



# Shifts of irrigation in Aleppo pine under semi-arid conditions reveal uncoupled growth and carbon storage and legacy effects on wood anatomy



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## ABSTRACT

Climate models forecast progressive aridification in the Mediterranean region. These warmer and drier conditions will probably lead to a decrease in carbon fixation and growth rates of drought-prone forests. To improve our knowledge on how water availability drives radial growth, wood anatomy and carbon storage we compared changes during a 40-year period in tree-ring width, wood-anatomical traits (tracheid lumen area, cell-wall thickness and parenchyma area), and stem sapwood non-structural carbohydrates (NSC) concentrations. We studied the drought-tolerant Aleppo pine (*Pinus halepensis*) comparing trees subjected to three irrigation regimes (control trees, no irrigation; IR trees, irrigated trees; TI trees, temporarily irrigated trees). Tree-ring width of TI trees widely overtook growth rates shown by IR trees during the irrigation treatment (1980s), whereas transversal lumen area and cell-wall thickness presented similar values in both groups of trees. Non-irrigated trees showed the lowest growth rates and also formed tracheids with the smallest lumen area and the narrowest cell walls. After the irrigation period, TI and trees without irrigation showed similar year-to-year growth variability. Lumen area of TI trees took 4–5 years to show values similar to those of the non-irrigated group. The TI trees had lower ray parenchyma area percentages during the irrigation period; afterwards both TI and non-irrigated trees formed similar amounts of ray parenchyma which were always higher than in IR trees. NSC concentrations were lower for IR trees suggesting either a dilution effect due to their significantly larger biomass or a higher demand for NSC by other carbon sinks such as primary growth. Aleppo pine may coordinate carbon supply and demand (growth) under changing conditions of water availability but long-term modification in soil moisture lead to legacy effects on wood anatomy.

## 1. Introduction

Drought is one of the major constraints to forest growth and productivity and is expected to become increasingly crucial in many regions because of the ongoing climate warming (Vicente-Serrano et al., 2013). Recent droughts have severely impacted forests worldwide causing: die-off events and tree mortality (Allen et al., 2010; Camarero et al., 2015; Sarris et al., 2007), transient declines in forest productivity (Baldocchi, 1997; Ciaies et al., 2005; Dorman et al., 2013; Leuzinger et al., 2005) and higher vulnerability to attacks by biotic agents (Bréda et al., 2006). Improving our knowledge on the factors controlling tree growth is thus a critical step to assess and predict the impact of a drier climate on forests. This is specially compelling for Mediterranean areas where climate models predict warming and aridification (IPCC et al., 2013), which may threaten the survival of some pine stands and tree species at very xeric sites (Sánchez-Salguero et al., 2017, 2012).

There is evidence supporting drought-induced sink limitation in

trees because low water availability restricts carbon sinks (growth) more than sources (photosynthesis) (Lempereur et al., 2015), leading to an accumulation of non-structural carbohydrates (NSC hereafter) and often uncoupling carbon use (growth) from carbon uptake (photosynthesis) (Körner, 2003; Muller et al., 2011). Consequently, drought-triggered growth reduction can lead to increases in the concentrations of NSC (Sala and Hoch, 2009). However, NSC accumulation may also be explained by an active growth suppression to avoid carbon starvation under prolonged water shortage (McDowell, 2011; Wiley and Helliker, 2012). In that case, carbon starvation could be adaptive and driven by other factors such as phloem malfunction (Sala et al., 2012; Sevanto, 2014). This agrees with the observations that drought-tolerant tree species increase NSC content in response to water shortage (Piper, 2011) or with the conversion of stored NSC (e.g. starch) into mobile osmolytes (e.g. soluble sugars) during drought (Salleo et al., 2009). Such controversial views on how water availability drives growth dynamics and NSC storage require further insight (Hartmann and

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Trumbore, 2016). Aleppo pine (*Pinus halepensis* Mill.) is one of the most common conifers in the Mediterranean Basin and presents a high growth plasticity and drought tolerance in response to changing water availability, which makes it an ideal subject for studying the effects of drought on tree performance in this region (Girard et al., 2012; Gazol et al., 2017). According to Borghetti et al. (1998) mature Aleppo pines subjected to long-term drought ( $\geq 12$  months) showed significant reduction in most growth parameters followed by a quick recovery of the overall plant hydraulic resistance a few months after the drought treatment. The low wood density in Aleppo pine roots and its vulnerability to xylem embolism has been proposed as a way to protect needles or twigs more exposed to xylem cavitation (Oliveras et al., 2003). At stem level, tracheid lumen area in earlywood can be up to 30% smaller in trees growing in dry areas which allow them to better cope with severe droughts (Pacheco et al., 2017). These strategies for withstanding drought may lead trees to adjust their water conducting tissues to a more negative hydraulic pressure (Bréda et al., 2006). This is a cumulative long-lasting process, as the sapwood consists of multiple annual rings, and such long-term adjustments can be analyzed retrospectively combining growth responses and changes in wood anatomical traits that are proxies of hydraulic functioning and resilience to drought (Montwé et al., 2014).

Drought effects on growth and NSC have mostly been studied on saplings or seedlings under imposed drought treatments or different irrigation regimes, indicating a reduction in stem biomass and growth rate, an accumulation of shoot starch in drought-exposed individuals, and the development of carbon starvation under extreme drought conditions (Villar-Salvador et al., 1999; de Luis et al., 2011; Klein et al., 2011). However, there is a lack of similar approaches on mature trees under field conditions.

In this study, we analyze three groups of mature Aleppo pine trees growing in semi-arid conditions at the same site. Throughout 40 years one group was permanently irrigated, another was irrigated only during a 10-year period, and the third was growing without any additional watering. Following this experimental design, the objective of our research is to describe and quantify the long-term effects of irrigation on radial growth, wood anatomical traits (lumen area, cell wall thickness, and parenchyma area percentage) and NSC storage in the sapwood. According to the current knowledge on water and carbohydrate balance formerly presented and using the experimental design proposed, we hypothesize that irrigation will cause an uncoupling between growth, wood anatomy and NSC storage leading to the formation of: wide rings, tracheids with ample lumen areas and thick walls, wood with less parenchyma area and sapwood with lower NSC concentrations. Consequently, we expect that drought would lead to the opposite features.

## 2. Materials and methods

### 2.1. Tree species, study area and climate

Aleppo pine (*Pinus halepensis* Mill.) is a drought-tolerant evergreen conifer species, widely distributed across the Western Mediterranean Basin, and covering areas subjected to seasonal water deficit, mainly lowlands under dry to semi-arid conditions (Ne'eman and Trabaud, 2000). In northeastern Spain, this species presents a growing season that extends from early April to early November (Camarero et al., 2010).

Our study sites are Aleppo pine plantations located in the south-eastern sub-urban area of Zaragoza (northeastern Spain) at 340 m. a.s.l. and on an almost flat topography (Table 1). Two of the sites (irrigated and non-irrigated trees) are located on the same stand but separated by a ground level difference, with the non-irrigated being few meters higher. The irrigated plot borders a residential area with permanent lawn water irrigation which indirectly maintains high water availability for the irrigated trees. The temporarily irrigated plot is 3 km to the west

on a similar terrain and soil features, and was artificially irrigated from 1980 to 1989 with sprinklers. Irrigation was done at early morning from March to October and corresponded to a supplementary rainfall of about 500 mm per year. In the currently-irrigated plot, irrigation corresponds to a supplementary rainfall of about 400 mm per year. The density and basal area of the Aleppo pine plantations of this area range between 162 and 542 stems  $\text{ha}^{-1}$ , and 4.12 and 20.82  $\text{m}^2 \text{ha}^{-1}$ , respectively. The understory vegetation is dominated by shrubs (*Genista scorpius*, *Thymus vulgaris* and *Rosmarinus officinalis*). The soils are cambisols poorly developed over gypsum outcrops. More details on sampling sites are available in Sangüesa-Barreda et al. (2015).

According to data from the nearby Zaragoza-airport weather station (41° 40' N, 1° 00' W, 263 m a.s.l.), 10 km from the study sites, the climate in the area is Mediterranean of semi-arid type. During the 1950–2012 period, mean annual temperature was 14.8 °C (the coldest and warmest months were January and July, respectively) and total annual precipitation was 325 mm (the wettest and driest months were May and July, respectively) (Supplementary material, Fig. S1).

### 2.2. Field sampling and tree-ring data

During the winter of 2016, a total of 30 dominant and mature trees were sampled (10 per class considering control, IR and TI trees). We took two radial cores per tree at 1.3 m with 5-mm Pressler increment borers. Sampled trees were randomly distributed across the plantation and field sampling followed standard dendrochronological methods (Fritts, 2001). Wood samples were air-dried and polished with a series of successively finer grits sand-paper until rings were clearly visible. Tree rings were measured to the nearest 0.01 mm using a binocular scope and a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating of the tree rings was checked using the COFECHA program (Holmes, 1983). Tree age at 1.3 m was determined by counting rings in the oldest core. With off-center cores we used a geometric pitch locator to estimate the number of missing rings (Duncan, 1989).

Chronologies of tree-ring width (as well as wood anatomy traits) were produced for each site using ARSTAN, a software developed to remove age-size related growth trends, which are also present in wood-anatomical data (Carrer et al., 2015), and potential disturbance pulses (Cook, 1985). Individual series were fitted using a cubic smoothing spline function with 50% frequency–response cutoff of 30 years. Subsequently, we divided observed by expected values to obtain detrended and dimensionless indices, which were then subjected to autoregressive modelling to remove the remaining serial autocorrelation. These residual or pre-whitened indices were finally averaged using the biweight robust mean to create the site chronology of each variable for each irrigation plot.

### 2.3. Wood-anatomy analyses

A third 10-mm core was obtained from each tree for wood-anatomy analyses. In the laboratory, these cores were divided into 4-cm long pieces, boiled in water to soften the wood and remove the resin, and sliced into 10–12  $\mu\text{m}$  thick transversal sections using a rotary microtome (Leica RM 2025, Heidelberg, Germany). The samples were then stained using a water-diluted mixture of safranin (1%) and astrablue (0.5%), and rinsed with water and ethanol. Afterwards sections were fixed on permanent slides with Eukitt (BioOptica, Milan, Italy) and scanned using a D-sight 2.0 System (Menarini Diagnostics, Florence, Italy) at 100 $\times$  magnification, with a resolution of 1.99 pixels  $\mu\text{m}^{-1}$ . The images were then processed with the image analysis software ROXAS v3 (von Arx and Carrer, 2014; Prendin et al., 2017) that provided the lumen area (LA), cell-wall thickness (CWT), and relative position within the dated annual ring for each of the > 3.5 million measured tracheids. Tree-ring borders were manually drawn on the images and cross-dating was checked using the reference curves obtained in the previous tree-ring measurements. Information related to

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