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Original Article

Wood density of silver fir reflects drought and cold stress across climatic and biogeographic gradients

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ABSTRACT

Climate influences wood density and this relationship affects the ability of conifer forests to uptake and store carbon. Some conifer species can show mixed responses to long-term climate variability in their within-ring width and density patterns. Here we analyze if tree-ring width and density differently respond to seasonal climate variability in silver fir (*Abies alba*) forests from the Spanish Pyrenees subjected to cold and Mediterranean influences. In these forests, early growing-season dry conditions increase minimum wood density, possibly by reducing lumen diameter and lowering growth rates. Cold conditions during the late growing season are associated to a decrease in maximum wood density, probably through a reduction in the lignification and thickening rates of latewood tracheids. We test if these associations follow climatic and biogeographic patterns since the Mediterranean influence, characterized by late-summer storms which alleviate drought stress, is prevalent eastwards in this region. Silver-fir intra-annual width and wood density data showed mixed responses to climate. Minimum wood density negatively responded to spring precipitation, particularly in dry sites forming the southernmost distribution limit of the species. Maximum wood density positively responded to mean maximum temperatures and sunshine duration during late summer and early autumn, mainly in eastern sites subjected to a dominant Mediterranean influence where late-summer drought stress is expected to be low. More extreme climate conditions including dry spells could shift minimum wood density and reduce hydraulic conductivity and growth in conifer species as silver fir which dominate mesic sites. Warmer conditions would lead to denser latewood in silver fir if accompanied by longer durations of sunshine.

1. Introduction

Wood is a major long-term carbon sink (Bonan, 2008). Tree-ring records allow reconstructing long-term changes in tree biomass increment, but these retrospective assessments are biased when going back to the past since they depend on how wood density changes through time as a function of climate and other factors (Briffa et al., 2004; Büntgen et al., 2010; Bouriaud et al., 2015). Consequently, we need a better knowledge on how climate influences wood density to assess the ability of forests to uptake and store carbon.

In conifers wood production involves lagged processes as stem-girth increase and tracheid maturation because different xylogenesis phases (cell production and expansion vs. cell-wall thickening and lignification) respond to diverse climate factors throughout the growing season (Cuny et al., 2015). These lags in xylogenesis stages translate into varied responses of wood properties such as radial increment and density to climate (Bouriaud et al., 2005; Vaganov et al., 2006). Therefore, we can expect different couplings between climate and tree-ring width or density during the growing season.

For instance, in continental and dry Mediterranean climates wet conditions during the early growing-season enhance radial increment but decrease minimum wood density (Camarero et al., 2014). Such lower minimum density can be interpreted as the production of narrower tracheid lumens in response to water shortage (Dalla-Salda et al., 2009; Ruiz Diaz Britez et al., 2014). Further, maximum wood density and summer temperature are usually related in boreal and temperate conifer forests (Conkey, 1986; Splechtna et al., 2000; Levanič et al., 2009; van der Maaten-Theunissen et al., 2013). This positive density-temperature association is interpreted as a thermal-induced enhancement of tracheid lignification during the late growing season (Gindl et al., 2001).

Here, we analyze if tree-ring width and density differently respond to seasonal climate variability in silver fir (*Abies alba* Mill.) stands from the Spanish Pyrenees, where woody biomass increment (growth and density) of this species may be constrained by dry conditions during the growing season but also by cold conditions during the late growing

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season (Büntgen et al., 2010; Camarero et al., 2011). In this range, warmer and more arid conditions are enhancing silver fir water stress and increasing growth variability (Macias et al., 2006). These changes are associated to ongoing growth decline and canopy dieback in stands located in the less humid sites, which contrasts to the growth enhancement observed in humid and cool sites across central Europe (Büntgen et al., 2014; Gazol et al., 2015). It is therefore interesting to investigate if stands subjected to drier conditions present climate-width/-density associations which differ from stands experiencing more cool-humid conditions. We expect that the driest and coldest sites will show the highest sensitivity of earlywood and latewood width and density to precipitation and temperature during the early and late growing seasons, respectively. Specifically, we anticipate that minimum wood density will respond to spring precipitation in the driest sites, whilst maximum wood density will respond to summer temperature in the coldest sites.

Since both precipitation and solar radiation can influence tree performance and radial growth (Stanhill and Cohen, 2001; Rozas et al., 2015; Dorado-Liñán et al., 2016), here we also explore if sunshine duration is related to changes in wood density. Recently, it was shown that latewood density of boreal trees responds to changes in light availability (Stine and Huybers, 2014). As 20th-century climate warming occurred while aerosols and clouds lead to more sunlight reflected to space and a net cooling from 1955 to 1975 (global dimming; Wild, 2009), it is relevant to disentangle these conflicting environmental signals on wood density. We hypothesize that eastern Pyrenean silver fir forests will show more pronounced responses to changes in sunshine during the late growing season when Mediterranean storms affect those sites more frequently than westwards (Camarero et al., 2011).

2. Materials and methods

2.1. Study area

In the Spanish Pyrenees, the abrupt northern-southern gradient leads to more continental-Mediterranean climate conditions as elevation decreases southwards (Fig. 1). Another western-eastern gradient leads to more winter-spring precipitation westwards and more summer-fall precipitation eastwards (Camarero et al., 2011). In this region, montane or subalpine silver fir forests dominate in mesic sites with deep soils, usually with N-NW exposure, and located at mid to high elevations, approximately from 1000 to 2000 m a.s.l. (Camarero et al., 2011). In the last centuries, Pyrenean silver fir forests were regularly logged, but exploitation decreased from the 1950s onwards (Cabrera 2001). These silver fir forests experience mild (mean annual temperature between 6.5° and 11.0° C) and wet conditions (annual precipitation between 850 and ca. 2000 mm) (see Table 1). Silver fir usually forms mixed forests with secondary tree species as European beech (*Fagus sylvatica*), Scots pine (*Pinus sylvestris*) and Mountain pine (*Pinus uncinata*) (Table 1). According to climate data for the second half of the 20th century, some study sites are experienced warmer conditions during the growing season (ORL, VIU, MAT and BOI) and only one eastern site (MOI) showed a significant decrease in August precipitation (Fig. S1, Supporting Information).

2.2. Field sampling

Based on the development of dendrochronological networks of silver fir forests (10 sites) distributed across the Spanish Pyrenees (Tardif et al., 2003; Macias et al., 2006; Camarero et al., 2011), we selected 8 sites subjected to very different climate conditions (Table 1). In each site, we randomly selected and sampled 10–15 dominant trees in ca. 1-ha large sampling areas (Table 2). Three 5-mm wide cores were extracted from each tree using Pressler increment borers. We took special care to sample the cores perpendicular to the main stem so as to capture the main fibre direction. We also measured diameter at 1.3 m (dbh) and total height of each sampled tree using tapes and clinometers, respectively. To estimate the basal area of each stand we measured the dbh of all trees found within 20 m × 20 m plots located in representative areas of each stand.

Trees selected for sampling had diameters ranging between 34.0 and 95.4 cm and their heights varied between 8.2 and 34.4 m (Table 1). In the study stands, basal area reached values between 28.0 and 66.2 m^2 ha^{-1}. In these forests, the relative basal area represented by silver fir oscillated between 60 and 94%.

2.3. Tree-ring width and density measurements

Two 5-mm cores were glued onto wooden mounts, sanded and visually cross-dated. Then, we measured tree-ring widths to a precision of 0.01 mm using a LINTAB measuring device (Rinntech, Heidelberg, Germany) and checked the measurements for dating accuracy using the COFECHA software (Holmes 1983), which calculates cross correlations between individual series of each core and the mean site series obtained averaging all measured series. These mean site series were used for dating the samples for wood density analyses. To estimate tree age at 1.3 m we calculated the number of innermost missing rings in samples without pith by using a geometrical pith locator (Norton et al., 1987).

We obtained one radial X-ray density profile from the third core by using indirect X-ray densitometry. Each core was cut carefully using a double-bladed saw to obtain ca. 1.5-mm thick cross sections. These samples were air dried to moisture equilibrium and then subjected to X-ray exposure for about 25 min. The resulting X-ray microfilms were scanned with a resolution of 10 μm using a microdensitometer DENDRO-2003 (Walesch Electronics Ltd., Switzerland). The measured grey levels of the X-ray films were transferred to density values by comparing them to a standard of known physical and optical density also exposed on the same film.

For each annual ring, the following variables were obtained from the density profiles: earlywood width (EW hereafter), latewood width (LW hereafter), minimum wood density (MN hereafter) and maximum wood density (MX hereafter). Since MN and MX are tightly related to earlywood and latewood mean densities, we only analysed the former two variables because they are easier to define and show strong responses to climate variables as previously demonstrated (Camarero et al., 2014). To define the earlywood-latewood transition we used the 50% level between the MN and MX values of each ring following Polge (1978), and confirmed this separation with a visual checking of the tree rings (Mäkinen and Hynynen, 2014).

2.4. Chronology building and series characterization

First, in each site we selected the 10 trees which best matched the mean site tree-ring width series. Second, in each site a subset of 5–10 cores was selected from those 10 trees for densitometry measurements (Table 2). All information provided and presented analyses refer to the tree-ring series of those subsets.

The tree-ring series produced in the previous step (EW, LW, MN and MX) were individually detrended to remove non-climatic biological growth trends (Cook and Kairiukstis, 1990). Prior to trend removal, a power transformation was applied to stabilize the variance of the MN and MX density series. A 2/3 cubic smoothing spline with 50% frequency-response cut-off was fitted to the individual records and indexed values were calculated. Then indexed tree-ring series were subjected to autoregressive modelling to remove most first-order autocorrelation so as to obtain residual indices. Finally, site chronologies for each variable and site were obtained by averaging the residual indices on a yearly basis using a bi-weight robust mean. These procedures were performed using the ARSTAN software (Cook and Holmes, 1984).

To compare the resulting chronologies, several statistics were