

Chapter 17

Intrinsic Water-Use Efficiency Derived from Stable Carbon Isotopes of Tree-Rings



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Abstract 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 CO₂, physiological information can be retrieved, namely the ratio of assimilation to stomatal conductance, which is termed the intrinsic water-use efficiency (iWUE). 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. iWUE is of great importance at the scale of individual plants because it can determine plant performance and survival. iWUE 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 iWUE of trees has changed in the past, e.g. due to increasing CO₂, nitrogen or other factors. Accordingly, many applications have explored this tool for various forest ecosystems across the globe, often reporting a strong increase in iWUE over the twentieth century. Explicit comparisons of tree-ring iWUE to growth-data obtained from the same rings can help distinguish among strategies plants employ under various environmental impacts, like increasing CO₂, light limitation, drought or too much water. In this chapter, we describe the theory behind iWUE, show some limitations of the method, give examples of the combined application of iWUE and tree-ring width, discuss photosynthetic limitations of iWUE and finally show how the method has been applied in large-scale tree-ring networks.

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R. T. W. Siegwolf et al. (eds.), *Stable Isotopes in Tree Rings*, Tree Physiology 8,
https://doi.org/10.1007/978-3-030-92698-4_17

481

17.1 Introduction

The development of the Farquhar-model of carbon isotope fractionation during photosynthesis was a milestone in the application of stable isotopes in ecology and many other fields (Farquhar et al. 1982). This model enabled a straightforward interpretation of carbon isotope values of plant organic matter in terms of physiology. One of the primary predictands of the Farquhar model is the internal CO_2 -concentration inside the leaf (c_i). Soon it was realized that this predictand can be directly linked to the so-called intrinsic water-use efficiency (iWUE), the ratio between assimilation (A) and stomatal conductance for water vapour (g) (Ehleringer and Cerling 1995; Farquhar et al. 1989) (see Sect. 17.2 for more details). The regulation of stomatal opening is one of the most intricate and essential functions of terrestrial plants, as water-limited systems demand that stomatal behavior simultaneously constrain water loss while assuring sufficient carbon gain for survival. This makes iWUE such a useful property to know, although the actual water-use efficiency (WUE), defined as the ratio of transpiration to assimilation, may even be more relevant in determining how plants respond to dry conditions. The analysis of carbon isotope values of organic matter is nowadays an efficient method to determine iWUE that integrates minute-to-minute signals in leaves over the days to months it may take to synthesize plant tissues. The isotopic composition can be determined efficiently via on-line coupling of elemental analysers to isotope-ratio mass-spectrometers (see Chap. 7), which has allowed for scientists to produce much larger data sets compared to studies taking place 20 years ago.

Given the advancements in isotopic theory and technical ability, it is not surprising that the Farquhar-model has found increasingly widespread application in tree-ring studies e.g. (Marshall and Monserud 1996; Penuelas et al. 2011; Waterhouse et al. 2004). In turn, many investigators have realized that the doors have been flung open to reveal retrospective insights on how physiological processes have shifted in response to myriad changing environmental conditions. Particularly important avenues of research for projecting carbon-climate-vegetation feedbacks within the biosphere have addressed how forests have responded to ongoing climate change and increasing CO_2 in the atmosphere (Saurer et al. 2014, Voelker et al. 2016). Although numerous studies of how plants have responded to CO_2 , temperature, drought and other factors have been carried out in greenhouses or growth chambers, such studies of small plants may not be representative of how adult trees in natural environments may have responded. Where tree longevity and size have made experimentation extraordinarily difficult, the use of tree-ring stable carbon isotopes can provide a more realistic view by studying trees in their natural habitat and over their entire life-cycle. Intriguingly, information on iWUE can be retrieved for times when CO_2 -concentration was different, for instance on the pre-industrial level of 280 ppm compared to current levels that exceed 400 ppm. We can thus obtain information on the ratio between A and g of trees living at times when scientific inquiry into plant function was in its infancy and when leaf gas-exchange equipment did not even exist. Stable carbon isotopes of tree-ring cellulose can therefore provide accurately

and absolutely dated archives of annual and intra-annual past plant physiological responses to climate, CO₂ and other environmental drivers that are unavailable from experimental methods and other paleoecological data sources.

Despite the power of pairing carbon isotope measurements and theory with tree-rings, some limitations should also be mentioned (Sect. 17.3). As *i*WUE only resolves the ratio of *A* to *g*, it often remains elusive, which of the two changed and to what degree. An increase in *i*WUE, for instance, can theoretically be caused by higher *A* or by lower *g* or a combination of the two. Furthermore, it should always be considered that *i*WUE is a different metric than the actual WUE (see Sect. 17.3 for details). Nevertheless, independent data confirm the usefulness of δ¹³C-derived *i*WUE-estimates from tree rings. Accordingly, *i*WUE-time series from multiple sites across the globe have provided numerous and invaluable insights into tree responses to global climate change. Increases in *i*WUE have been documented by essentially all studies spanning multiple decades of tree-ring isotope data and have occurred within the last ca. 100 years. However, the rate of change of increase in *i*WUE is quite variable and the reason for this range of responses not well understood. To provide additional insights, some studies have combined tree-ring derived *i*WUE with growth data originating from the same tree-rings. This can help the interpretation of growth trajectories by adding a physiological perspective, for instance in studies of drought-related decline (Sect. 17.4). While most studies focused on stomatal limitations of *i*WUE, photosynthetic limitation may be an under-explored topic (Sect. 17.5). Finally, due to the construction of large networks of sites with tree-ring isotope data, it recently became feasible to study spatial patterns of *i*WUE on regional to continental scales (Sect. 17.6). Hence, with these examples, the breadth and success of *i*WUE-reconstructions using tree-ring isotopes is on full display and portends many novel findings in the future.

17.2 Model and Scenarios

The potential to derive physiological information from δ¹³C of plant material (δ¹³C_{plant}) is strongly based on the Farquhar-model (1982), which in its simplest form is given as:

$$\delta^{13}C_{plant} = \delta^{13}C_{atm} - a - (b - a)\frac{c_i}{c_a}, \quad (17.1)$$

where δ¹³C_{atm} is the carbon isotope ratio of atmospheric CO₂, *a* (4.4‰) is the fractionation associated with the diffusion of CO₂ through the stomata, *b* (27‰) the fractionation resulting from enzymatic C fixation by RubisCO, and *c_i/c_a* is the ratio of leaf internal to ambient CO₂-concentrations. This mechanistic model for C₃-plants was experimentally verified in many studies (Evans et al. 1986) and predicts

a depletion in the isotope ratio in the plant compared to the isotope ratio in the atmosphere, but to a varying degree depending on c_i/c_a . Equation (17.1) can be applied directly to tree-rings by using the measured tree-ring isotope value of a specific year as $\delta^{13}C_{plant}$, provided the corresponding value for $\delta^{13}C_{atm}$ for the same year is used. The $\delta^{13}C_{atm}$ -values have declined over the past 150 years due to fossil CO₂ emissions and are known either from atmospheric measurements or derived from ice-core studies (Leuenberger 2007). A modified equation is sometimes used in biological studies, based on carbon isotope discrimination (Δ), which approximates the difference between $\delta^{13}C_{atm}$ and $\delta^{13}C_{plant}$, thus a positive number:

$$\Delta^{13}C_{plant} = \frac{\delta^{13}C_{atm} - \delta^{13}C_{plant}}{1 + \delta^{13}C_{plant}} = a + (b - a) \frac{c_i}{c_a}. \quad (17.2)$$

These equations can be solved for c_i/c_a . In the following, we explain how the intrinsic water-use efficiency *iWUE* is derived from this information, which is the ratio of net photosynthesis (*A*) to conductance for water vapor (g_{H_2O}) (Ehleringer and Cerling 1995):

$$iWUE = \frac{A}{g_{H_2O}}, \quad (17.3)$$

expressed in units of $\mu\text{mol mol}^{-1}$. Using the equation for net photosynthesis

$$A = g_{CO_2}(c_a - c_i), \quad (17.4)$$

with g_{CO_2} as the conductance for CO₂, and considering

$$g_{H_2O} = 1.6g_{CO_2}, \quad (17.5)$$

we obtain the following relationship

$$iWUE = \frac{(c_a - c_i)}{1.6}. \quad (17.6)$$

Finally, using c_i/c_a derived from Eq. (17.1), we find:

$$iWUE = c_a \frac{b - (\delta^{13}C_{atm} - \delta^{13}C_{plant})}{1.6(b - a)}. \quad (17.7)$$

Such derived *iWUE* has been widely employed in tree-ring isotopic studies.

A and g_{H_2O} and thus c_i depend on various environmental drivers (light, CO₂, VPD, etc.) and are dependent on species and site conditions. To group different

tree physiological responses, a useful heuristic has classified three primary leaf gas-exchange scenarios (Saurer et al. 2004): In response to changing CO_2 and other environmental variability over time, there can be trees that (1) tend to keep c_i constant representing a homeostatic gas-exchange regulation (Marshall and Monserud 1996), (2) trees that keep c_i/c_a constant like a set-point (Ehleringer and Cerling 1995), or (3) trees that keep $c_a - c_i$ constant, which is the equivalent of no increase in iWUE. Over large gradients in c_a , however, meta-analysis of empirical data indicates there is a shift between scenarios (Voelker et al. 2016). Equations (17.1 and 17.7) shown here are easily applicable due to their simple form, but additional fractionation effects occur during and after photosynthesis that could in principle also be included. Such effects are, for instance, due to the mesophyll conductance and other diffusive limitations within the leaf as well as photorespiration (discussed in Chap. 9), post-photosynthetic fractionations during biochemical reactions and phloem transport (Chap. 13) as well as effects related to timing of wood formation, use of stored carbohydrates and subsequent mixing of carbon pools of different age (Chap. 15).

17.3 Limitations and Verifications

While iWUE has proven useful in numerous studies, one needs to be aware of some limitations of this metric. The actual WUE is a closely related, but still different concept, which is calculated as the ratios of net photosynthesis (A) to transpiration (E) (rather than A to $g_{\text{H}_2\text{O}}$ only):

$$WUE = \frac{A}{E}, \quad (17.8)$$

with E defined as:

$$E = g_{\text{H}_2\text{O}}(e_i - e_a) = g_{\text{H}_2\text{O}}VPD, \quad (17.9)$$

whereby e_i and e_a are the vapor pressures in the leaf cellular air space and ambient air, respectively. Such WUE may be ecologically more relevant than iWUE because it is based on the water fluxes and depends directly on VPD, which has been shown to be important in amplifying recent warming trends (Breshears et al. 2013; Szejner et al. 2019). Furthermore, WUE can be calculated over different periods, for instance, as the ratio of carbon uptake to water loss at the plant level over a growing season or plant life, which is also influenced by respiratory losses. It has been shown that different concepts of WUE, like intrinsic and actual WUE, are sometimes poorly correlated (Seibt et al. 2008). WUE can also be considered at a larger scale: at the ecosystem-level, where it is defined as gross primary production (GPP) relative to evapotranspiration (ET). In our opinion, it is of great importance to be aware of the different scales at which WUE can be calculated and be cognizant that one is

not compared directly with another without acknowledging how they may differ. It should be quite obvious that plant-level and, for instance, ecosystem level WUE are not the same and therefore should also not be expected to respond similarly to environmental variability. Nonetheless, comparisons of WUE-estimates obtained by different techniques may yield new insights on leaf, plant and ecosystem functioning.

As an example where different techniques resulted in comparable WUE estimates, a study in a *Quercus petraea* forest indicated that seasonal iWUE data obtained via a process-based physiological model matched well with iWUE derived from intra-annual $\delta^{13}\text{C}$ of tree-rings (Michelot et al. 2011). The authors concluded that latewood may be a good proxy for assessing seasonal variations of the ratio of assimilation to stomatal conductance, despite some delay in organic matter deposition in the ring. In contrast, WUE at the ecosystem level determined as GPP/ET at eddy-covariance-based ecosystem flux tower monitoring sites across North America showed that WUE at the ecosystem scale has been increasing much faster than that recorded by tree-ring isotope-based iWUE (Guerrieri et al. 2019). The authors speculated that reasons for this discrepancy could be different time-scales of the two approaches or fluxes not accounted for, like non-transpirational water fluxes and contribution from understory vegetation. In a study using satellite-based NPP estimates, a relationship between tree-ring $\delta^{13}\text{C}$ values of an Eastern US network of sites and NPP was found, rather than with WUE (Levesque et al. 2019). Finally, at a site in California, Keen (2019) showed that intra-annual tree-ring derived iWUE responded positively to VPD, whereas ecosystem-level WUE responded negatively to VPD, and this opposing VPD-response drove a negative response between iWUE and WUE during a range of wet to historically severe drought conditions. Together, these studies demonstrate that tree-ring carbon isotopes can contain valuable information on large-scale fluxes, but that more studies are needed to determine under what conditions iWUE is related to ecosystem-scale WUE (Seibt et al. 2008).

A complication of interpreting tree growth patterns and iWUE-estimation that needs careful consideration are the effects of age, tree size or height (Brienen et al. 2017; McDowell et al. 2011). Dendrochronologists have conventionally used empirical detrending methods to remove age-related growth patterns from ring-width data prior to assessing climate-sensitivity of tree growth. In recent decades it has become popular among ecologists and ecophysiologicalists to convert tree-ring data to basal area increment (BAI) or BAI/basal area for a given year, often putatively as a means to avoid the need to detrend ring-width data that decline with tree size and age. However, the often-stated or implied contention that these variables overcome the need for detrending is a misconception. For example, BAI tends to increase with tree size, but trees with initially greater BAI tend to have steeper positive relationships between BAI and tree age (Voelker et al. 2008). Likewise, BAI/basal area has a negative trend with age that is particularly steep when trees are young and BAI/basal area is nearer to one. Hence, it should be obvious that use of BAI or BAI/basal area may include biases in tree growth trends and should not be compared when groups of trees differ in age or size. Overall, BAI or BAI/basal area methods may not be an improvement over conventional detrending methods for comparison to stable isotopes in the

same tree rings, particularly for studies of trees that are young (i.e., <100 years in age).

The carbon isotopes of tree-rings can change as trees grow, and depending somewhat on species and stand density, foliage is displayed at further distances from soil water sources as they get taller and form larger branches (McDowell et al. 2011). This change in stature results in a greater hydrostatic gradient in water potential and higher hydraulic resistance that impacts canopy-level stomatal conductance and thus iWUE. Such long-term trends owing to changes in tree stature can be mistakenly attributed to climate and/or CO₂, so care should be taken to minimize the potential for this bias by considering it in assessments of carbon isotope responses to long-term environmental change (Brienen et al. 2017). If neglected, this bias could result in an over-estimation of how CO₂ modifies leaf gas exchange. Several studies have, however, highlighted that $\delta^{13}\text{C}$ mainly has age-related trends in the first few decades, forming a so-called juvenile trend, but not later on (Gagen et al. 2007; McCarroll and Loader 2004). This problem can be avoided by simply not using the juvenile phase or by applying appropriate corrections if known for a specific species or site (Vadeboncoeur et al. 2020). The age-trend can well be tested for trees growing in pre-industrial times where there are no strong variations in CO₂-concentration by aligning them according their cambial age. This was done in a recent study with coastal redwood trees where indeed the age-trend was strongest in the first few decades of their life, but extended several centuries before finally levelling off (Voelker et al. 2018) (Fig. 17.1). These trees are, however, almost 100 m tall and take exceptionally long to reach this height, showing that there is no universal juvenile phase that is applicable across species and forest types.

Some studies have tried to exclude age-effects by comparing different age cohorts, i.e. comparing iWUE of young trees with mature trees during the same time period (Bert et al. 1997; Brienen et al. 2017; Marshall and Monserud 1996). These studies have not addressed a potential sampling bias, whereby mature trees are the survivors of decades to centuries of mortality processes and also may not reflect the overall stand structure and history (Brienen et al. 2017). Microclimatic conditions are also different for saplings near the ground as compared to larger trees, e.g. regarding light and VPD, which affects the relationship between $\delta^{13}\text{C}$ and growth (Fardusi et al. 2016). In other studies, stand structure has been shown to affect $\delta^{13}\text{C}$ -trends of understory beech and spruce trees, emphasizing the effects of competition and light (Klesse et al. 2018) as well as in overstory ponderosa pine and grand fir trees (Voelker et al. 2019a) due to increasing competition for water in the absence of wildfire. Clearly, more research is needed to reliably separate the effects of CO₂, climate, age and tree height. Nevertheless, the strong increases in iWUE as a result of the atmospheric CO₂-increase has been found to be widespread and thereby clearly cannot be an artefact (Guerrieri et al. 2019).

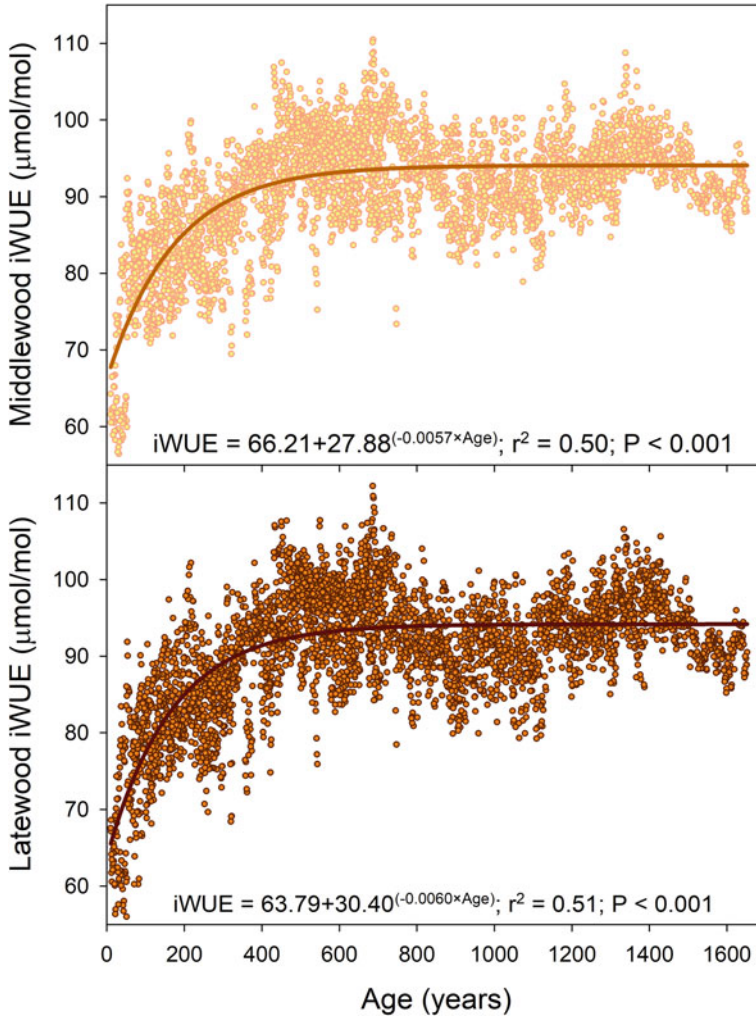


Fig. 17.1 Examples of inter-annual iWUE, sampled for two intra-annual ring divisions (latewood and middlewood), from seven coastal redwoods (*Sequoia sempervirens*) growing in northern California, USA (after Voelker et al. (2018)). Tree age data were corrected to ground level from tree cross-section sampling height and pith dates were estimated using conventional techniques. To minimize the potential impact of atmospheric CO₂ concentrations or ¹³CO₂, no data from years later than 1880 were used. Finally, tree-level variation was minimized by iteratively fitting negative exponential curves and correcting each data point with the tree-level mean residual. There were no significant changes to the relationship after three iterations. Note that middlewood was defined as the central 60% of each ring while the latewood occupied the last 25% and the first 15% of each ring was discarded

17.4 Combination of Growth and iWUE: The Case of Drought

The combination of conventional dendrochronological analyses of growth and stable isotope methods can be very powerful. With a multi-proxy approach, the particular strength of tree rings is taken full advantage of as all the measurable parameters originate from the same absolutely dated rings, but contain different environmental information. Tree ring widths or basal area increments provide cumulative growth information that is related to the complex interplay of environmental conditions and limiting factors to xylogenesis during the growing season, whereas stable isotopes measured in the cellulose of these tree rings are rather recording the physiological conditions at the canopy level. Stable isotopes are also influenced by seasonal timing of wood formation as periods of extreme growth limitation, e.g. drought, may not be reflected in the isotope signal of the tree ring when xylogenesis is halted (Sarris et al. 2013). Furthermore, drought legacy effects may differ between tree-ring width and stable isotopes as the recovery after an extreme event may be different for the two parameters (Szejner et al. 2019). Hence, stable isotopes can help decipher causes of growth variations more clearly in many cases. Tree growth and iWUE may or may not show similar trends and may also display positive or negative correlations. With careful consideration of biological trends due to tree age and size, the combined analysis of tree growth and iWUE or carbon isotope discrimination can help to decipher what relevant environmental mechanisms may be impacting trees by affecting leaf gas exchange, growth, or both factors together (Brienen et al. 2021; Sun et al. 2018; Voelker et al. 2014). This multi-proxy approach may be particularly relevant for better understanding tree responses to climate warming and various aspects of drought (Levesque et al. 2014). Indeed, the area of land classified as very dry has more than doubled globally in the last 50 years and accordingly drought conditions are affecting many forest ecosystems, resulting in reduced growth and increased stress and tree mortality (Allen et al. 2010). For example, in areas such as the Central Mediterranean, Central and Western Europe, California and much of the Western United States and elsewhere, warmer temperatures have amplified droughts (Dai 2013). California and the west US coast in particular has undergone recent extremes (Keen et al. 2022) that are expected to become more severe in the future based on climate model predictions (Wang et al. 2017; Yoon et al. 2015). These projections are further supported by long tree-ring isotope chronologies that demonstrated greater hydroclimate variability during the warmer Medieval Climate Anomaly and the period of recent warming compared to the colder Little Ice Age (Voelker et al. 2018).

Considering projections of increased drought frequency and severity, there is a crucial need to understand mechanisms leading to drought-induced tree mortality, which may be provided by investigating how some trees, species and different forest ecosystems have responded to acute or chronic drought stress (Allen et al. 2010). Although drought-related physiological effects on trees have long been studied, the significance of different mechanisms is still unclear (McDowell et al. 2008). When

pests and pathogens do not act as the primary cause of tree mortality, the most important processes leading to death are hydraulic failure (desiccation) in extreme drought events and a reduction of the trees' carbon storage through gradual depletion of carbohydrates (starvation) induced by protracted drought episodes. The mechanism of carbon starvation is likely related to water-use efficiency, as plants may reduce stomatal conductance strongly to avoid loss of water, and therefore this process may be elucidated using stable carbon isotopes. In such a situation, the plant is no longer capable of producing enough non-structural carbohydrates to maintain essential metabolic functions and stored non-structural carbohydrates are inaccessible due to compartmentalization and lack of enzymatic energy (Sala et al. 2010).

Studies of trees that survived or died during intense periods of drought have been particularly effective at applying tree-ring growth and stable carbon isotopes to highlight physiological factors that ostensibly predisposed trees to mortality. One of the first such investigations to do so used a rather narrow time window for assessment, but nonetheless found that trees that died during a severe drought had similar *i*WUE, but lower tree growth rates, compared to co-occurring trees that survived (McDowell et al. 2010). However, the surviving trees showed a strong climatic sensitivity of gas exchange (i.e. $\delta^{13}\text{C}$) in contrast to dying trees, which was attributed to dead trees having undergone chronic drought stress and carbon starvation prior to death. Other more recent studies have further refined this type of approach. For example, high mortality rates of Scots pine (*Pinus sylvestris* L.) in lower altitudes in inner-Alpine valleys such as the Valais (Switzerland) (Rigling et al. 2013) exemplify a region that was undergoing drought-induced forest decline. At one site, analyses of growth and stable carbon isotope ratios in tree rings over the twentieth century were combined with a 10-year irrigation experiment that doubled annual precipitation (Timofeeva et al. 2017). There was a strong growth increase and concurrent depletion of $\delta^{13}\text{C}$ values for irrigated trees, indicating reduced *i*WUE. This demonstrated that progressive limitation of leaf gas-exchange by drought-induced stomatal closure was reversible when extra water was supplied. In the same stand, Scots pine trees that had recently died had more than 100 years of lower growth and higher *i*WUE derived from $\delta^{13}\text{C}$ values compared with surviving trees. This indicates a conservative water-use strategy for trees that had died, which resulted in a lack of carbohydrates, reduction of the needle mass and long-term weakening. In contrast, a study with Norway Spruce (*Picea abies* L. Karst.) indicated a different cause for mortality, as dying trees grew significantly better and had higher *i*WUE in the earlier life phase than surviving trees (Hentschel et al. 2014). Similarly, it was found for Scots pine (Voltas et al. 2013) and for a Mediterranean oak species (Colangelo et al. 2017) that "fast growing" and "less efficient" individuals were more affected, whereas (Heres et al. 2014) observed that declining trees were less sensitive in *i*WUE than non-declining trees. Such differences in tree response strategies to drought could be summarized in a conceptual diagram (Fig. 17.2).

The diagram shows differences between surviving and dead trees, where the surviving trees are considered as the reference. These two tree groups have differed in their past growth patterns and physiology prior to the actual, final decline phase. Trees following a conservative strategy are located in the upper, left-hand sector of

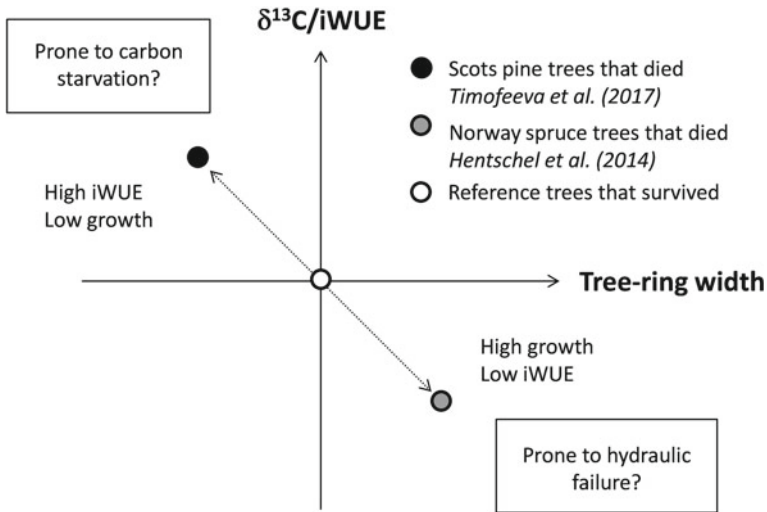


Fig. 17.2 Conceptual diagram for explaining death or survival of trees from the same stand based on their earlier physiology and growth patterns. The location of the black circle indicates the position of dead trees from the Scots pine site in Switzerland (Timofeeva et al. 2017), while the grey circle refers to Norway spruce trees from southern Norway (Hentschel et al. 2014). Surviving trees indicated as open circle are considered as the reference in both studies

the diagram, as was observed for Scots pine at the Swiss study site (Fig. 17.2). These trees are expected to be prone to carbon starvation rather than to hydraulic failure. It should be considered that carbon starvation may just mean a lack of carbohydrates and energy to maintain vital functions, although not a complete exhaustion of storage pools (Hartmann and Trumbore 2016). In contrast, for Norway spruce (Hentschel et al. 2014), trees that died later had higher growth and were not following a strict water-use strategy. Therefore, these trees were prone to hydraulic failure rather than carbon starvation. This less conservative water-use strategy falls in the lower, right-hand sector of the diagram (Fig. 17.2).

Absolute values of growth and iWUE can provide one continuum on which trees can be ordered that can provide valuable physiological interpretations (Fig. 17.2). Additional insights may be gained by assessing the sensitivity of growth or carbon isotopes to various metrics of meteorological drought or the coupling of growth to carbon isotope variation each provide additional windows on the relative degree of drought stress and how that response may have changed over time (Keen 2019, McDowell et al. 2010, Urrutia-Jalabert et al. 2015, Voelker et al. 2014, Voelker et al. 2019a). Overall, stable isotope analysis in combination with the study of growth patterns is therefore a promising approach for elucidating relevant physiological processes under drought, even more so when including oxygen isotope ratios as their changes are influenced by transpiration rate, but not photosynthesis (Gessler et al. 2018) (Chap. 10). This may ultimately result in improved predictions of forest ecosystem changes in the future.

17.5 Photosynthetic Limitations to iWUE

Most investigations of tree-ring carbon isotopes have highlighted how interannual variability in iWUE is driven by stomatal closure during drought and that this pattern is superimposed on how gradually rising CO₂ has driven long-term changes in A . Since so few studies have demonstrated evidence for how A has formed the primary physiological constraint on interannual variability on tree-ring carbon isotopes and iWUE, a few examples warrant specific mention here because they may continue to lead to particularly novel insights. Two forest health studies on species located in the eastern United States have shown that iWUE has been strongly influenced by sulfur emissions and associated acidic deposition that increased during most of the twentieth century and then showed a reversal in trend near 1980 after US federal legislation and enforcement was increasingly implemented from 1963 through 1990 (Mathias and Thomas 2018; Thomas et al. 2013). The authors concluded that increasing A was an important component for explaining recent tree recovery. Other records where inter-annual variability in tree-ring isotopes were controlled by how A was modified by temperature and/or sunshine occurred in cold northerly regions such as Northern Norway and Sweden (Loader et al. 2013; Young et al. 2012). Alternatively, Voelker et al. (2019b) showed that similar constraints on A by temperature could be identified in temperate trees growing adjacent Lake Superior, which modulates near-lake air temperature regimes due to the large heat capacity of the lake reflecting previous winter conditions during spring and early summer. The last study was careful to utilize only “middlewood” formed during the early growing season, which contrasts with many other studies of drought stress that focus on whole rings or latewood. Hence, this emphasizes the need for future studies of tree-ring isotopes to carefully consider which intra-annual sampling scheme may be most appropriate where differences in the primary constraints on leaf carbon uptake may shift on a seasonal basis between photosynthetic rates and stomatal conductance (see also Chap. 15). Finally, Breinen et al. (2021) has shown that during understory phases of tree development, tree growth is often negatively correlated to carbon isotope discrimination but had neutral or weak positive correlations once the same trees were in canopy dominant positions, which implies that both the photosynthetic rates and growth of these trees were limited by irradiance when they were in the understory.

17.6 Large-Scale Patterns

Earth System Models and Dynamic Global Vegetation Models (DGVMs) are the workhorses to explore many large-scale terrestrial processes and climate-land biosphere interactions. These models are routinely used to project future changes in climate and Earth System processes under anthropogenic forcing in a detailed spatio-temporal context (Sitch et al. 2003). DGVMs represent the basic physiological processes responsible for plant growth via sets of interconnected equations

such as those for photosynthesis, respiration, and stomatal conductance, and the dependence of these physiological processes on the environmental (e.g., atmospheric CO₂ concentration, temperature, and water availability) conditions. A particular challenge for these models is to correctly capture and project changes at decadal-to-century timescales of utmost relevance for predicting short-term anthropogenic climate perturbations. For example, mechanisms of the contemporary terrestrial carbon sink are poorly understood which leads to large uncertainties in twenty-first century climate projections (Cox et al. 2000). The representation of many physiological mechanisms and plant-atmosphere interactions is still crudely or not at all implemented in these DGVMs, and appears to significantly contribute to uncertainties in predictions. Improving and validating the modeling of key processes with empirical data are thus particularly important.

Based on development of tree-ring isotopic networks over the past two decades (Saurer et al. 2014; Treydte et al. 2007), it has become feasible to link such tree-ring data to DGVMs on a large spatial and temporal scale. While not strictly leading to a validation of either model nor tree-ring data, this comparison can be profitable for both fields of scientific inquiry, as independent assessment of similar variables, like iWUE. Furthermore, DGVMs can also add more interpretation to a tree-ring network, as variables like *g_s* and *A* can be obtained. In a recent study using a 35-site network across Europe with coniferous and deciduous species, changes in iWUE from 1901–2000 and the spatial distribution of these changes across Europe were investigated (Saurer et al. 2014). On average, iWUE increased in European forests by 28%, with clear spatial differences across the continent. Moreover, comparison of these data with iWUE simulations by a dynamic vegetation model (LPX-Bern 1.0) showed good agreement with spatial patterns and overall twentieth century trends in tree ring derived iWUE. Across the 27 conifer sites, tree-ring derived iWUE showed strong differences between sites grouped in three latitudinal bands, i.e. <45°N, 45–60°N, and >60°N (Fig. 17.3). The northernmost sites showed the lowest iWUE and also the lowest increase over the twentieth century (60.3–70.3 μmol/mol from the first to last decade of twentieth century, i.e. an increase by 16.6%). They also showed a rather homogenous signal as reflected in relatively low variability among sites. In comparison, the most southern sites, from Mediterranean climate, showed the highest overall values, an increase of 23% over the twentieth century, and also were characterized by relatively high variability among sites, showing that different ecosystems react rather differently to increasing CO₂ depending on local site factors. Sites from temperate climates, i.e. intermediate latitudes, showed intermediate overall iWUE, the strongest increase over the twentieth century by 31%, and further a notable increase in the variability over time. This patterns of iWUE-increase might reflect a generally strong, but variable sensitivity to increasing CO₂, compared to where temperature (i.e. northern latitude sites) or precipitation (i.e. low latitude mediterranean sites) have historically been strongly limiting to leaf gas-exchange and growth.

These analyses clearly demonstrate the usefulness of such networks of tree-ring data for better understanding physiological tree responses to climate and CO₂ across

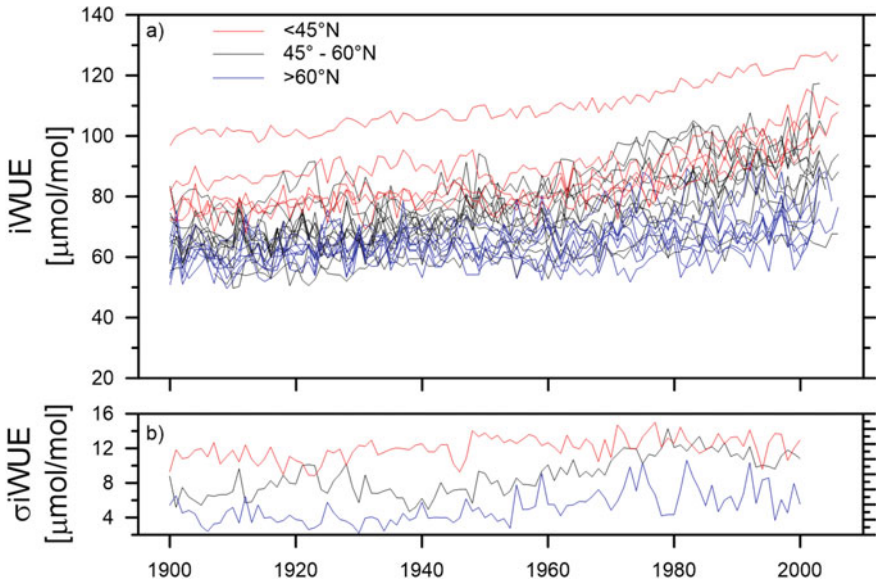


Fig. 17.3 Reconstructed iWUE from 27 conifer sites across Europe grouped into different latitudinal bands (a). Variability of iWUE between sites (standard deviation) for these latitudinal bands (b)

different ecosystems. It might be further interesting to consider that net photosynthesis tends to play a larger role in determining growth and $\delta^{13}\text{C}$ in more energy-limited environments, such as boreal forests, than in drought-prone environments. Under scenarios of increasing drought, this may imply that changes in the relative weight of energy and water limitations could be assessed through the combined use of $\delta^{13}\text{C}$ and tree-rings. Nevertheless, the interpretation of iWUE-trends is not straightforward and can be enhanced by DGVM-results as shown in another recent study (Frank et al. 2015). Here, increases in European forest transpiration were calculated over the twentieth century, although a general decrease in stomatal conductance was also inferred, which seems at first view to be contradictory. The increased model transpiration results were due to longer growing seasons, enhanced evaporative demand in a warmer climate, and increased leaf area, which in total were outweighing the effect of reduced conductance. These results suggest caution may need to be applied when interpreting iWUE-results physiologically from $\delta^{13}\text{C}$ of tree-rings without additional information on seasonality of tree-ring growth, but also shows the enormous potential of combining tree-ring isotopes and DGVM- or other large-scale model outputs for yielding new insights on carbon and water cycling.

Acknowledgements Steve Voelker was supported by US-NSF Award #1903721.

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