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Simultaneous assessment, through sap flow and stable isotopes, of water use efficiency (WUE) in thinned pines shows improvement in growth, tree-climate sensitivity and WUE, but not in WUEi

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ABSTRACT

In water-limited regions, adaptive management of forest and water relationships has been put forward, to implement hydrology-oriented silviculture to reduce stand evapotranspiration and, at the tree level, to improve growth and water use efficiency (WUE). The main goal of this study was to evaluate the effect of thinning in the short and medium term on tree growth, climate (drought) sensitivity, WUE performed using growth and sap flow measurements and WUEi performed using $\delta^{13}C$ and $\delta^{18}O$ isotopes, in a typical semiarid forest. This approach also evaluated the reliability of isotopes as indicators of the effects of adaptive forest management. A stagnated Aleppo pine plantation was experimentally thinned at high intensity (H98) in 1998 and at High (H), Medium (M) and Low (L) intensities in 2008, along with a control (C). Substantial limitation of tree growth was observed in C. Thinning not only increased growth, but also changed the tree growth–precipitation relationships, with C trees depending more on precipitation than thinned trees did. WUEi after thinning was significantly affected only in the medium term, with C trees being more efficient (94.4 $\mu molCO_2/molH_2O$) than H98 trees (88.7), especially in dry spells (100.7). WUEi was found to increase when precipitation decreased, regardless of the treatment. However, WUE increased sharply from C (1.26 g biomass/L H_2O) to H (3.20 g/L), showing a clear difference with WUEi observed in the same years. Thinning caused an increase in $\delta^{18}O$ in the short term, but no relationship was found between $\delta^{18}O$ and tree water use. It can be concluded that forest management improved WUE in spite of higher tree transpiration, but WUEi remained unchanged, probably due to an underestimate of photosynthetic capacity. The dual isotope ($\delta^{13}C$ and $\delta^{18}O$) conceptual model was not consistent with our experimental data. Thus, the question of whether stable isotopes can be used as a tool for addressing the ecophysiological impacts of thinning remains open.

1. Introduction

Water resource availability in the Mediterranean will be seriously jeopardized in the foreseeable future (García-Ruiz et al., 2011), which may have a substantial impact on the semiarid forests growing in the region (Lindner et al., 2010; Torras et al., 2012). To improve forest resilience, forest managers need adaptive strategies that help make forest management more efficient and effective under changing water resource availability (Sjölund and Jump, 2013). However, although many studies have addressed this need in recent years, reliable guidelines for adaptive management in line with the eco-regional and social context are still scarce (Fitzgerald et al., 2013).

In water-limited regions, adaptive management usually focuses on forest and water relationships based on hydrology-oriented silviculture (Del Campo et al., 2014; Ungar et al., 2013). Guidelines for this silviculture should be developed through a full approach covering tree to stand scales. Stand scale is related to the hydrologic performance of the physical structure of forests (density, LAI, canopy storage etc.), in which thinning is known to affect water cycle components such as rainfall interception, throughfall, transpiration, soil moisture and deep infiltration (Del Campo

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et al., 2014; Molina and Del Campo, 2012). On the other hand, tree-scale studies provide fundamental information about how changing forest structure and microclimate might lead to modifications in the ecophysiology of photosynthesis, transpiration and tree water relations (Aussenac, 2000). In this context, tree climate–growth relations, water use (WU) and water use efficiency (WUE) are central topics to be tackled when relating forest management and tree water (Brooks and Mitchell, 2011; Forrester et al., 2012; Kruse et al., 2012; Sohn et al., 2013; Ungar et al., 2013). While WU is the amount of water transpired by trees (Burgess et al., 2001), WUE is the ratio of carbon gain per WU (Brienen et al., 2011). In most of the literature, WUE is discussed either in terms of an instantaneous measurement of the efficiency of carbon gain per water loss, i.e. intrinsic water-use efficiency (WUEi), or as an integral of such efficiency over time, commonly expressed as the ratio of water use to biomass accumulation or to harvestable yield (Dye, 2000; Hubbard et al., 2010).

Plant carbon stable isotope composition ($\delta^{13}C$) provides a time-integrated proxy of WUEi during the growing season (Dawson et al., 2002; Farquhar et al., 1989), because the isotopic carbon discrimination of plants is linearly linked to the C_i/C_a ratio, where C_i is the partial pressure of CO_2 in the leaf intercellular spaces and C_a that of the ambient air (Farquhar et al., 1982; Scheidegger et al., 2000). However, increases in $\delta^{13}C$, interpreted as a reduction in C_i, may be the result of either (i) reduced stomatal conductance (gs) at a constant photosynthetic capacity (A) or (ii) increase in A at a constant gs, i.e. changes in WUEi are due to changes in transpiration rate or in photosynthesis activity. To overcome this, the dual-isotope model (Scheidegger et al., 2000) was developed to constrain the interpretation of $\delta^{13}C$ variations in organic matter by measuring $\delta^{18}O$ in the same material. In principle, the latter as a proxy for evaporative demand would be modified by gs but not by A, thus allowing for a better interpretation of WUEi. This model is conceptually sound and many authors have used it to interpret $\delta^{13}C$ results measured in tree rings (Brooks and Mitchell, 2011). However, Roden and Siegwolf (2012), on analysing the systematic use of this conceptual model, warned about specific situations in which its applicability might be compromised.

Studies of WUEi and of the use of stable isotopes in Aleppo pine have been profuse in the literature. Previous studies used this technique to assess climate–growth relations (Ferrio et al., 2003), intraspecific differences in WUEi related to seed origin (Voltas et al., 2008) and differences in plantation performance (Querejeta et al., 2008), or to specifically address tree water use in the species (Klein et al., 2013a). Some of these studies provide key information for improving silviculture in the face of increasing water scarcity in Mediterranean regions. However, how forest management affects WUE, how long these changes may last and how stable isotopes can study these effects remain unclear for this species. For instance, Moreno-Gutiérrez et al. (2011, 2012) report no variation in WUEi in Aleppo pine after reducing forest density; similar results were found by Martín-Benito et al. (2010) for black pine. In addition, Gyenge and Fernández (2014) report that thinning increased the amount of water reaching the soil, but that WUEi was unrelated to growth, nitrogen and light use efficiencies. On the other hand, Querejeta et al. (2008) report a significant effect of the afforestation method on WUEi of Aleppo pine saplings. In addition, in most studies WUE is addressed by studying $\delta^{13}C$ in tree-rings (i.e. WUEi), although some divergences may appear when $\delta^{13}C$ results are compared to other techniques such as leaf-scale gas exchange (Klein et al., 2013a).

The present study complements our previously published stand-scale results from a stagnated Aleppo pine plantation (Del Campo et al., 2014) and specifically addresses: (i) What are the short- and medium-term effects of thinning intensity on WUE and growth of trees? (ii) Do these effects change in drought periods? (iii) Is there congruency between WUEi findings with the isotope-based approach and WUE findings obtained from tree growth and tree water use by sap flow measurements? We also addressed the question of whether the dual isotope technique ($\delta^{13}C$ and $\delta^{18}O$) could be used to explain further the WUE results.

2. Material and methods

2.1. Experimental site and design

The experimental site and design have been described elsewhere (Del Campo et al., 2014). Briefly, "La Hunde" site is located in Valencia, Spain (39°5′N; 1°13′W, 943 m a.s.l.). The climate is Mediterranean with an average total annual precipitation of 477 mm and a mean annual temperature of 14.1 °C. The soils are shallow (50–60 cm) with a sandy–silty texture and basic pH. The area is occupied by *Pinus halepensis* Mill. plantations about 50–60 years old and with high tree density (ca. 1500 trees/ha) due mainly to low forest management. The experimental set-up encompassed five treatments. One of them was selected within a non-replicated plot heavily thinned in 1998 (H98), leaving approximately 10% of the trees. This 0.2 ha plot was established and sampled to assess the medium-term effects of thinning. Adjacent to this plot, another experimental area was set up. This consisted of a randomized block design with three blocks (0.36 ha each) to assess the short-term effects of thinning. Each block was further divided into four plots (30 × 30 m), three of them with thinning treatments performed in 2008 at different intensities (High-H, Medium-M and Low-L) and a control plot (C) common to both experimental areas (Table 1).

2.2. Tree growth

Between eight and twelve trees per treatment were cored (north and south) by a 5 mm increment borer at 1.30 m height. Each core was mounted on a wooden support and sanded until wood cells were clearly identified under the stereomicroscope. All cores were visually cross-dated and measured to the nearest 0.01 mm with a measuring table (LINTAB 6.0, Frank Rinn, Heidelberg, Germany) coupled with the TSAP-Win software package (Rinn, 2011). Cross-dating of the tree-ring width (TRW) series was evaluated by the COFECHA software (Holmes, 1983). Cores with missing rings were ruled out for any further analysis. The average series length was 50.2 ($\sigma = 2.51$) years; autocorrelation at 1-year average was 0.76 ($\sigma = 0.09$); and the Gini coefficient, which describes annual changes in the inequality of size and size increment, was 0.42 ($\sigma = 0.08$), where 0 indicates perfect equality (the size or growth of all individuals is the same) and 1 indicates perfect inequality. The average series correlation to the master chronology was 0.79 ($\sigma = 0.07$), excluding the H98 treatment, which was analysed separately, obtaining a correlation of 0.80 ($\sigma = 0.09$).

The tree ring width (TRW) series were detrended to reduce the systematic noise caused by tree age (Cook and Briffa, 1990), using a cubic smoothing spline function with a wavelength fixed at 67% (Cook et al., 1990) of the length of the series, and a 50% frequency response. In some cores a negative exponential method was used instead. Each measured series was standardized by dividing the observed values by the predicted ones to obtain dimensionless TRW index series (TRWi). TRWi was averaged using a robust bi-weight mean. Additionally, the temporal autocorrelation was removed from each series by an autoregressive model (Cook and Briffa, 1990) to obtain the standard and residual chronology. To determine the length of the residual chronology for which climatological responses would be tested, a running (20-year) mean of the