



Inter- and intra-annual stable carbon and oxygen isotope signals in response to drought in Mediterranean pines

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ABSTRACT

Interpreting the isotopic tree-ring responses of pines to drought provides insight into the causes of tree mortality. For this reason, we examine such responses for low elevation *Pinus halepensis* subsp. *brutia* trees that neighbor recently desiccated pine stands. A strong correlation between ^{13}C discrimination (Δ) signals recorded in tree-rings and concurrent drought indicates a rapid transfer of newly synthesized assimilates to wood formation. However, in dry years the limited moisture allows only early- to mid-spring and mid- to late-autumn as productive periods. Thus, isotopic signals for summer drought may be missing in tree-rings. Yet, over a 30 year observation period, drought clearly reduced both, tree-ring width and $\Delta^{13}\text{C}$. Intra-annual microtome slices (1/10 mm) indicate the highest $\delta^{13}\text{C}$ signals in autumn (after growth resumed in response to rainfall) as a likely result of autumn wood (late-wood) incorporating carbon fixed and stored during the summer drought related growth cessation. Thus, non structural carbon reserves accumulating under drought are likely to leave a $\delta^{13}\text{C}$ fingerprint when complete tree-rings (early-plus late-wood) are analyzed. Both inter- and intra-annually, $\delta^{18}\text{O}$ in tree-rings from these pines declined following precipitation and in contrast to the rise in temperature. Any evaporative enrichment of leaf water in the heavier isotope under drought appears to be masked by the source water utilized for tree growth. Source water from deeper moisture pools is less enriched in ^{18}O than surface water. Therefore, as inter- or intra-annual drought intensifies, pines appear to use this deep water, which accumulates from precipitation over a series of years. This was also confirmed by $\Delta^{13}\text{C}$ and tree growth data, as both were best correlated with multiple years of past precipitation rather than with seasonal precipitation. Consequently, the most likely cause of drought induced mortality for such plants is chronic depletion of deeper moisture pools and hydraulic failure rather than C starvation.

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1. Introduction

Severe droughts have been associated with regional-scale tree mortality worldwide with climate change expected to exacerbate such trends. The physiological mechanisms underlying drought mortality are still poorly understood and in some cases may be related to carbon starvation, while in others to hydraulic failure (McDowell et al., 2008). Short drought periods (a couple of weeks to months) or the early part of longer drought periods can even produce carbon overflow, because sink activity (meristems) is more affected than source activity (photosynthesis; Körner, 2003; Gruber et al., 2012; Sala et al., 2012). Over longer periods (one to multiple

years) drought is likely to induce carbon starvation (McDowell et al., 2008) or a combination of hydraulic failure and carbon shortage.

Drought conditions in the eastern Mediterranean are related to reduced winter rainfall (December–February), which normally supplies more than 50% of the annual precipitation (Xoplaki, 2002). When winter rainfall is low for a number of years (chronic drought) tree growth is reduced or even inhibited in this region as evidenced by decreased annual radial increment for low elevation pines without access to permanent ground water supplies (Körner et al., 2005; Sarris et al., 2011). As topsoil moisture pools dry out under severe drought, the availability of deeper soil moisture pools determines annual tree-ring width. These reserves in deeper soil layers are suggested to originate from rainfall of multiple years prior to the current year's growth, and when these pools get depleted, this may lead to pine mortality (Sarris et al., 2007). Surplus winter precipitation infiltrates into deeper ground layers, available to deep rooted trees later during the growing season (Schenk and Jackson, 2002; Sankaran et al., 2004).

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Table 1

Scheme for ecophysiological responses of *Pinus brutia* trees to wet and dry years in Mediterranean climate conditions investigated here and expected isotopic signals captured by their tree rings. (+) = increase and (–) = reduction, e.g. in wet years we expect increased stomatal conductance indicated by increased $\Delta_{\text{std}}^{13\text{C}}$ tree-ring signals.

Tree response	Climate		Recorded isotopic signal		
	Wet	Dry	Climate		
			Wet	Dry	
Stomatal conductance	+	–	$\Delta^{13\text{C}}$	+	–
Deeper soil water uptake	–	+	$\Delta^{13\text{C}}$	+	–
Late spring growth	+	–	$\delta^{18\text{O}}$	+	–

Carbon and oxygen isotopes ($\delta^{13\text{C}}$, $\delta^{18\text{O}}$) in tree-rings have been shown to bear relevant climatic signals. However, little is known about the interrelationship between both isotopes in wood constituents for species from other than relatively wet climates (Ferrio and Voltas, 2005). If deep moisture pools are indeed important for pine survival under severe drought, this should be reflected in isotope signatures of their tree-rings. For such Mediterranean pines, reduced stomatal conductance (indicating increased drought stress) and reduced late spring growth in dry years, as well as an increased utilization of water from deeper soil layers should be reflected in reduced ^{13}C discrimination (Δ) and reduced $\delta^{18\text{O}}$ values in tree-rings compared to more humid years (Table 1).

More specifically, the $^{13}\text{C}/^{12}\text{C}$ isotope ratio in tree-rings can be used to estimate the degree of drought stress experienced by trees during photosynthesis (Porté and Loustau, 2001) and particularly in seasonally dry climates and where variation in other environmental factors can be accounted for (Warren et al., 2001). Farquhar et al. (1982, 1989) showed that the carbon isotope discrimination (Δ) is proportional to the c_i/c_a ratio where c_i is the leaf intercellular and c_a the ambient CO_2 concentration. The c_i/c_a ratio reflects the balance between the stomatal conductance (g_i) and the rate of Photosynthesis (P_N). If g_i decreases at a given P_N , and as a consequence, c_i/c_a decreases, then Δ decreases as well. The same is true if P_N increases at a given g_i . Under dry conditions (low soil water availability and/or dry air, expressed as a high vapor pressure deficit; VPD), g_i usually decreases to a greater degree than P_N , resulting in a decrease of c_i/c_a and, consequently, in Δ . Thus, the plant incorporates more ^{13}C . Part of this ^{13}C will be invested in structural growth to the extent that past C reserves are not diluting the signal.

In years of severe drought a strong correlation between ^{13}C signals recorded in tree-rings and concurrent climate conditions may indicate a direct transfer of newly synthesized assimilates to growing tree-rings as a result of low C reserves. These findings suggest that tree mortality may also be caused or accelerated by a continuous carbon depletion (Eilmann et al., 2010).

Besides reflecting the temperature signal from precipitation water, tree-ring $\delta^{18\text{O}}$ signals are enhanced by the evaporative $\text{H}_2^{18\text{O}}$ enrichment of leaf water during warm and dry weather conditions (Dongmann et al., 1974; Cernusak et al., 2002). Thus, the $\delta^{18\text{O}}$ signal in tree-rings represents the mean temperature signal during the period of tree rings formation, provided there is sufficient water to support meristematic activity. This $^{18\text{O}}$ enriched water leaves a signal in the carbohydrate synthesis, and thus, wood (Saurer and Siegwolf, 2007; Sidorova et al., 2009). As the summers get warmer and drier over the years, one would expect an increase in the $^{18\text{O}}/^{16\text{O}}$ isotope ratio in the tree-ring cellulose. Such a signal would be enhanced by the reduction in transpiration, due to stomatal limitation and a reduced contribution of the so-called Péclet effect, which expresses the degree of dilution of the enriched leaf $\text{H}_2^{18\text{O}}$ (due to discrimination of $^{18\text{O}}$ in the course of transpiration) with non $^{18\text{O}}$ enriched source water coming from

the root infiltrated soil (Farquhar and Lloyd, 1993; Barbour et al., 2004). This low $^{18\text{O}}$ water replenishes the water in the leaf, which is lost during transpiration. Therefore the higher the sap flux the stronger the ‘dilution effect’ of $\text{H}_2^{18\text{O}}$ at the evaporative surfaces in the leaf. When stomata close, the Péclet effect is hardly effective and the needle water should become highly enriched.

Yet, the tree-ring $\delta^{18\text{O}}$ signals are predominantly given by the isotopic composition of the source water utilized for tree growth (Dansgaard, 1964; Saurer et al., 1997; Ferrio and Voltas, 2005). It is known that the isotopic composition of oxygen in rain water varies with the condensation temperature throughout the season (Dansgaard, 1964). This signal is amplified by the evaporation of water from upper soil layers, which is expected to be highest during the warm season (for any moisture supplied during late spring rainfall events) and lowest during the wet and cold season. Thus, winter precipitation in the Mediterranean is expected to be less enriched in $\text{H}_2^{18\text{O}}$ than spring and summer precipitation. Rain-water that infiltrates into the ground during the winter months is also low in $\text{H}_2^{18\text{O}}$. The $^{18\text{O}}/^{16\text{O}}$ isotopic composition of water stored in deeper soil layers will remain low all year round, since most water evaporates from top soil. Therefore, deeper moisture pools are less enriched in $\text{H}_2^{18\text{O}}$ compared to top soil moisture (Kurz-Besson et al., 2006; Wingate et al., 2008). If under increasing drought, deeper moisture pools are utilized by trees (Dawson, 1993; Kurz-Besson et al., 2006; David et al., 2007) this can produce a decline in $^{18\text{O}}$ of tree-rings, masking possible evaporative enrichment of leaf water in the heavier isotope. By analyzing the isotopic composition of tree-ring $^{18\text{O}}$ and its variation through time it is possible to estimate the origin of moisture utilized by these trees to sustain their growth.

However, the above described processes are not the only possible explanation for declining $^{18\text{O}}$ in tree-ring series. During spring, cambial activity is at its peak promoted by favorable temperatures and abundant soil moisture. This is the season when most of the annual tree-ring increment occurs before summer drought stalls growth. A smaller fraction of growth occurs later in mid to late autumn before the cambium falls into winter dormancy (Liphshitz et al., 1984; De Luis et al., 2007; Sarris et al., 2007). In wet years we expect trees, to utilize the abundant top soil moisture pools (supplied from winter rainfall and enhanced by rainy spring weather), allowing growth to continue into early summer (until these reserves are used up) resulting in wider tree rings. In this case, trees would incorporate $^{18\text{O}}$ enriched water from the top soil (due to enhanced evaporation during May and June). On the other hand, in dry years, these surface reserves soon become exhausted resulting in a shorter growth period (Eilmann et al., 2010). Temperatures in April are lower than in May or June. Hence, in dry years, when spring growth ends earlier (e.g. late April), less enriched $\text{H}_2^{18\text{O}}$ from top soil moisture would be absorbed by the upper roots of trees. As water gets scarce, the proportion of enriched leaf water is also reduced. Thus, the less enriched $\text{H}_2^{18\text{O}}$ from early to mid spring growth may decrease the long-term $^{18\text{O}}/^{16\text{O}}$ signal in tree rings. In this case, a decline in $^{18\text{O}}$ in a tree-ring series (as precipitation declines) would also indicate a shortening of the period of spring growth (summer growth being very low even in wet years).

The aim of this paper is to demonstrate the impact of extreme drought (associated with declining precipitation and climatic warming) on *Brutia* pine, the dominant Mediterranean conifer in the Eastern Mediterranean at low elevation. Isotopic signals from its tree-rings are investigated at inter- and intra-annual scales in order to illuminate whether the path leading to pine mortality under drought is more likely caused by carbon starvation or by lack of deeper ground moisture to sustain tree hydraulics and plant cell turgor pressure. The correct interpretation of isotopic signals in tree-rings is also important to support and improve the reliability of stable isotopes for environmental reconstructions.

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