

Chapter 22

Stable Isotopes in Tree Rings of Tropical Forests



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22.1 Introduction

The analysis of growth rings in the stems of trees is a relatively new tool in tropical forests, as the existence of annual rings in tropical trees was not commonly recognized until recently. For a long time, the tropical environment was associated with year-round favorable growth conditions that were thought to prevent the formation of distinct annual growth rings. However, most tropical environments are seasonal to a various extent (Fig. 22.1), and the formation of annual tree rings in deciduous species growing in tropical climates with a pronounced dry season has been known for a long time (Coster 1927). Although ring boundaries of trees in the humid tropics are generally less clear than those in temperate trees, the formation of distinct annual growth rings has been shown for a large number of tropical tree species (Worbes 2002; Rozendaal and Zuidema 2011; Zuidema et al. 2012; Brienen et al. 2016; Schöngart et al. 2017). In addition to drought, other seasonally changing environmental factors, such as flooding and soil salinity, are known to induce the formation of annual ring boundaries (Schöngart et al. 2002; Chowdhury et al. 2008).

Supplementary Information The online version contains supplementary material available at (https://doi.org/10.1007/978-3-030-92698-4_22).

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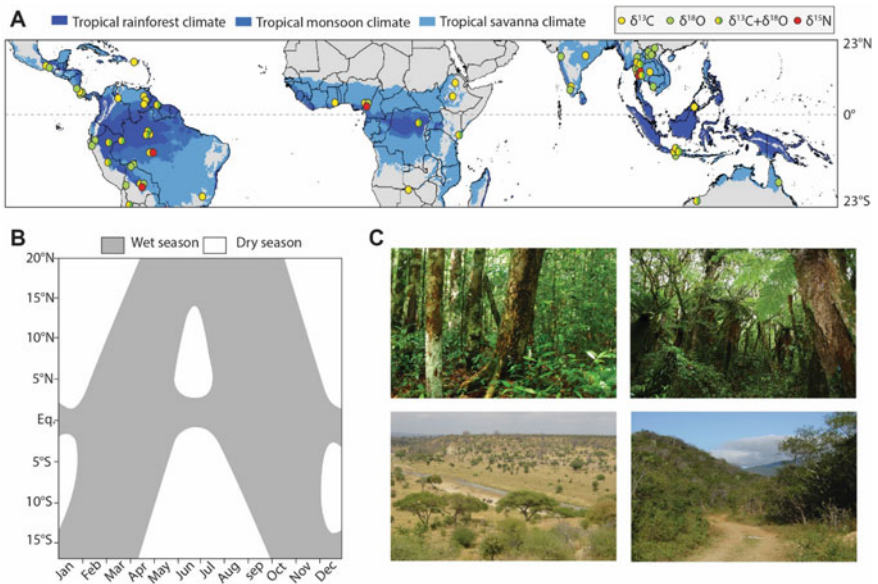


Fig. 22.1 **a** Map of the tropics showing locations of studies on stable isotopes in tropical tree-rings. Main findings of these studies summarized in Table 22.1. Background map showing tropical climates according to Köppen classification (map from Beck et al. 2018), with grey continental areas belonging to arid (mostly treeless) climate types. **b** Diagram showing general rainfall seasonality in the tropics, with a dry month defined as a month with <100 mm average precipitation. Figure adapted from Kricher (2011). **c** A few examples of tropical (woody) ecosystems. Clockwise from top left: evergreen rainforest close to the equator (no dry season) in Brazil, mountain cloud forest in Bolivia (moderate dry season; but moist year round), deciduous dry forest in Mexico (long dry season), and savanna vegetation in Tanzania (long dry season)

The “re-discovery” of annual growth-ring formation in tropical trees, and developments in stable isotope analyses has triggered studies on the variation of the natural abundance of isotopes in tropical trees, with the number of publications on stable isotopes in tropical tree rings increasing rapidly in recent years (Fig. 22.1). In this chapter, we provide an overview of research on stable isotopes in tropical tree rings, and the insights gained on the functioning of tropical forests and the impacts of global change. This chapter is a condensed and updated version of our earlier review (van der Sleen et al. 2017), with a main focus on lowland forests in the wet tropics between 23.5°N/S (Fig. 22.1).

22.2 Tropical climate

The tropics are generally warm (mean annual temperature of $>24\text{ }^{\circ}\text{C}$) and wet (except for dry grasslands and deserts). Most tropical ecosystems are seasonal to some extent, but in contrast to temperate regions, seasonal weather patterns are primarily driven by variation in precipitation amount and not temperature fluctuations. Across the tropics, rainfall seasonality is a result of large-scale atmospheric circulation patterns. At the equator, heat builds up, causing warm and moisture-laden air to rise. The ascending air diverges at the top of the troposphere and flows to more northern and southern latitudes. As the air cools, it loses its moisture as precipitation, becomes more dense, and ultimately descends as dry air in the subtropics, from where it returns equatorward near the surface, giving rise to the trade winds. These circulation patterns, on both the northern and southern hemisphere, are called the Hadley cells. The great equatorial convection zone, where the trade winds meet is known as the Intertropical Convergence Zone (ITCZ), and characterized by violent thunderstorms and high quantities of precipitation. The ITCZ moves north during the Northern hemisphere summer, and south during the austral summer, as a consequence of the Earth's tilt. This seasonal movement induces wet and dry seasons in most tropical regions (Fig. 22.1). At locations lacking a true dry season, forests will remain evergreen throughout the year. At locations with a longer or drier dry season, the number of deciduous species increases. Further away from the Equator, forests give way to savanna, shrubland or grassland (Fig. 22.1). Although climate is an important factor determining forest type, it is also affected by other factors, such as soil characteristics and fire regime.

Another important climatic feature in tropical regions is the El Niño–Southern Oscillation (ENSO), which are irregular periodic variations in winds and sea surface temperatures over the tropical eastern Pacific Ocean. Although the factors responsible for the occurrence of ENSO events remain incompletely understood, the phenomenon occurs when the ITCZ migrates more southwards than normal. This raises sea surface temperature and disrupts the normal upwelling pattern along the west coast of South America. Eventually, this reduces the transport of warm surface water across the Pacific Ocean toward Asia, and as a result affects weather systems throughout the tropics and subtropics, causing heavy downpours and flooding in some regions and severe droughts in others. El Niño occurs every two to seven years and tends to alternate with another climatic phenomenon with opposite effects. This is called La Niña, and happens when trade winds gain abnormal strengths, increasing upwelling along the west Coast of South America and strengthening the flow of warm surface water westwards across the Pacific.

Local climate conditions, and its variability (including ENSO-driven anomalies), affect tree physiology and thus tree-ring isotope values. In addition, large-scale circulation patterns affect the $\delta^{18}\text{O}$ signature of precipitation, which can be recorded in tree rings (Table 22.1).

Table 22.1 Summary of the main usage and outcomes of studies measuring stable isotopes in tropical tree rings. References given in chronological order (detailed version of the table is available, see Supplementary Table S1)

Stable isotope	Main usage	Main outcome	Number of species*	References
¹³ C	Proxy for iWUE	iWUE generally increased over time	21(3)	Hietz et al. (2005), Brienen et al. (2011), Loader et al. (2011), Locosselli et al. (2013), van der Sleen et al. (2015a), Rahman et al. (2020)
	Identification of annual rings in ring-less wood	Moderate potential to identify annual rings through intra-annual sampling	12(8)	Leavitt and Long (1991), Ohashi et al. (2009), Krepkowski et al. (2013), Schubert and Timmermann (2015)
	Unravelling isotope-climate relationships	Negative correlation with rainfall	16(0)	Gebrekirstos et al. (2009), Fichtler et al. (2010), Brienen et al. (2011), Gebrekirstos et al. (2011), van der Sleen et al. (2014), Schubert and Timmermann (2015), Boakye et al. (2019)
	Reconstruction of past climate	Some prospect for rainfall reconstruction	1(0)	Wils et al. (2010), Mokria et al. (2018)
¹⁸ O	Unravelling isotope-climate relationships	Correlations with rainfall, humidity and ENSO in shallow rooting trees	11(0)	Anchukaitis et al. (2008), Anchukaitis and Evans (2010), Managave et al. (2011b), Managave et al. (2011a), Xu et al. (2011), Brienen et al. (2012), Zhu et al. (2012a), Zhu et al. (2012b), Sano et al. (2012), Brienen et al. (2013), Xu et al. (2013), Boysen et al. (2014), van der Sleen et al. (2015b), Schollaen et al. (2015), Xu et al. (2015), Volland et al. (2016), Cintra et al. (2019)

(continued)

Table 22.1 (continued)

Stable isotope	Main usage	Main outcome	Number of species*	References
	Reconstruction of past climate	Good prospect for rainfall reconstruction	14(0)	Managave et al. (2011b), Managave et al. (2011a), Brienen et al. (2012), Zhu et al. (2012a), Zhu et al. (2012b), Sano et al. (2012), Xu et al. (2013), van der Sleen et al. (2015b), Baker et al. (2015), Xu et al. (2015), Pumijumnong et al. (2020)
	Identification of annual rings in ring-less wood	Good potential to identify annual rings through intra-annual sampling	6(6)	Evans and Schrag (2004), Evans (2007), Anchukaitis et al. (2008), Managave et al. (2010), Xu et al. (2014)
	Identification of annual rings in ring-less wood	Good potential to identify annual rings through intra-annual sampling	20(17)	Verheyden et al. (2004), Poussart et al. (2004), Poussart and Schrag (2005), Pons and Helle (2011), Ohashi et al. (2016), Managave et al. (2017), Cintra et al. (2019)
¹³ C and ¹⁸ O	Unravelling isotope-climate relationships	Correlations with rainfall and ENSO	6(0)	Cullen and Grierson (2007), Ballantyne et al. (2011), Schollaen et al. (2013), Colombaroli et al. (2016), Managave et al. (2017)
	Identification of drivers of changes in iWUE (stomatal conductance vs. photosynthesis)	Some evidence that iWUE increased through decreased <i>g_s</i>	4(0)	Cullen et al. (2008), Nock et al. (2011)
¹⁵ N	Effects of increased N deposition on N cycling	Potential to record aspects of nitrogen cycle	9(0)	Hietz et al. (2010), Hietz et al. (2011), van der Sleen et al. (2015c)

ENSO, el Niño Southern Oscillation; iWUE, intrinsic water-use efficiency; *g_s* stomatal conductance

* Total number of species and those with non-distinct growth rings between brackets. Some species were involved in multiple studies, notable *Tectona grandis*, *Cedrela odorata*, and *Fokienia hodginsii*

22.3 Carbon Stable Isotopes

22.3.1 Carbon Isotope Ecophysiology in the Tropics

The stable carbon isotopic signature in the wood of tropical trees is influenced by a variety of factors related to rainfall, temperature, light conditions and species' responses to drought (for the basics of the $^{13}\text{C}/^{12}\text{C}$ isotope fractionation in plants see Chap. 9). The combined effects of these factors determine $\delta^{13}\text{C}$ values measured in tropical tree rings. In some cases, contributions of individual environmental factors are hard to disentangle, as they can covary and exert similar effects on tree-ring $\delta^{13}\text{C}$.

Ontogenetic trends in tree-ring $\delta^{13}\text{C}$ series can be substantial for tropical trees, as was illustrated for *Cedrela odorata* from Bolivia (Brienen et al. 2017). Juvenile trees growing under a forest canopy are exposed to reduced irradiance that is associated with a high ratio of intercellular over atmospheric CO_2 concentration (c_i/c_a), and young trees possibly also absorb ^{13}C -depleted CO_2 near the forest floor (Medina and Minchin 1980; Medina et al. 1991; Buchmann et al. 1997). Both factors contribute to low $\delta^{13}\text{C}$ values in the stem wood of small trees. Sub-canopy trees are exposed to higher light levels and slightly ^{13}C -enriched CO_2 due to high photosynthetic activity in the canopy, leading to higher $\delta^{13}\text{C}$ values in their wood. Canopy and emergent trees are exposed to high light levels and CO_2 with an atmospheric $\delta^{13}\text{C}$ signature (Buchmann et al. 1997). In addition, ontogenetic trends in tree-ring $\delta^{13}\text{C}$ may be driven by increased vapor pressure deficit (VPD) from understory to canopy and increases in hydraulic resistance with tree height. Therefore, changes in $\delta^{13}\text{C}$ with tree size can provide valuable information in an ecological context (e.g. on light conditions; van der Sleen et al. 2014), but are an important confounding factor in a dendroclimatological context.

Decreasing water availability, or increasing VPD, results in stomatal closure, and therefore lowers the C_i/C_a ratio (e.g. Gebrekirstos et al. 2011). As a result, drought increases tree-ring $\delta^{13}\text{C}$ values and intrinsic water-use efficiency (iWUE; the ratio of photosynthetic rate over stomatal conductance; A/g_s) (e.g. Lambers et al. 2008; Cernusak et al. 2009; Craven et al. 2013). The available evidence suggests that the relationship between water availability and tree-ring $\delta^{13}\text{C}$ also holds in regions with humid climatic conditions: $\delta^{13}\text{C}$ of leaves collected in the rainy season was lower than in leaves collected in the dry season (French Guyana, Buchmann et al. 1997), and wood $\delta^{13}\text{C}$ of trees growing near a creek was lower than that of trees growing on a comparatively drier ridge (Guyana, Pons et al. 2005).

Changes in light and nutrient conditions can also affect tree-ring $\delta^{13}\text{C}$ values when photosynthetic activity increases (A) more than stomatal opening (g_s) (e.g. Cernusak et al. 2009; van der Sleen et al. 2014). Interestingly, average tree-ring $\delta^{13}\text{C}$ values and the impact of environmental conditions on $\delta^{13}\text{C}$ ratios is species specific. Co-occurring tree species of similar DBH can exhibit large variations in $\delta^{13}\text{C}$ values, which has been related to differences in successional status (Bonal et al. 2007), shade tolerance (Guehl et al. 1998; Bonal et al. 2000), leaf phenology patterns (Bonal et al. 2000), and drought tolerance (Craven et al. 2013).

22.3.2 Seasonal Variation in Tree-Ring $\delta^{13}\text{C}$

Early studies on $\delta^{13}\text{C}$ in tropical wood showed the presence of intra-annual variation, similar to what was found for other climatic regions (Leavitt and Long 1991). Subsequent studies confirmed this seasonality (e.g. Poussart et al. 2004; Verheyden et al. 2004; Ohashi et al. 2009), suggesting seasonal variation in water availability as underlying cause. Variation in $\delta^{13}\text{C}$ within a single growth ring can however, not be unequivocally understood from current photosynthesis on the basis of the Farquhar et al. (1989) model. Other processes may interfere with patterns driven by climate seasonality, such as utilization of stored reserves early in the growing season, potential fractionation downstream from the carbon fixation in the leaves, and a varying fraction of C allocated to other processes than diameter increment in the growing season (Helle and Schleser 2004; Kagawa et al. 2006; Krepkowski et al. 2013; Fu et al. 2017). Although attempts have been made to identify annual rings in tropical trees that lack visible increment ring boundaries based on intra-annual $\delta^{13}\text{C}$ patterns, $\delta^{18}\text{O}$ proved to be more useful for that purpose.

22.3.3 Annual and Decadal Variation in Tree-Ring $\delta^{13}\text{C}$

Several studies have investigated the inter-annual variation of $\delta^{13}\text{C}$ and its correlation with precipitation amount (Table C). Strong negative correlations between tree-ring $\delta^{13}\text{C}$ and annual precipitation were found for species from various sites in tropical America, Asia and Africa, whose growing conditions differed widely in annual precipitation (e.g. Fichtler et al. 2010; Rahman et al. 2020). Such climate sensitivity was further linked to ENSO variability in some studies (e.g. Brienen et al. 2011). In semi-arid Ethiopia, Gebrekirstos et al. (2009) also found a strong correlation of $\delta^{13}\text{C}$ with precipitation for three *Acacia* species, but less so in *Balanites aegyptiaca*. Such differences may relate to water-use strategies, with drought-tolerant species showing a lower sensitivity to inter-annual variability in precipitation amount (Gebrekirstos et al. 2011; Craven et al. 2013).

Other studies combined $\delta^{13}\text{C}$ sequences with measurements of $\delta^{18}\text{O}$. In some of these, $\delta^{13}\text{C}$ showed correlation with other precipitation variables than those found for $\delta^{18}\text{O}$ (Cullen and Grierson 2007; Schollaen et al. 2013). Nevertheless, $\delta^{18}\text{O}$ series generally yielded stronger correlations with precipitation variables than $\delta^{13}\text{C}$ series (Poussart and Schrag 2005; Ballantyne et al. 2011: and see discussion in the next section).

Studies using longer tree-ring sequences have consistently shown a declining $\delta^{13}\text{C}$ trend over the last century in tropical trees (Hietz et al. 2005; Brienen et al. 2011; Loader et al. 2011), also when explicitly correcting for potential ontogenetic effects (Nock et al. 2011; van der Sleen et al. 2015a). After correcting for decreasing atmospheric $\delta^{13}\text{C}$ over that period (the Suess effect), a rather constant ^{13}C discrimination ($\Delta^{13}\text{C}$) generally remains. This leads to the conclusion that C_i/C_a remained constant

over time and that, as a result of the increasing atmospheric CO₂ concentration, iWUE has increased consistently over time (Silva and Anand 2013, see Chap. 17). A sustained increase of photosynthesis and/or a higher water-use efficiency under elevated CO₂ are expected to stimulate tree growth if carbon and/or water are limiting factors (Körner 2009). A few studies also quantified temporal trends in tree growth using the same tree-ring sequences as used to determine $\delta^{13}\text{C}$ trends (Nock et al. 2011; van der Sleen et al. 2015a). Interestingly, these studies found no indications for a growth stimulation over the past century. Stem diameter growth is not necessarily linearly linked to photosynthetic activity, because other aspects of the carbon balance of trees may have changed as well, such as phenology, leaf turnover, respiration and biomass allocation. However, if it is reasonable to assume that diameter growth can reflect changes in the total carbon balance of a tree, in particular on longer time scales, than the available tree-ring studies suggest that photosynthesis did not increase as a result of rising atmospheric CO₂ concentration. This scenario could arise if tree growth is ultimately limited by nutrient availability in most tropical regions, or if a CO₂-induced stimulation of photosynthesis has been compensated by an external climate-related stressor, such as increased temperature or decreased precipitation.

22.4 Oxygen Stable Isotopes

22.4.1 Oxygen Stable Isotope Ecophysiology in the Tropics

Water taken up by trees becomes enriched in ¹⁸O in leaves as a result of transpiration. The strength of this enrichment is mediated by environmental conditions (Barbour 2007; Chap. 10). CO₂ taken up by the leaves exchanges its oxygen atoms with that of leaf water, causing a transfer of the isotopic signature of leaf water to sucrose. In addition, when cellulose is synthesized from sucrose in the stem, about 42% of the oxygen atoms are again exchanged with xylem water. This exchange causes the effect of enriched leaf water to be partly reverted, and results in a strong imprinting of the isotope signature of source water in the wood of trees. Unfortunately, the $\delta^{18}\text{O}$ signature of absorbed source water is commonly unknown, especially over longer time scales. In addition, it is often unknown from what depth the root systems of tropical trees take up water, which further complicates the determination of the $\delta^{18}\text{O}$ of source water, and thus the interpretation of intra- and inter-annual variation in $\delta^{18}\text{O}$ in wood. Shallow-rooting trees, growing in dense canopies where isotopic enrichment at the soil surface is minimal, likely absorb water that consists mainly of recent precipitation, and hence tree-rings are imprinted with an ¹⁸O signal that is rather similar to that of rainwater. As rainwater resides only shortly at the soil surface before percolating down to the groundwater, the $\delta^{18}\text{O}$ signature of groundwater likely integrates variation in $\delta^{18}\text{O}$ in precipitation over several years (Chap. 18). The depth of water uptake has been estimated by measuring natural abundance of ¹⁸O in the soil

profile and in xylem water (Jackson et al. 1995; Hasselquist et al. 2010; Ellsworth and Sternberg 2015) or by labelling soil water (Stahl et al. 2013). These studies show that deciduous trees tend to take up water from shallower depths than evergreen trees and that the depth of water uptake generally increases with tree age and size.

22.4.2 *Seasonal Variation in Tree-Ring $\delta^{18}\text{O}$*

The first $\delta^{18}\text{O}$ studies on tropical trees quantified radial variation of $\delta^{18}\text{O}$ in tree stems to reconstruct annual ring boundaries of tree species without anatomically distinct rings or to confirm the annual nature of ring formation (Evans and Schrag 2004; Poussart et al. 2004; Verheyden et al. 2004; Poussart and Schrag 2005; Evans 2007). In some of these studies, $\delta^{13}\text{C}$ was also measured, but $\delta^{18}\text{O}$ was found to be generally superior for this purpose. The suitability of $\delta^{18}\text{O}$ for the identification of annual rings is based on its seasonal change in precipitation: rainwater $\delta^{18}\text{O}$ is low during the rainy season and with heavy precipitation events (Dansgaard 1964; Villacis et al. 2008; Kurita et al. 2009). High $\delta^{18}\text{O}$ values of precipitation during the dry season can be further amplified in both soil and leaves due to higher evaporation at low humidity (Jackson et al. 1995; Cintra et al. 2019). This seasonality in $\delta^{18}\text{O}$ was confirmed in tropical trees with distinct annual rings (Poussart et al. 2004; Managave et al. 2010; Ballantyne et al. 2011; Managave et al. 2011a; Schollaen et al. 2013). The identification of annual rings in homogeneous (ring-less) wood is most successfully done when intra-annual variation in source $\delta^{18}\text{O}$ is large. This is the case in the western parts of the Amazon basin, where $\delta^{18}\text{O}$ in precipitation is low in the rainy season due to rain-out of the heavy isotopes as water vapor travels from the Atlantic ocean across the basin (Sturm et al. 2007). Evidence for this effect is provided by the lower intra-annual variation in $\delta^{18}\text{O}$ in evergreen trees from Guyana (1–4‰; Pons and Helle 2011) compared to trees sampled near Manaus, Brazil (3–6‰; Ohashi et al. 2016). A special case are trees in montane forests where the uptake of water during the rainy season is from precipitation, whereas moisture can also be directly absorbed from clouds in the dry season. These two water sources differ in $\delta^{18}\text{O}$ values, which can result in large seasonal variation of tree-ring $\delta^{18}\text{O}$ (Anchukaitis et al. 2008; Anchukaitis and Evans 2010). As the strength of intra-annual variation in $\delta^{18}\text{O}$ varies across species (Poussart and Schrag 2005; Anchukaitis et al. 2008) and climatic conditions, selection of species and sites will determine the ability to identify annual rings in homogeneous wood.

22.4.3 *Annual and Decadal Variation in Tree-Ring $\delta^{18}\text{O}$*

Because some trees incorporate the $\delta^{18}\text{O}$ signature of rainwater in stem wood, time series of tree-ring $\delta^{18}\text{O}$ can be used to quantify past variability in precipitation. Tree-ring $\delta^{18}\text{O}$ has been correlated with basin-wide precipitation in the Amazon

(Ballantyne et al. 2011; Brienen et al. 2012; Baker et al. 2015, 2016), and regional precipitation in Thailand (Poussart and Schrag 2005; Pumijumng et al. 2020), Costa Rica (Anchukaitis and Evans 2010), India (Managave et al. 2011b), Indonesia (Schollaen et al. 2013, 2015), Laos and Vietnam (Xu et al. 2011), West Africa (van der Sleen et al. 2015b), and central Africa (Colombaroli et al. 2016). Particularly El Niño Southern Oscillation (ENSO) variability is often evident in $\delta^{18}\text{O}$ sequences either from positive anomalies (Verheyden et al. 2004; Anchukaitis and Evans 2010; Zhu et al. 2012a) or negative ones (Evans and Schrag 2004; Brienen et al. 2012). The analysis of tropical tree-ring $\delta^{18}\text{O}$ is developing into a powerful tool for reconstructing the variability of precipitation on regional scales.

Good synchronization of $\delta^{18}\text{O}$ patterns among individual trees was found for several species (e.g. Poussart and Schrag 2005; Managave et al. 2011b; Brienen et al. 2012; van der Sleen et al. 2015b), sometimes over large spatial distances (Baker et al. 2015; Schwendenmann et al. 2015; Volland et al. 2016). Synchronous variability in $\delta^{18}\text{O}$ can be higher than for ring-width, thus providing an alternative tool for cross dating (Baker et al. 2015; van der Sleen et al. 2015b; Volland et al. 2016) and identification of false and missing rings (Boysen et al. 2014). However, $\delta^{18}\text{O}$ synchronization between individuals may be low for certain species or sites (e.g. Poussart and Schrag 2005; Baker et al. 2015). For $\delta^{18}\text{O}$ in *Toona ciliata* from Thailand, low $\delta^{18}\text{O}$ synchronization occurred (van der Sleen 2014), in spite of the ring-width series showing strong synchronization (Vlam et al. 2014). It is likely that trees that lack a common signal in tree-ring $\delta^{18}\text{O}$ values exploit other water sources than recent precipitation (e.g. ground water). These results suggest that shallow rooting tree species on well-drained soils have the highest probability to record the $\delta^{18}\text{O}$ variability of precipitation and thus have the highest potential as tools for climate reconstructions.

In several studies the two stable isotopes ^{18}O and ^{13}C were combined using a mechanistic interpretation, the so-called dual isotope approach (see Chap. 16), where A/g_s obtained from $\Delta^{13}\text{C}$ and g_s derived from $\Delta^{18}\text{O}$ could potentially provide an estimate of A (Scheidegger et al. 2000). This approach was used by Nock et al. (2011), who interpreted an increase of $\Delta^{18}\text{O}$ over time as an indication of a decreasing g_s in trees from Thailand. The observed decrease of $\Delta^{13}\text{C}$, and thus increasing A/g_s , would then be the result of this decreasing g_s and not an increasing A . However, the underlying assumptions in this approach are that the $\delta^{18}\text{O}$ signature of source water is known and that the leaf to air vapor pressure difference (LAVPD) has remained constant over the period studied. In many tropical regions, this LAVPD may have increased as a result of global warming and/or decreased precipitation, leading to increased transpiration and $\delta^{18}\text{O}$ over time. Even though g_s is also partly controlled by LAVPD, this makes it nonetheless difficult to separate the g_s effect from the LAVPD effect on transpiration.

A long-term increase of $\delta^{18}\text{O}$ values has been encountered in several studies conducted on tropical tree species (Poussart and Schrag 2005; Xu et al. 2011; Brienen et al. 2012; van der Sleen 2014; van der Sleen et al. 2015b; Volland et al. 2016). Some of these trends could be caused by ontogenetic changes, but a consistent small trend over the past century was also found in studies that did correct for ontogenetic trends (van der Sleen 2014; van der Sleen et al. 2015b; Volland et al. 2016). For

the Amazon region, these results are consistent with similar increases of $\delta^{18}\text{O}$ in Andean ice cores (Thompson et al. 2006) and Andean lake sediments (Bird et al. 2011). Thus, the increasing trend in $\delta^{18}\text{O}$ in tree rings likely reflects a pan-tropical phenomenon. The cause of this increase is yet unknown, and it is unclear whether it relates to climate change.

22.5 Nitrogen Stable Isotopes

22.5.1 Nitrogen Stable Isotope Ecophysiology

The value of plant $\delta^{15}\text{N}$ depends on the $\delta^{15}\text{N}$ of the N taken up and N losses in leaves, fruits, etc. Uptake can be in the form of nitrate, ammonium, organic N compounds or N_2 in the case of nitrogen fixation. The $\delta^{15}\text{N}$ of these sources varies in a complex manner (except for N_2 , which is used as standard and is thus 0‰ by definition; Chap. 12).

Higher soil and foliage $\delta^{15}\text{N}$ are generally reported for tropical lowland forests, compared to temperate and boreal forests (Martinelli et al. 1999; Amundson et al. 2003), and tropical montane forest (Brearley 2013). This pattern is considered as evidence of more N losses and thus a more open N cycle in tropical lowland forests, because nitrate lost through leaching and/or denitrification is ^{15}N -depleted. Temperate forests are generally more N-limited, whereas tropical forests tend to be more P-limited (Vitousek and Howarth 1991), which is consistent with their higher $\delta^{15}\text{N}$. Leguminous trees are abundant in tropical forests, although not all can form an effective symbiosis with Rhizobia. Yet, facultative leguminous N_2 -fixers can still be abundant (Menge and Chazdon 2016) and contribute to N-accumulation also in late successional stages of tropical forests (Roggy et al. 1999; Pons et al. 2007). This could be the reason for an alleviation of N-limitation, whereas N_2 -fixing trees are virtually lacking in temperate forest (except for early successional stages; Menge et al. 2009).

22.5.2 Annual and Decadal Variability in Tree-Ring $\delta^{15}\text{N}$

So far, only three studies on temporal variation or trends $\delta^{15}\text{N}$ in tree rings have been carried out in tropical forests (Hietz et al. 2010, 2011; van der Sleen et al. 2015c). Hietz et al. (2010) using two species in a Brazilian forest, found a gradual increase of tree-ring $\delta^{15}\text{N}$ over time after statistical correction for tree age. The authors suggested that this result could be caused by an increase in tree turnover and thus gap formation that generates NO_3^- losses and thereby increasing $\delta^{15}\text{N}$ of the remaining soil N pool. In a subsequent study, Hietz et al. (2011) reported also an increase in $\delta^{15}\text{N}$ in three species from a monsoon forest in Thailand. They

also found a similar increase when comparing 40-year-old herbarium leaves with recent leaves from the same species and sample location in a Panamanian forest (BCI). The two forests are intensively monitored and there are no indications that the level of disturbance has increased over the past century. Such a consistent trend in $\delta^{15}\text{N}$ in three widely separated tropical forests may therefore indicate an effect of increased anthropogenic N-deposition, which causes higher NO_3^- losses (and thus $\delta^{15}\text{N}$ enrichment of remaining soil nitrogen). However, in the most recent study, van der Sleen et al. (2015c) sampled annual rings in six species from three sites at different continents. They corrected for possible tree size effects by comparing wood sampled at a fixed diameter (20 cm) from different sized trees. Ten-year pooled samples were also collected between 1955 and 2005 from single trees, which showed increasing trends of $\delta^{15}\text{N}$ in Bolivia and Cameroon. Surprisingly, the trends were absent in the fixed diameter sampling, showing evidence of potential ontogenetic effects. The discrepancy between the results of Hietz et al. (2011) and van der Sleen et al. (2015c) may also have been caused by a lower statistical power in the latter. Unfortunately, the interpretation of temporal changes in $\delta^{15}\text{N}$ in the few available tropical tree-ring studies remain strongly hampered by a limited understanding of the factors that influence soil- and tree $\delta^{15}\text{N}$ values.

22.6 Conclusion and Perspective

Tropical forests harbor an incredible biodiversity and provide ecosystem services on which millions of people depend. They are a major component of the global carbon cycle, storing some 25% of the total terrestrial carbon and accounting for a third of net primary production (Bonan 2008). Understanding the functioning of these forests and their responses to global change is therefore an urgent need for ecology, climate science and conservation. The study of stable isotopes in tropical tree rings offers unique opportunities to quantify how these trees respond to their environment, and can fill an important void in many tropical areas where the availability of climate data is limited or of short duration. In fact, stable isotopes in tree rings are essentially the only tools available to obtain cost-effective, high-resolution, long-term retrospective data on tree physiology and the environmental conditions affecting it.

Currently, stable isotopes research in the tropics has mainly focused on (i) quantifying the effects of rising atmospheric CO_2 and climate change on tree physiology, (ii) identifying the drivers of growth variability and reconstruction of past climate, and (iii) the identification of annual rings in wood lacking anatomically distinct growth boundaries. The main findings of the available studies are shortly summarized for each isotope in Table 22.1. The application of stable isotopes continues to expand. New applications are numerous, and include the potential use of stable isotopes for timber tracing and to identify illegally logged wood (e.g. Vlam et al. 2018), to benchmark the predictions of dynamic global vegetation models (e.g. Zuidema et al. 2018), and for reconstructions of atmospheric CO_2 and $\delta^{13}\text{C}$ values (using trees with a C4 photosynthetic pathway; Ben et al. 2017).

Although tropical isotope research has centered on three stable isotopes (C, O, and to a lesser degree N), advances in analytical techniques and reductions in associated costs continue to broaden these analyses. This not only includes the analyses of other stable isotopes, but also the analyses of the intramolecular distribution of isotopes. For example, the position of ^{18}O in the glucose moiety in cellulose can be used to separate source water from leaf water enrichment effects (Sternberg 2009; Waterhouse et al. 2013), and the position of ^2H was related to the oxygenation/carboxylation ratio that depends on C_i (Ehlers et al. 2015). These techniques can be used to infer more details about environmental effects on tropical trees than is possible with bulk isotopic ratios as done so far. Even though stable isotope research in the tropics still faces methodological and interpretation issues, we anticipate that it will continue to play a crucial role for our understanding of the functioning of tropical forests and their resilience to global change.

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