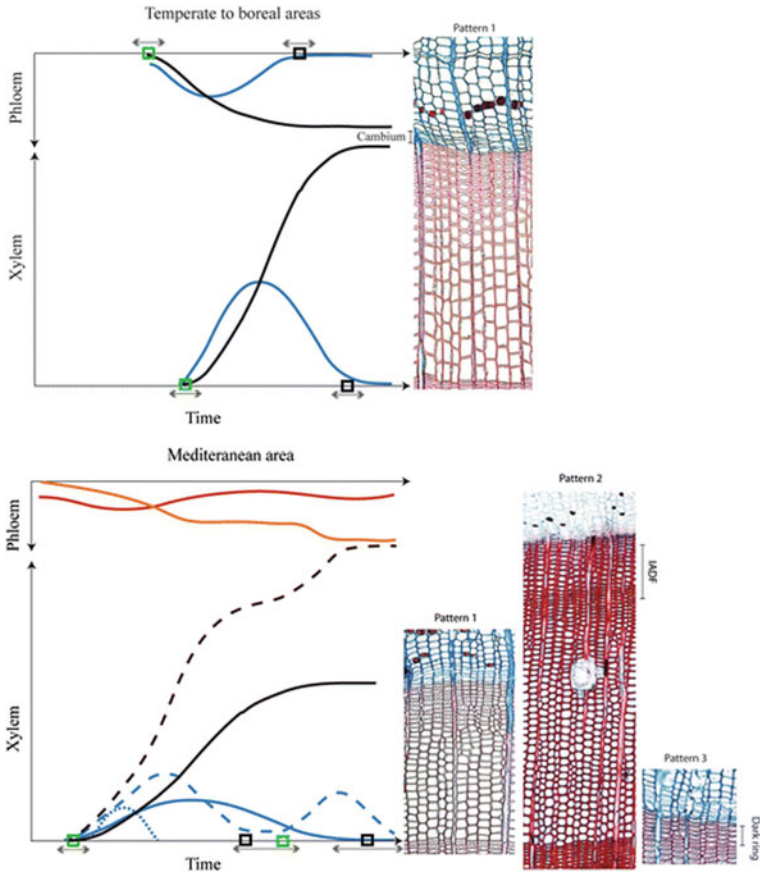


Fig. 14.3 Variation of growth patterns in two contrasting biomes. Xylem and phloem growth over one growing season resulting from cambium activity in (top) boreal or temperate and (bottom) Mediterranean forests. In each case, the periods of growth are defined by the onset (green squares) and cessation (black squares) while the arrow represents the time variability in the onset and cessation. For both xylem and phloem, the progress of growth over time (black lines) is quantified either as the number of cells or ring width produced within a year. A general rate of growth (blue lines), which indicates how fast the process occurs in terms of the measured quantity per time unit, can be represented as the first derivative of the progress of growth (black lines). Only one pattern of xylem and phloem growth over time was represented for temperate- boreal areas illustrated as the S-shaped (top, pattern 1) growth pattern (black line). The general rate of growth of this pattern is typically bell shaped (top, blue line in pattern 1). For Mediterranean areas, three patterns of growth over time were represented: (bottom, pattern 1) S-shaped growth, such as for temperate-boreal conifers with its bell-shaped rate of growth (solid black and blue lines); (pattern 2) Intra-annual density fluctuation (IADF, dashed black line) with its bimodal rate of growth (dashed blue line); (pattern 3) missing rings or dark rings (illustrated as the rate of growth only, dotted blue line) where few xylem cells are formed (less than five cells), which slowly differentiate and can look like latewood cells. Orange and red lines indicate the progress of phloem growth over time and phloem growth rate, respectively. Phloem growth rate (in red) is hypothetical and has been shown to be bimodal like the xylem of pattern 2. [Source figure and text: (Deslauriers et al. 2017)]. Reprinted by permission from Springer Nature: Springer, *Ecophysiology and Plasticity of Wood and Phloem Formation* by Deslauriers et al. (2017), license number 4971200864679

to the adjacent trees via mycorrhiza (Klein et al. 2016a). However, high rates of transfer does not necessarily indicate a high, direct and lasting incorporation of new assimilates into structural growth, because the mobile carbohydrates can mix, and thus, get diluted by the old carbon pool, with only the mixture becoming invested in new growth (Keel et al. 2007; Mildner et al. 2014).

14.5.2.1 Assimilation at Leaf Level (Tree Carbon Source)

At the canopy level during the photosynthetic assimilate production (Fig. 14.4) the

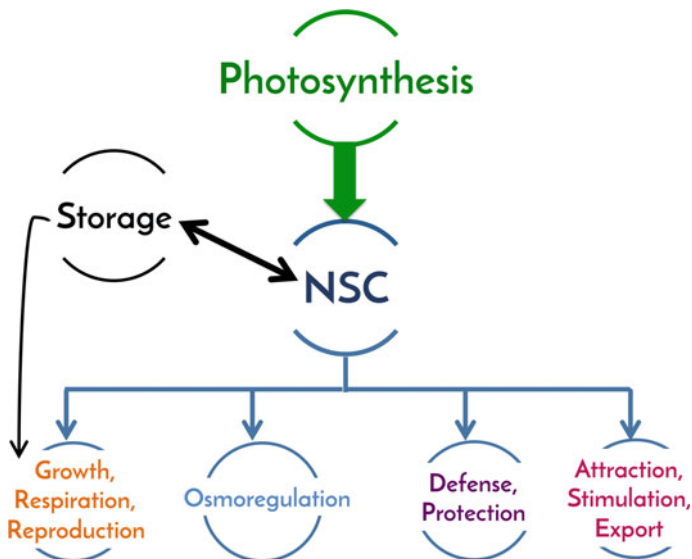


Fig. 14.4 Scheme showing the fate of non-structural carbohydrate (NSC) in trees. Modified from (Hartmann and Trumbore 2016)

$\delta^{13}\text{C}$ signature of new carbohydrates at leaf level reflects the dominant climate factors controlling stomatal conductance and/or photosynthetic rates (see Chap. 9). The $\delta^{18}\text{O}$ signature of new carbohydrates is driven by climate variations responsible for the isotopic fractionations before water is incorporated in the plants (Chap. 18) and in leaves controlling transpiration and stomatal conductance (see Chap. 10).

14.5.2.2 Non-structural Carbohydrates

Non-structural carbohydrates (NSC) are photassimilates produced during a given growing season in the leaves and are mostly composed of starch and sugars, but also fructans, sugar-alcohols and other compounds. NSC are not directly invested

in growth but they are used by trees to fulfill different functions (Fig. 14.4) such as storage, reproduction, growth and respiration (maintenance of life sustaining processes). Furthermore, they are used for osmoregulation, defense (synthesis of biogenic volatile organic compounds, BVOCs), protection, attraction, stimulation and export (e.g., root exudates). They also provide a neutral disposal avenue for overabundant photoassimilates, similar to storage lipids (Hartmann and Trumbore 2016; Martinez-Vilalta et al. 2016), or may simply be exuded for no other reason than a C overflow (Prescott et al. 2020).

However, the hierarchy or priority of certain uses of fresh photoassimilates is unclear. Evidence is accumulating that storage has a very high priority. Plants tend to prioritize storage even under C shortage (Weber et al. 2018), indicating that survival has a higher rank than adding structural biomass (growth). When meristematic activity is inhibited or slowed because of critically low temperatures, drought, lack of nutrients, or phenology, photosynthates are simply stored, since photosynthesis is commonly less sensitive to such stressors or limitations than meristem activity (Körner 2003, 2015; Muller et al. 2011). Under such conditions, the concentration of C stores rises and these stores either become mobilized as meristems resume their activity when conditions improve (Würth et al. 2005) or they remain disposed forever in heartwood. The only alternative is down regulation of photosynthetic capacity. Seasonal changes in cambial activity are coupled with a higher sugar concentration in the cambial zone, with highest demand during the cell differentiation and wall-thickening phase (Deslauriers et al. 2009; Perez-de-Lis et al. 2016). The NSC pool also undergoes seasonal variation, and is negatively correlated with the rate of structural growth. Whenever growth slows, NSC content increases, when growth resumes, NSC declines (Körner 2003; Würth et al. 2005; Streit et al. 2013). The alternatives are down regulation of photosynthetic capacity or export of excess carbon as discussed by Prescott et al. (2020).

14.5.3 *Coherency Between C-Sources and Sinks*

There is no evidence that mature trees in forest ecosystems with a natural nutrient cycle are carbon limited at current atmospheric CO₂ concentrations (Norby and Zak 2011; Bader et al. 2013; Sigurdsson et al. 2013; Klein et al. 2016b; Ellsworth et al. 2017); for a review see also Palacio et al (2014). The proposed trade-off between C storage and growth (Wiley and Helliker 2012) is not driven by C shortage but rather reflects investment opportunities driven by meristem activity (C sink limitation to growth) as set by environmental cues. In other words, the allocation of new assimilates to storage is an active or passive response by trees, particularly under limiting environmental conditions (Körner and Paulsen 2004; Dietze et al. 2014; Hartmann 2015; Galiano et al. 2017; Piper et al. 2017), and depends on when trees prioritize growth over storage or defense (Huang et al. 2019).

At the beginning of seasonal growth, some stored carbohydrates that were produced in previous years, or during the non-growing season in evergreen species,

are used for the onset of tree growth. Therefore, the isotope signals of stored carbohydrates used for growth in the current growing season are not necessarily representative of the concurrent climate. With the ongoing foliage development, tree growth is progressively supplied with freshly formed assimilates, which carry the isotope signals representing the current climate, stored in the late wood formation (see Sect. 14.6). Thus, in the short term, environmental signals are well represented in fresh photoassimilates, but only to a minor degree in lasting tissue signals such as those captured in bulk stem wood.

14.5.3.1 Evidences from Intra-annual Ring Measurements

Recent improvements in dendro-isotopic analysis, such as sampling thin sections of tree rings either by microtome slicing (Sarris et al. 2013) or by laser ablation techniques (Schollaen et al. 2014; Rinne et al. 2015; Soudant et al. 2016; Loader et al. 2017) have greatly enhanced the possibility to simultaneously study xylogenesis and isotopic composition at high-temporal intra-annual resolution (Chap. 7). High-resolution intra-annual analyses of tree-ring isotope ratios (Rinne et al. 2015; Belmecheri et al. 2018) disclosed time lags in the isotope ratios resulting from climatic impacts, remobilization of carbohydrates and tree-ring formation. Intra-annual analyses assessing tree response to the seasonal variation of climatic conditions have mostly separately analyzed the isotopic ratios in early- and latewood sections (Kress et al. 2009; Lévesque et al. 2014). Kimak and Leuenberger (2015) confirmed that $\delta^{13}\text{C}$ in earlywood material was strongly dependent on previous year reserves (although the usage of stored versus fresh assimilate can vary between species and seasons depending on the prevalent climatic conditions), while latewood material was mostly formed from assimilates of the current growth year. Thus, earlywood and latewood need to be analyzed separately for their isotopic composition, even for trees from cold environments with narrow rings if possible (Kagawa et al. 2006a).

The examination of the xylogenesis dynamics can help to identify temporal lags between cell formation and cell thickening such as lignification (Cuny et al. 2015). The interactions between cambial phenology and seasonal climate result in seasonal lags of the isotope ratios, stressing the importance of properly aligning isotopic measurements with the phenology of the xylogenesis (Belmecheri et al. 2018; Castagneri et al. 2018). The amount of cellulose produced during the development of the primary cell wall (cell enlargement) is smaller than during the cell wall thickening phase (Cuny et al. 2015), with the latter (reflecting the concurrent climate conditions) having a greater weight in the overall tree-ring isotope signal. This implies a bias toward the climatic controls of the main part of cell wall thickening (Cuny et al. 2015; Castagneri et al. 2017; Belmecheri et al. 2018). Finally, lignification, the last stage of cell maturation, can last until the end of the growing season, so it can be also associated with late season climate. By aligning tree-ring isotope series with xylogenesis and climate conditions, the robustness of ecological and paleoclimatic studies will improve considerably (Monson et al. 2018). Consequently, the need

of cellulose extraction prior isotopic analysis should be carefully considered based on the questions being addressed. Removing other wood constituents could prevent the detection of the full dynamics of carbon allocation during tree-ring formation. Indeed, lignification can last up to one month after growth cessation (Cuny et al. 2015), hence potentially losing physiological and environmental signals associated with these compounds (Barbour et al. 2001; Guerrieri et al. 2017). See also Chaps. 3 and 5.

14.5.3.2 Species Specific Dynamics in Xylogenesis and the Use of Stored and New Carbohydrates

The seasonal stages of xylogenesis are also species-specific. These NSC dynamics (i.e., production in the canopy and NSC investment during xylogenesis in the stem) differ among species (Hoch and Körner 2003). In ring-porous species, earlywood formation relies almost exclusively on previous year(s) carbohydrates, exhibiting isotopic carry-over effects (Helle and Schleser 2004). The onset of cambial activity and vessel formation in ring porous tree species occurs prior to budburst and depends on the remobilization of carbohydrates from storage (Gonzalez-Gonzalez et al. 2013; Perez-de-Lis et al. 2017). Yet a large fraction of these C storages is never mobilized, but rather stays in ray tissues, with the climatic signal related to the time when they were assimilated. This lack of synchronicity between photosynthesis and stem growth leads to temporal shifts between C assimilation and investment in secondary tissues, which is reflected in the isotopic values.

In contrast, diffuse-porous species rely mostly on new assimilates to build up new woody biomass (Keel et al. 2006; Palacio et al. 2011; Michelot et al. 2012; Carbone et al. 2013; Vincent-Barbaroux et al. 2019). Conifers use mostly newly formed sugars (see early studies from Glerum 1980; Michelot et al. 2012; Rinne et al. 2015; Deslauriers et al. 2016). These potential lags between C assimilation and xylem formation can also be bimodal if spring and autumn activity are separated by a dry summer such as in the southwestern United States (Belmecheri et al. 2018) or in Mediterranean regions (Sarris et al. 2013; Castagneri et al. 2018). In contrast, when trees were irrigated in precipitation manipulation experiments after a long drought period (e.g. *Pinus sylvestris* in a dry valley in the Alps), the $\delta^{13}\text{C}$ signals were more depleted in ^{13}C , for both, earlywood and latewood, evidencing an almost synchronic coupling between new assimilates and xylem formation (Eilmann et al. 2010).

Generally deciduous conifer species (i.e. *Larix* spp.) show a lower use of stored assimilates produced in previous years as indicated by $\delta^{13}\text{C}$ intra-annual patterns of sucrose and tree-ring samples of *Larix sibirica* (Rinne et al. 2015). Still earlywood formation relies on both carried-over photoassimilates from the previous year(s) and to the degree as current photoassimilates are available, whereas latewood formation depends predominantly on current assimilates, as demonstrated with $\delta^{13}\text{C}$ pulse-labeling and intra-annual $\delta^{13}\text{C}$ analysis (Kagawa et al. 2006a, b).

14.5.3.3 Coupling and Decoupling Between Carbon Source and Sinks and Their Isotopic Coupling

Under the assumption that source (canopy physiology) and sink (stem growth) are strongly linked and synchronized, tree-ring width and isotope compositions are an ideal proxy to reconstruct changes in leaf physiological responses to environmental limitations retrospectively. However, this agreement is rare (Michelot et al. 2012; Belmecheri et al. 2014; Guerrieri et al. 2016, see also Chap. 9). When trees are exposed to severe environmental limitations, photosynthesis and tree growth are uncoupled to the degree that an isotopic decoupling occurs, i.e., the isotopic signals in tree rings do not correspond with the prevalent environmental conditions. For example, drought can stop radial growth and cold conditions can slow it significantly, even though there are no changes in NSC concentration (Lempereur et al. 2015; Fernandez-de-Una et al. 2017; Dietrich et al. 2019) while photosynthesis is still ongoing (Pflug et al. 2015). As mentioned before, growth is more drought sensitive than photosynthesis (Muller et al. 2011; Piper et al. 2017). Source and sink activities were also found not to be fully coupled in a mesic forest, with growth being more sensitive to atmospheric, soil moisture limitation and low temperature than canopy C uptake in a temperate oak forest (Delpierre et al. 2016). At the world's highest elevation treeline in the South American Altiplano, a coupling and decoupling between physiological processes at leaf level (carbon source) and wood formation (carbon sink) was observed along an aridity gradient likely associated to similar or different climate sensitivity of these carbon source and sink processes (Rodríguez-Catón et al. 2021). The accumulation of soluble NSC under drought conditions in the cambium zone could be a strategy for trees to prioritize maintenance of cell turgor (Deslauriers et al. 2014; Piper et al. 2017) and to keep an efficient vascular system (including phloem and xylem (Sala et al. 2012)). However, the quantities required for osmoregulation are small, with one mole of solutes already creating an osmotic pressure of 2.24 MPa, and cells already operate under 'normal' conditions at an osmotic pressure between 0.5 and 1 MPa. The increase in NSC with increasing elevation (Hoch and Körner 2002, 2012; Fajardo et al. 2013), although not always observed (Simard et al. 2013), was associated with sink rather than source limitation (Körner 2003) and hence, to environmental control on cambial activity (Rossi et al. 2016).

Beside the time lag in the transfer and mixing between recently fixed and old assimilates, other factors may contribute to mask the isotopic tree-ring signal. First, soluble sugars may undergo biochemical transformation (e.g., synthesis of cellulose or lignin) within the canopy and later they are loaded to the phloem (during the export) and used during the annual ring formation, with associated isotope fractionations (Cernusak et al. 2013; Gessler et al. 2014). This can cause an offset between sink and source in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. Its magnitude has shown to be species-specific (Cernusak et al. 2005; Gessler et al. 2009b; Bögelein et al. 2019), and can partially uncouple tree rings from isotopic signals in fresh assimilates in the canopy (see also the post-photosynthetic fractionation in Chap. 13; Cernusak et al. 2013; Gessler et al. 2014).

Another aspect to consider is the confounding effect of changes in atmospheric CO₂ and air pollutants (Ozone, SO₂, NO_y and NH_x) on tree physiological processes. This topic is discussed in detail in Chap. 24.

14.6 Concluding Remarks

The dendro-isotope approach is one of the few reliable methods allowing for the assessment of tree carbon and water relations in response to changes in environmental conditions. It facilitates the reconstruction of climate signals (Chap. 1) and environmental changes retrospectively over long temporal and large spatial scales and at high spatial and time resolution (Babst et al. 2017). Yet this approach has also some weak points in particular when trees are exposed to chronic or severe stress episodes: (1) an isotopic decoupling between leaves and tree rings occurs under limiting environmental conditions when growth is restricted e.g., either by low temperatures (<5–6 °C) or drought. (2) A temporal decoupling related to the different carbon pools used for growth, with different isotopic signals. While stored assimilates (starch, sugars) carry a mixture of isotopic signals from past and current growing seasons, they are distinctly different from the isotopic values of freshly synthesized assimilates. (3) Shifts in the oxygen isotope signals can occur due to usage of different water sources that vary in their temporal origin. In temperate sites during the growing season, trees can utilize large proportions of winter water deeper in the soil profile, which can lead to an asynchrony between the $\delta^{18}\text{O}$ values in tree rings and recent precipitation water carrying the growing season temperature/humidity signal. (4) Post photosynthetic fractionations can dampen the amplitude of the initial signal in the leaves, to a degree, that a poor signal to noise ratio hampers a straightforward data interpretation.

To overcome these difficulties, we suggest an isotopic intra-annual assessment (IAA) of tree rings (using microtomes, laser ablation, etc.) to gain access to isotopic signals, which are formed under boundary conditions, particularly for trees living under extreme environments (cold/hot, dry). Moreover, the interpretation of the intra-annual stable isotope-climate relationships, with particular reference to the seasonal changes in the NSC and water source for $\delta^{18}\text{O}$, could be greatly improved when different stages of xylogenesis are accounted for (Szejner et al. 2016; Belmecheri et al. 2018). Furthermore, the IAA facilitates the study of physiological processes at a finer temporal resolution. In a combined effort with controlled experiments and field studies one could be looking at dynamics and isotopic composition of NSC with the help of CSIA (Compound Specific Isotope Analysis) in autotrophic and heterotrophic tissues, which reflect the instantaneous changes in leaf gas exchanges better (e.g. Keitel et al. 2003). Thus it is possible to account for the lag between C assimilation in foliage and investment in the annual ring formation through xylogenesis (Rinne et al. 2015).

The development for fine resolution intra annual tree-ring analysis is highly promising, thanks to the recent instrumental development (Chap. 7). Not only it will help to improve the interpretation of tree-ring isotope values, but it will widen the field

of tree-ring analyses and advance the detection of tree physiological mechanisms we can gain from them.

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