

Chapter 21

Stable Isotopes in Tree Rings of Mediterranean Forests



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21.1 Introduction

Tree-ring studies in the Mediterranean Basin and in regions characterized by Mediterranean climates are scarce because of a lack of old trees and difficulties related to the clear identification of individual rings. Old trees are lacking because most regions with a Mediterranean climate have long histories of human activity; logging, grazing, and human-induced fires have occurred over millennia. Annual rings are difficult to identify in some woody plant species because highly variable climatic conditions can lead to the formation of intra-annual density fluctuations, which hamper the cross-dating of tree-ring series (Cherubini et al. 2013). Stable isotopes may help in identifying intra-annual density fluctuations (De Micco et al. 2007) and in understanding the physiological processes behind tree-ring formation, carbon uptake, and water use (Battipaglia et al. 2010a, 2014a).

Most of the tree-ring stable isotope studies carried out on Mediterranean tree and shrub species include the use of both carbon and oxygen stable isotopes (Table 21.1), which help to reconstruct past climate and retrospectively assess tree responses to the environment (McCarroll and Loader 2004). The values of the isotopic ratios reflect the extent to which the heavier isotope is discriminated compared to the lighter one during the physical and chemical processes involved in the synthesis of plant organic matter (Farquhar et al. 1989).

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Table 21.1 Summary of the main aim and outcomes of studies measuring stable isotopes in Mediterranean tree rings. References given in chronological order

Stable isotope	Main usage	Main outcome	Number of species	References
^{13}C	Unravelling isotope-climate relations	Negative correlation with precipitation; water availability triggers tree growth and stomatal conductance	15	Shestakova et al. (2019), Castagneri et al. (2018), Fernández-de-Uña et al. (2017), Shestakova et al. (2017), Voelker et al. (2014), Bogino and Bravo (2014), Granda et al. (2014), del Castillo et al. (2013), De Micco et al. (2012), Battipaglia et al. (2010a; b), De Micco et al. (2007), Ferrio et al. (2003), Liñán et al. (2012)
	Proxy for iWUE	Generally, an increase in iWUE shows that the potential <i>fertilization effect</i> of increasing atmospheric CO_2 does not <i>compensate</i> for the negative <i>effects</i> of stress factors such as drought	41	Camarero et al. (2018), Martínez-Sancho et al. (2018), Paris et al. (2018), Brito et al. (2016), Fernández-de-Uña et al. (2016), González-Muñoz et al. (2015), Lucas et al. (2013), Peñuelas et al. (2011), Linares et al. (2011), Di Matteo et al. (2010), Linares et al. (2009)
	Reconstruction of past climate	Good prospect for temperature and past precipitation regimes	3	Heinrich et al. (2013), Szymczak et al. (2012a; b), Aguilera et al. (2009)
^{18}O	Reconstruction of water resources	Trees show contrasting patterns of water use	4	Sargeant et al. (2016), Singer et al. (2013)
^{13}C & ^{18}O	Drought effect on trees	Dying trees showed reduced productivity and lower intrinsic water-use efficiency compared with healthy trees due to enhanced water loss through transpiration	7	Barbeta & Peñuelas (2017), Colangelo et al. (2017), Sarris et al. (2013), Brooks & Coulombe (2009), Battipaglia et al. (2009), Voltas et al. (2013)

(continued)

Table 21.1 (continued)

Stable isotope	Main usage	Main outcome	Number of species	References
	Proxy for species iWUE	Variations in stable carbon and oxygen isotope compositions of co-occurring plant species reflect their different water-use strategies	10	Battipaglia et al. (2016a, 2017; b), Altieri et al. (2015), Moreno-Gutierrez et al. (2015), Shestakova et al. (2014), Maseyk et al. (2011)
	Effects of fire on tree physiology	Fire increases tree iWUE, decreases tree growth and relative conductivity. Prescribed fire reduces stress competition for water and nutrients	3	Niccoli et al. (2019), Valor et al. (2018), Battipaglia et al. (2014a, 2016a; b, c, b), Beghin et al. 2011)
	IADF characterization	IADFs formation is mainly species and site specific, related to high temperature, precipitation patterns, and/or soil water availability, which differ at the selected study sites	3	Zalloni et al. (2018), Battipaglia et al. (2014a, b, c)
	Effect of natural CO ₂ spring	Downward adjustment of photosynthesis under elevated CO ₂ in a dry, nutrient-poor environment	1	Saurer et al. (2003)
	Solar flare effects on trees	No clear effects on ecophysiology	2	Bartolomei et al. (1995)
	Reconstruction of past climate	Summer climate influences trees performance	5	Konter et al. (2014), Hafner et al. (2011), Aguilera et al. (2011)
	Methodological approach	Necessity of cellulose extraction depends on species and research questions	1	Szymczak et al. (2011, 2014), Battipaglia et al. (2008)

(continued)

Table 21.1 (continued)

Stable isotope	Main usage	Main outcome	Number of species	References
¹⁵ N	Climate change effect on carbon and nitrogen cycles	Decreasing trend in $\delta^{15}\text{N}$ in both herbarium material and tree rings, indicating that ecosystems might cope with higher plant N demand by decreasing N losses and increasing N fixation and mineralization	4	Peñuelas & Estiarte (1996)
	Effect of fire and drought on trees	The post-fire growth responses and changes in wood C and N isotope composition depend on site water availability and fire severity	1	Alfaro-Sanchez et al. (2016)
	Pollution effects on trees	N deposition influences iWUE and photosynthetic activity	4	Guerrieri et al. (2009, 2010, 2011), Battipaglia et al. (2010a, b)

In this chapter, we highlight the importance of stable isotope research in Mediterranean ecosystems and explain the link between the morphological and functional characteristics of Mediterranean species and the climatic and environmental adaptations that have occurred over millennia.

21.2 Mediterranean Climates

Mediterranean climates occur around the world: in California, central Chile, western and southwestern Australia, southwestern South Africa, and in the Mediterranean Basin. As most tree-ring studies have been carried out in the Mediterranean, we focus on this region in this chapter. In a typical Mediterranean climate, winters are wet and rather mild, although frost and cold stress can occur (Larcher 2000; Mitrakos 1980; Terradas and Save 1992). Rainfall starts in September and continues until April, with a total precipitation amount of 400–1200 mm (Pignatti 2008). Summers are hot and dry; rainfall events are rare, and the season is often characterized by an extremely dry period, the so-called *summer drought*. These general features can vary

in different coastal areas of the Mediterranean Basin depending on their elevation and local geomorphological and soil features, but the summer drought is always present (see Fig. 21.1). The main factors leading to the formation of Mediterranean-type climates are air circulation, latitude, topography, and the surface temperature of the surrounding water.

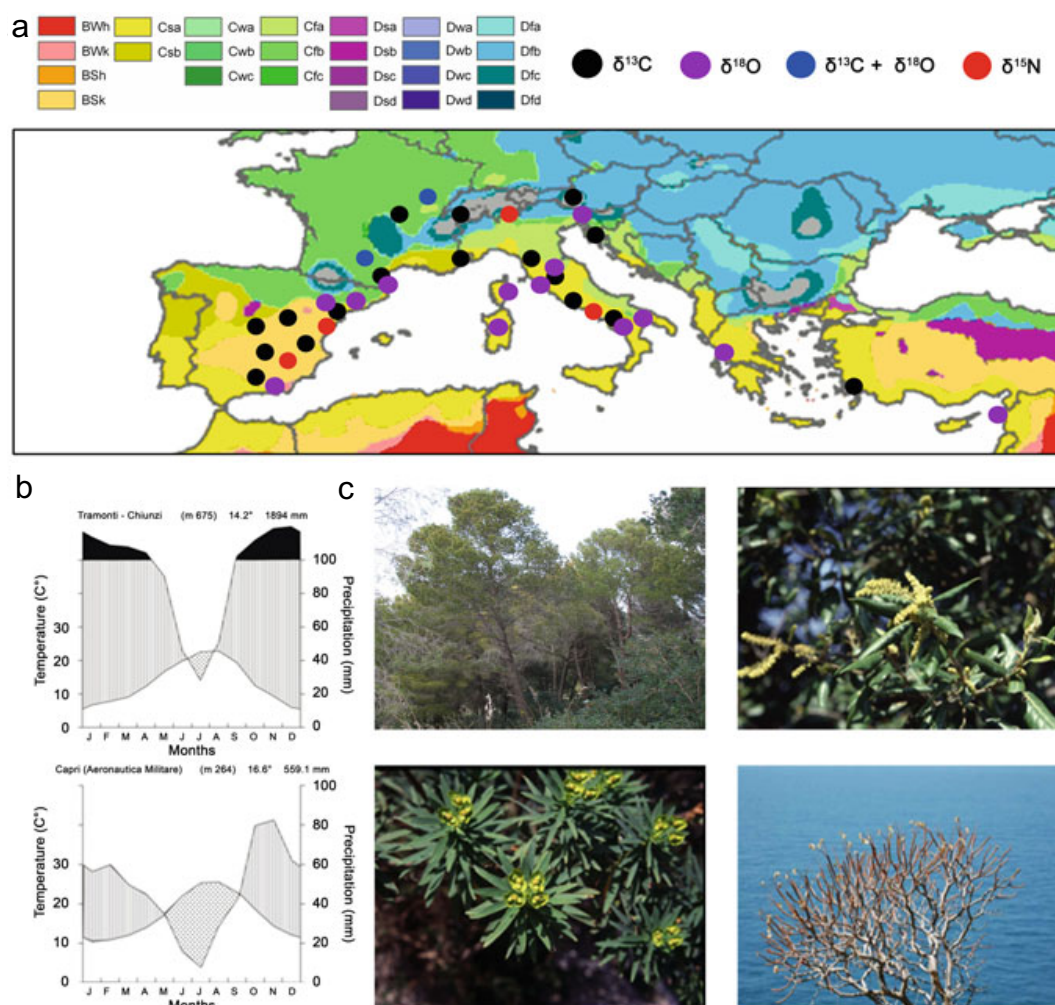


Fig. 21.1 **a** Map of the Mediterranean Basin showing locations of stable isotope tree-ring studies. The main findings of these studies are summarized in Table 21.1. Background map showing Mediterranean climates according to Köppen classification. **b** Two Walter and Lieth climate diagrams depicting the climate of two typical Mediterranean areas. Lower diagram: Capri (an island in the Tirrenic sea); upper diagram: Tramonti, at a higher altitude (period 1960–2010). **c** A few examples of Mediterranean species. Clockwise from top left: *Pinus halepensis* Mill. of southern Spain; *Quercus ilex* L. from southern Italy; *Euphorbia dendroides* L.: winter habitus and summer habitus

21.2.1 *Mediterranean Climate and Vegetation*

Mediterranean plants are adapted to this climate and cope with summer drought through several changes at the phenological, morphological, physiological,

or biochemical levels (Pignatti 2008). These adaptations influence all relevant ecophysiological processes, i.e., transpiration and carbon assimilation, as well as the isotopic signal imprinted in plant organic matter. Hence, the isotopic composition of the wood material of Mediterranean trees reflects their functionality and adaptation strategies. To cope with drought stress, two main strategies are observed in Mediterranean plants: avoidance and tolerance (Pignatti 2008).

Many species survive summer drought by avoiding it through summer dormancy. This strategy is adopted by annual and perennial herbs and by woody species. Annual herbs have a very short life cycle that starts in late winter so that fruits are mature at the beginning of summer. Seeds then remain dormant until conditions are optimal for successful growth. Perennial herbaceous species often have a geophyte life-form, in which the above-ground parts of the plants (leaves, stems) are shed at the beginning of summer and the individual remains dormant by means of a perennating below-ground organ (bulb, tuber, rhizome). Some woody species also have summer dormancy, shedding all their leaves (e.g. *Euphorbia dendroides* L.) at the end of spring or summer. Several species, such as *Cistus*, change their leaves according to the season and are characterised by the alternation of a winter and a summer *leaf habitus*.

Plants without summer dormancy present tolerance attributes, which help them to face summer drought. Many species have a low leaf surface area, e.g., the needle-like leaves of *Rosmarinus officinalis* L. or *Juniperus phoenicea* L. subsp. *phoenicea*, whose juvenile needle-like leaves turn into scale-like leaves that are densely arranged around the stem in older branches. Other species have sclerophyllous leaves, with very dense mesophyll and thick cuticles to constrain water loss. Regulation of stomatal activity is a good strategy to cope with summer drought: stomatal closure can reduce transpiration rate and water loss. Several *species* count on *stomata*, which are *sunken* into the leaf surface and protected by dense, short trichomes, to reduce water loss. The lower leaf blades of *R. officinalis*, *Quercus ilex* L., and *Olea europaea* L. are examples of this feature. Other plants without summer dormancy tolerate high solar radiation by means of a reflecting cuticle (e.g., *Myrtus communis* L. subsp. *communis*) or long (often white) hairs on the upper leaf blade (e.g., *Centaurea cineraria* L. subsp. *cineraria*) that protect inner tissues from excessive radiation.

The adaptation mechanisms of Mediterranean plants are often linked with human activity, since their long association with humans has left its mark across much of the landscape. Human activities have influenced not only the type of community and forest composition, but also their main characteristics.

Four major types of vegetation can be recognized in the Mediterranean-European region according to the bioclimate type and the elevation (Quézel and Médail 2003; Rivas-Martínez et al. 2007; Médail 2008). First, a thermo-Mediterranean vegetation rises from sea level to ~200–500/800 m a.s.l. and is dominated by sclerophyllous communities (e.g., *Olea europaea*, *Ceratonia siliqua*, *Chamaerops humilis*,

Pistacia lentiscus, *Pinus halepensis*, *Pinus brutia*, etc.). A meso-Mediterranean vegetation takes over between ~100–500/1000 m a.s.l. and is dominated by sclerophyllous forests (*Quercus ilex*, *Quercus suber*, and *Q. coccifera*) or *Pinus halepensis*/*P. brutia* forests in drought-prone forest systems. This then transitions to a supra-Mediterranean vegetation between ~500–1500/1800 m a.s.l., with deciduous oaks forests (e.g. *Acer*, *Carpinus*, *Ostrya*, *Quercus*, and *Sorbus*) in the more humid areas. Finally, a mountain-Mediterranean vegetation belt between ~1500–2000 m a.s.l. includes *Fagus* and deciduous and semi-deciduous *Quercus* forests, as well as several coniferous forests with *Pinus nigra*, *Pinus sylvestris*, firs (*Abies alba* and most of the Mediterranean *Abies* spp.), and even cedar (*Cedrus libani* s.l.) on Cyprus (Médail et al. 2019).

21.3 Mediterranean Wood Formation in Mediterranean Tree Species

The Mediterranean basin has an extension of more than 2 million square kilometers, and it is the largest of the world's five mediterranean-climate regions, as well as the world's second largest biodiversity hotspot (Myers et al. 2000).

The Mediterranean region is considered to be one of the climate-change hotspots, being a transition zone between temperate and arid and tropical regions (Diffenbaugh and Giorgi 2012). It has experienced an increase in drought frequency in the past three decades, and forecasts predict increased irregularity of the intra-annual precipitation pattern, and increasing temperature in the next decades (IPCC 2017). Water availability is considered the key factor driving ecophysiological processes in Mediterranean vegetation. It influences cambial activity, photosynthetic rates, dry matter production, phenology, allocation of carbon to roots and leaves, and overall growth activity of woody plants (Margaris and Papadogianni 1977; Lo Gullo and Salleo 1988; Orshan 1989; Gratani 1995; Salleo et al. 1997; Davis et al. 1999).

In Mediterranean ecosystems, tree species are adapted to cope with the so-called “double stress” of summer drought and winter low temperatures (Mitrakos 1980; Cherubini et al. 2003). These stressors trigger the formation of Intra Annual Density Fluctuations (IADFs) (Campelo et al. 2007; Battipaglia et al. 2016a; De Micco et al. 2016), which are caused by the interruption of the normal course of growth during the growing season. When favorable growth conditions resume, growth resumes, resulting in a change in wood density (Tingley 1937; Schulman 1938). In Mediterranean regions, this happens irregularly in space (at different sites at the same time), time (in different years at the same site), and among species (as well as individual trees). This ability to stop and restart growth within a growth season is indicative of the high plasticity of Mediterranean species, whose wood functional traits enable them to preserve hydraulic conductivity throughout the different seasons, achieving a trade-off between hydraulic efficiency and safety (see Beeckman 2016).

IADFs make it difficult to clearly identify individual annual rings; as a result, the tree rings of Mediterranean species are used less often for dendroecological purposes less than those of plants growing in temperate environments. However, a variety of recent research techniques have provided valuable information about the short-term growth variability of Mediterranean trees and shrubs. These include the intensive monitoring of stem radial variation using dendrometers (Sánchez-Costa et al. 2015), the assessment of cambial phenology (Camarero et al. 2010; Vieira et al. 2017), the measurement of xylem anatomical traits (De Micco et al. 2019; Carvalho et al. 2015; Pacheco et al. 2016), stable isotopes within tree rings (on tree-ring sub-sections, Klein et al. 2005; in continuum by laser ablation, Battipaglia et al. 2010a, b; 2014a) and a combination of methodologies (Zalloni et al. 2018, 2019; Balzano et al. 2018; Castagneri et al. 2018).

21.4 Carbon and Oxygen Stable Isotopes in Tree Rings of Mediterranean Species

21.4.1 Carbon Isotopes

Mediterranean species, which grow in climates characterized by summer drought and wet periods during the growing season, show wood structure adjustments that are mostly related to the need to maintain high conductivity when water is available, and to prevent xylem embolism when dry conditions occur (Cherubini et al. 2003; De Micco and Aronne 2012; Meinzer et al. 2010; Sperry et al. 2008). Tree-ring formation is therefore directly influenced by these adjustment processes and carbon stable isotopes can investigate the link between xylem hydraulic properties and the related physiological mechanisms.

Water shortage negatively influences carboxylation rates by reducing the CO₂ concentration in the gaseous spaces within the plant (C_i) due to stomata closure, causing a decrease in carbon isotope discrimination (Farquhar et al. 1989; Scheidegger et al. 2000). Many studies conducted in Mediterranean climates have shown that plants growing under water stress (stress induced by low soil water content and high evaporative atmospheric demand) produce tree-rings with higher $\delta^{13}\text{C}$ (Ferrio et al. 2003; Battipaglia et al. 2010a; Maseyk et al. 2011). However, leaf water availability ultimately influences tree-ring $\delta^{13}\text{C}$. This availability is a consequence not only of soil water content, but also of the physical structure and hydraulic resistance along the plant xylem and the way the plant transports and uses water (e.g. leaf phenology) (Masle and Farquhar 1988; Warren and Adams 2000). Further, tree $\delta^{13}\text{C}$ is influenced by the leaf-to-air vapour pressure deficit (VPD), which is the driving force for transpiration. Studies on isotope-climate relationships have shown that mean annual precipitation controls carbon discrimination ($\Delta^{13}\text{C}$) in several forest ecosystem types (Schulze et al. 1998; Diefendorf et al. 2010; Kohn 2010), as well as in tree rings of a large range of Mediterranean species (Shestakova et al. 2019;

del Castillo et al. 2013). These studies generally suggest a stronger influence of precipitation on $\Delta^{13}\text{C}$ in drier environments (Warren et al. 2001).

21.4.2 Carbon Isotope Discrimination as a Proxy for iWUE

Carbon isotope composition has been used to calculate intrinsic water-use efficiency (iWUE) (see Chap. 17) in Mediterranean species (Ehleringer et al. 1993; Altieri et al. 2015; Battipaglia et al. 2016b; Dawson and Ehleringer 1993; Moreno-Gutiérrez et al. 2012). iWUE is key to the survival of Mediterranean species under drought conditions (Farquar et al. 1989); according to Medrano et al. (2009), a high iWUE can be considered an adaptive trait of Mediterranean species. Inter- and intra-species interactions influence iWUE, and iWUE can vary with inter- and intra-annual climate variability, stand density, and tree size (Forrester 2015). Within and across tree species, variations in iWUE reveal a continuous ecophysiological gradient of plant water-use strategies ranging from “profligate/opportunistic” (low iWUE) to “conservative” (high iWUE) (Moreno-Gutierrez et al. 2012). Several factors can affect iWUE at individual and stand levels, such as tree age and height (Francey and Farquhar 1982; Farquhar et al. 1982, Bert et al. 1997; McDowell et al. 2011a, b; Brien et al. 2017), site density and characteristics (Battipaglia et al. 2010a; Zalloni et al. 2018), forest management, climate, and increasing atmospheric CO_2 (Silva and Horward 2013, De Micco et al. 2019).

Both network studies and case studies have highlighted a general increase in iWUE in Mediterranean species (Linares et al. 2009; Di Matteo et al. 2010; Linares et al. 2011; Peñuelas et al. 2011; González-Muñoz et al. 2015; Brito et al. 2016; Fernández-de-Uña et al. 2016; Paris et al. 2018; Shestakova et al. 2019). All studies agree that the increase in iWUE does not translate into growth enhancement in response to increasing atmospheric CO_2 . However, it is not yet clear why this occurs because it is extremely difficult to disentangle the influence of single factors on iWUE variation and to quantify the extent to which drought overrides a positive CO_2 fertilization effect (see Peñuelas et al. 2011). Moreover, iWUE can vary due to both photosynthetic and stomatal conductance rates, since both affect the ratio between CO_2 partial pressure in leaf intercellular space and in the atmosphere. To better understand the role of assimilation on iWUE, several authors have coupled tree-ring $\delta^{13}\text{C}$ values with wood $\delta^{18}\text{O}$ values (the dual isotope approach; Chap. 16, paragraph 5).

21.4.3 Oxygen Isotopes as a Proxy for Source Water

Oxygen isotopes can provide valuable information about changes in source water, which is typically either precipitation or groundwater (Dansgaard, 1964). No fractionation occurs when water is taken up by the roots (Wershaw et al. 1966), so the

$\delta^{18}\text{O}$ of xylem water can be used to investigate plant water source use in a range of environmental conditions (Sternberg and Swart 1987; Ehleringer and Dawson 1992; Dawson et al. 1998a, b). Very few studies, however, have focused on Mediterranean environments (Sargeant and Singer 2016; Singer et al. 2013), where water sources are quite complex and subject to strong seasonal fluctuations. The interface between the influx of marine water and the freshwater table depends strongly on climatic factors and on the exploitation of groundwater for urban or rural purposes, both of which influence the quality of water available for plant communities.

The isotopic composition of rainfall is typically subject to seasonal patterns that are influenced by geographic and climatic factors. Generally, autumn–winter precipitation has a more negative isotopic signature (ranging between ~ -7.8 and -6.0 ‰) than spring–summer precipitation (ranging between ~ -4.0 and $+0.8$ ‰) (Alessio et al. 2004). Consequently, the freshwater table is labelled by meteoric water, and primarily by the abundant autumn–winter and spring precipitation events (Wu et al. 1996). In contrast, soil water in the shallow layers depends on spring–summer precipitation. Further, water occurring 10–50 cm below the dry soil surface is subject to evaporative enrichment and therefore attains less negative or even positive $\delta^{18}\text{O}$ values (Craig and Gordon 1965; Allison and Leaney 1982; Yakir et al. 2000). A further source of water is the marine water table, which is typically characterized by enriched values of $\delta^{18}\text{O}$ (~ 0 ‰).

Thus, the $\delta^{18}\text{O}$ composition of tree rings will reflect the isotopic signature of the tree's water source: rings will have a depleted $\delta^{18}\text{O}$ signature if trees take up water from the groundwater table (Dawson and Ehleringer 1998), and an enriched $\delta^{18}\text{O}$ signature if trees take up water from the vadose zone. Indeed, water in the vadose zone is generally linked to recent precipitation and is subject to high evaporative enrichment of $\delta^{18}\text{O}$ (Dawson and Ehleringer 1998). These source-water signatures will be different for individual rings within a given species depending on the annual position of the water table and the degree of mixing between precipitation, surface flow, and groundwater during periods of xylem uptake (McCarroll and Loader 2004). It should also be noted that considerable fractionation occurs at the leaf/needle level, where lighter isotopes are preferentially lost via transpiration, leading to an enrichment in plant tissue $\delta^{18}\text{O}$ of up to 20‰ compared to soil water (Craig and Gordon 1965; Saurer et al. 1998; McCarroll and Loader 2004; Barbour 2007; Cernusak et al. 2016). Indeed, it has been demonstrated that the source water signal can be modified by large changes in evaporative enrichment in drought-adapted Mediterranean species. These species tightly regulate transpiration through their stomata (Ferrio and Voltas, 2005), an ability that is thought to be a functional adaptation to drought (Pallary et al. 1995; Battipaglia et al. 2009).

Singer et al. (2013) and Sargeant and Singer (2016) used annual tree-ring $\delta^{18}\text{O}$ analyses to interpret plant water use at various temporal and spatial scales as a function of regional hydrology and climate. Both studies underlined the great plasticity of plants as evinced by their ability to take up different sources of water and to modulate their root depth to take up water from different compartments in order to avoid competition. This promising approach needs to be exploited further, as it

could provide important information regarding the ability of plants to survive drought events cooperatively (Altieri et al. 2015).

21.5 Application of Carbon and Oxygen Isotopes in Tree-Rings of Mediterranean Species

The carbon and oxygen composition of tree-rings has been used for elucidating whether plant functional responses are related to stomata control of water losses (g_s) or to varying assimilation rates (A), since $\delta^{18}\text{O}$ shared a dependence on g_s with $\delta^{13}\text{C}$, but is thought to be independent of variation in A (Scheidegger et al. 2000; Grams et al. 2007; Roden and Farquhar 2012).

Indeed, even if the interpretation of the double model $\delta^{13}\text{C}$ — $\delta^{18}\text{O}$ is not straightforward (Roden and Siegwolf 2012), and may sometimes be hampered by changes in the source water isotopes (Gessler et al. 2014), it can still provide important information when applied in strongly water-limited ecosystems, such as the Mediterranean (Ripullone et al. 2009; Moreno-Gutiérrez et al. 2012; Voltas et al. 2013; Gessler et al. 2014; Altieri et al. 2015; Battipaglia et al. 2016a). In the next paragraphs, we will illustrate specific examples of a double $\delta^{13}\text{C}$ — $\delta^{18}\text{O}$ model that is relevant for the Mediterranean region.

21.5.1 Carbon and Oxygen Isotopes and Forest Dieback in the Mediterranean Basin

Forest vulnerability is reported to be increasing worldwide; forest dieback episodes have been recorded for different species in all biomes (Allen et al. 2015; Adams et al. 2017; Hartmann et al. 2018) and particularly for tree and shrub species in Mediterranean ecosystems. Manifested by a loss in tree vigour (leaf shedding, canopy and shoot dieback) and growth declines, these dieback cases reveal the high vulnerability of forest ecosystems. Increased tree mortality seems to be a response to the rapid rise in temperature and associated drying trends (Camarero et al. 2015; Colangelo et al. 2017). In the Mediterranean, trends of increasing temperature and altered precipitation patterns lead to higher probabilities of extreme events, such as heat waves and fires (IPPC 2014). Species-, age- and microsite-specific plant responses to changing climatic conditions are responsible for the degree of adaptation and survival under limiting conditions. These factors also determine interspecific competition, and thus vegetation dynamics.

The main mechanisms triggering tree decline and mortality have been identified as carbon starvation and hydraulic failure, but the relative importance of the two processes and their link are not clear yet (McDowell et al. 2008, Sala 2009, Sala et al. 2010, Gruber et al. 2010, Sevanto et al. 2014, Gaylord et al. 2015, Hartmann

2015, Rowland et al. 2015, Salmon et al. 2015; Adams et al. 2017). Plants experience hydraulic failure when more water is lost by transpiration than a plant can take up through its root. This creates high xylem water tension and results in progressive cavitation and conductivity loss of the xylem (Sperry et al. 1998; McDowell et al. 2008; Sevanto et al. 2014; Salmon et al. 2015). This process may be most relevant during very severe, short-term droughts (McDowell et al. 2008). On the other hand, carbon starvation occurs when plants close their stomata to prevent desiccation under drought conditions (McDowell et al. 2008). Low water supply leads to a reduction of photosynthetic activity, which, when coupled with the depletion of non-structural carbohydrates (NSC), can induce a negative carbon balance, leading to so-called starvation (McDowell et al. 2008; McDowell and Sevanto 2010; Hartmann 2015; Salmon et al. 2015).

Gessler et al. (2018) developed a conceptual model, based on the Scheidegger model (Scheidegger et al. 2000, see Chap. 16), to assess the mechanisms of drought-induced tree mortality. Using a synchronic approach, they investigated the tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data for different species and found that an increase in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in dying trees as compared to surviving ones indicates low photosynthetic activity and stomatal conductance. These conditions can lead to a slow or continuous decline in growth, possibly followed by carbon starvation-induced death. On the other hand, the long-term reduction of iWUE in dying trees seems to be associated with increased growth and higher stomatal conductance, inducing possible hydraulic failure in dying trees. However, those findings show a huge variability among species and sites. This variability is linked to the complex processes regulating growth and, in particular, the fractionation processes that take place during the mobilization of photosynthetic assimilates from the leaf to the wood (Gessler et al. 2014). Indeed, it has been demonstrated that trees may use remobilized carbohydrates (primarily starch) for the formation of tree rings. These stored carbohydrates may have been produced months or even years earlier (Gessler et al. 2014). This is especially possible in Mediterranean biomes, where the growing season is very long (Castagneri et al. 2018) and where xylogenesis can be interrupted more than once during the year (Balzano et al. 2019, 2018). In this case, a multidisciplinary approach is required to disentangle the different processes underpinning changes in growth and iWUE, and to better understand the causes of tree diebacks (Cailleret et al. 2017; Colangelo et al. 2017; Camarero et al. 2015, 2019).

21.5.2 Carbon and Oxygen Isotopes and IADF

Intra-annual density fluctuations (IADFs) are abrupt changes in density within a tree ring, and are frequently found in Mediterranean species as a response to seasonal climate fluctuations between dry and wet periods (Bräuning 1999; Campelo et al. 2007; Cherubini et al. 2003; Rigling et al. 2001; Schulman 1938; Tingley 1937; De Micco et al. 2016). Although IADF frequency is related to tree age, size, and tree-ring width, as well as to genetic and site conditions, it mainly depends on drought. IADF

frequency is the result of wood functional trait adjustments to preserve hydraulic conductivity under Mediterranean “double stress” conditions (De Micco et al. 2016). The ability to adapt to highly seasonal Mediterranean conditions may depend on a species’ capacity to adjust cambial activity in order to cope with the prevailing environmental conditions. Trees that are not able to quickly adjust their wood traits to respond to climate are more vulnerable to drought (Martinez-Meier et al. 2008). Nevertheless, the question of whether these adaptations result from a hydraulic structure adjustment to avoid stressful conditions or to take advantage of favorable ones is still open (Battipaglia et al. 2016a).

Carbon and oxygen stable isotopes have been used both separately and together to study IADF formation in *Pinus pinaster* (De Micco et al. 2007), *Arbutus unedo* (Battipaglia et al. 2010a; b), *Erica arborea* (Battipaglia et al. 2014a), *Quercus ilex*, and *Pinus pinea* (Zalloni et al. 2018, 2019), and to infer information about IADF functionality. In particular, the position of IADF within the rings is linked with several microclimatic factors and varies within the same species according to the soil water availability, reflects different $\delta^{13}\text{C}$ signals (Battipaglia et al. 2010a). An increase in $\delta^{13}\text{C}$ is almost always found in the first half of the ring (in the so-called E-IADF band of latewood-like cells in the earlywood; see De Micco et al. 2016) as a consequence of stomatal closure under drought stress, when the tree reduces its vulnerability to cavitation, with a low hydraulic conductivity (De Micco et al. 2007, Battipaglia et al. 2010a, 2014a). A decrease in $\delta^{13}\text{C}$ is typically found in the second half of the ring in the so-called L-IADF (earlywood-like cells in the latewood) and corresponds with a reactivation of the cambium and of photosynthetic activity due to late-summer or early-autumn water availability following summer dormancy (Battipaglia et al. 2014a). The importance of the position of IADFs and their link to a common ecophysiological process was analysed using a network approach to examine $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in several species (*P. pinea* from Italy, *Pinus halepensis* from Spain and Slovenia; *P. pinaster* from Portugal, *Larix decidua* from Poland, and *L. decidua xkaempferi* from Austria). For all the different sites and species, the types of IADF and their positions had the same isotopic signals in terms of carbon and oxygen. E-IADFs presented $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in the range of $-23 \pm 0.6\text{‰}$ and $32 \pm 1\text{‰}$, respectively; L-IADFs had $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of $-27 \pm 0.7\text{‰}$ and $29 \pm 0.5\text{‰}$, respectively (Battipaglia et al. 2016a). These results should be extended to a larger database in order to assess how the isotopic composition of IADFs could help with dating problematic samples and support the interpretation of phenomena that trigger the formation of IADFs in the Mediterranean environment.

21.5.3 Carbon and Oxygen Isotopes and Fire

Fire has been a frequent and important disturbance in Mediterranean forest ecosystems throughout the Holocene (Heinselman 1981; FAO, State of Mediterranean Forest 2018), shaping landscapes and determining vegetation distribution and dynamics. Tree rings have been used to reconstruct fire history and to determine

the effects of fire on forest productivity. In recent years, carbon and oxygen isotopes measured in tree rings have proved to be a useful tool for understanding the complex ecophysiological processes that occur in Mediterranean tree species following a wildfire or prescribed burning (Beghin et al. 2011; Battipaglia et al. 2014b, c, 2016b, 2019; De Micco et al. 2014; Valor et al. 2018; Niccoli et al. 2019). Because conifers are widespread in the Mediterranean Basin and highly prone to fire damage, many studies have focused on conifer species, including *Pinus sylvestris* (Beghin et al., 2011), *Pinus halepensis* (Battipaglia et al. 2014b; c; Valor et al. 2018), *Pinus pinea* (Battipaglia et al. 2016b), and *Pinus pinaster* (Niccoli et al. 2019). Stable isotopes studies indicate that tree response and their potential to recover over the short- and long-term depends on fire severity. Strong wildfires produce a simultaneous increase in tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, suggesting a strong reduction in stomatal conductance and assimilation rate, which are often linked to crown damage (Battipaglia et al. 2014b; Niccoli et al. 2019). When fire severity is low to moderate, the effect on trees is less pronounced; often, the tree rings only report a small variation in $\delta^{13}\text{C}$, with no change of $\delta^{18}\text{O}$. In these cases, a reduction in tree growth is largely due to the reduced photosynthetic capacity of the burned trees (Battipaglia et al. 2016b). Following prescribed burning s, however, trees show a decrease in both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, indicating a possible favorable effect of reduced competition between the surviving plants. In addition to reducing competition, prescribed burning seems to lead to a release of nutrients, which can also stimulate the growth of surviving trees (Battipaglia et al. 2014c, 2016b; Valor et al. 2018; Niccoli et al. 2019).

21.6 Nitrogen Stable Isotopes

Nitrogen availability is an important factor limiting productivity in Mediterranean ecosystems (Noy-Meir 1973; Gutierrez and Withford 1987; Lloret et al. 1999) and therefore influencing wood formation. Tree-ring $\delta^{15}\text{N}$ is mainly influenced by the isotopic ratio of the available nitrogen sources (Nadelhoffer and Fry 1994; Peñuelas and Estiarte 1997; Evans 2001, Stewart et al. 2001). Thus, tree-ring $\delta^{15}\text{N}$ allows for the reconstruction of the nitrogen source and the relative activity of the different biogeochemical processes that affect the $\delta^{15}\text{N}$ of nitrogen compounds taken up by trees in the surrounding ecosystem (i.e., mineralization, nitrification, denitrification and, NO_3 leaching; see Chap. 12). However, other fractionation events that occur in plants during assimilation processes can also influence tree-ring $\delta^{15}\text{N}$ and complicate interpretation of the nitrogen sources (Evans 2001). Indeed, tree-ring $\delta^{15}\text{N}$ may also depend on nitrogen reabsorption or re-translocation (Kolb and Evans 2002) or fractionation by different mycorrhizal associations (Michelsen et al. 1998; Craine et al. 2009). The incorporated tree-ring $\delta^{15}\text{N}$ signature thus results from an integration of nitrogen sources and internal transformations. These complications may explain why only a limited number of studies have been carried out in Mediterranean ecosystems, most of which have focused on understanding the effects of climate change on carbon and nitrogen cycles (Peñuelas et al. 1996; Alfaro-Sanchez et al. 2016).

Tree-ring $\delta^{15}\text{N}$ has also been used to assess changes in nitrogen availability due to (i) variations in atmospheric nitrogen deposition and (ii) their influence on ecosystem nitrogen dynamics, since the nitrogen isotope ratio in compounds produced as a result of anthropogenic activities may be significantly different from the natural background $\delta^{15}\text{N}$ in the soil (Freyer 1991). Guerrieri et al. (2009, 2011) and Battipaglia et al. (2010b) showed that increases in nitrogen deposition from the atmosphere or from fertilization are reflected in tree-ring $\delta^{15}\text{N}$ signals as a result of source $\delta^{15}\text{N}$ (e.g., NO_x , NH_x forms, or NH_4^+ vs NO_3^-) and the processes occurring during different phases of soil biogeochemical processes (i.e., losses caused by NO_3^- leaching, denitrification, and NH_3 volatilization; see also Chap. 12). Changes in $\delta^{15}\text{N}$ in annual tree-rings reflect the causes of variation in the tree's iWUE due to climatic or anthropogenic impacts, suggesting that an increase in nitrogen input from the atmosphere (Guerrieri et al. 2011) or from consociation from nitrogen-fixing species could lead to an increase of trees iWUE under a scenario of reduction in precipitation, such as in Mediterranean area (Guerrieri et al. 2011; Battipaglia et al. 2017). Measurement of $\delta^{15}\text{N}$ of the different possible sources, and a better understanding of the fractionation processes in the different species, is needed for a proper interpretation of tree-ring $\delta^{15}\text{N}$ data.

21.7 Conclusions and Outlook

Tree-ring isotope studies in the Mediterranean Basin have increased in the last years for two main reasons. First, there is general agreement regarding the importance of reliable information about how Mediterranean trees are responding to a changing climate. Such information informs assessments of the future state of such vulnerable forests, as well as their role in carbon sequestration and ecosystem services. Second, stable isotopes help to identify the ecological behavior and vulnerability of Mediterranean tree and shrub species, information that can improve management options. Further research is needed to improve our knowledge about the xylem plasticity of the different Mediterranean species. This will help pinpoint how cambial activity affects the functional processes of trees and their responses to climate change. The combination of multiple approaches, including stable isotopes, xylogenesis, wood anatomy, and long-term growth and isotope-based gas exchange data, may provide more insight on how plants optimize growth and minimize costs.

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