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Water availability controls *Pinus pinaster* xylem growth and density: A multi-proxy approach along its environmental range

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ABSTRACT

Deciphering climatic factors limiting cambial activity is critical to forecast the potential of trees to respond to ongoing climatic change. We explored multiple xylem traits, including tree-ring width, inter-annual micro-density variation and intra-annual density fluctuations (IADF), to unveil the climatic factors constraining cambial activity of a Mediterranean conifer (*Pinus pinaster*) along a continental-aridity gradient. Secondary growth responded mainly to water availability, explaining as much as 64.7% of earlywood growth variance for earlywood growth. The continuous and non-overlapping timing of the climatic signals of earlywood and latewood growth reflected a continuous water limitation of secondary growth along the growing season. Drought also had an extraordinary impact on minimum (D_{min}) and maximum (D_{max}) density, with maximal explained variances reaching 47.4% and 39.1%, respectively. D_{min} was negatively associated to water availability during the initiation of earlywood formation, whereas D_{max} responded positively to water availability during two distinct periods: previous winter and the initiation of latewood formation. IADFs in the latewood were quite common along the gradient, occurred in 21–51% of the rings, and responded to episodes of high rainfall and elevated temperature at different phases of latewood formation. Xylem traits identity outperformed site as a driver of climatic signal, revealing the potential of a multi-proxy approach to unveil multiple facets of the xylogenetic cycle. Cambial plasticity, i.e. the ability to adjust the xylogenesis rate and to arrest and resume cambial activity to exploit favorable climatic windows, was critical for *Pinus pinaster* to thrive within wide climatic envelopes. Nevertheless, the pervasive effect of water availability on all analyzed traits indicates that forthcoming reduced precipitation and increased evapotranspiration, as predicted by climate change models, will negatively impact *P. pinaster* secondary growth along its whole environmental range.

1. Introduction

Trees have a pivotal position in CO_2 dynamics, contributing with the largest fraction of photosynthesis in terrestrial ecosystems (Lal, 2008). Moreover, a significant fraction of the fixed carbon is converted into durable compounds and stored as xylem cell walls that act as a carbon reservoir. Higher temperatures and shifts in precipitation patterns associated to climate change will impact photosynthetic and respiratory rates (Frank et al., 2015, affecting carbon gain capacity, but also tree secondary growth (Granda et al., 2013), thus potentially modifying carbon storage patterns. These phenomena may disrupt the role of trees as CO_2 sinks (Frank et al., 2015), compromising this critical ecosystem service.

Understanding how climate constrains xylogenesis is critical to forecast whether trees will be able to provide carbon storage services under future climatic scenarios (IPCC, 2014). Deciphering factors limiting cambial activity along climatic gradients captures the adjustments of species to thrive in a wide range of environmental conditions, predicting its potential adaptive capacity to ongoing climatic change. Ideally, this information could be achieved by monitoring cambial activity of the species along environmental gradients (Camarero et al., 2010; Pérez-de-Lis et al., 2016b; Rossi et al., 2006). Nevertheless, long-term studies of xylem phenology are usually lacking (Antonucci et al., 2017). Information on cambial activity, however, can be mostly inferred by analysing the permanent imprint of cambial activity on xylem structure (Rossi et al., 2006; Fonti et al., 2010).

Abbreviations: D_{max}, maximum ring density; D_{min}, minimum ring density; EW, earlywood width; IADF, intra-annual density fluctuations; LW, latewood width; LW_{adj}, adjusted latewood index; PCA, Principal Component Analysis; RDA, Redundancy Analysis; RW, tree-ring width; SPEI, Standardized Precipitation Evapotranspiration Index

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Ring-width series are routinely used to analyze the effects of climate on cambial activity, including their spatio-temporal dimensions (Fonti et al., 2010). Xylem structure stores additional information to tree-ring width (Speer, 2012). Therefore, multi-proxy approaches, including several xylem traits, may improve our insight on the factors controlling cambial activity (Cleaveland, 1986; Olano et al., 2012; Vaganov et al., 2009). Wood density integrates xylem anatomical traits related to mechanical strength, water transport and carbon storage capacities (Chave et al., 2009), with changes in density mirroring climate variability (Camarero et al., 2014; Rosner et al., 2014). Abrupt intra-annual changes in wood density, namely intra-annual density fluctuations (IADF) – also termed as false rings, double rings or multiple rings (Rigling et al., 2001) – echo sharp changes in weather at an intra-annual level (Fritts, 1976; Schweingruber, 1988). IADFs reveal short-term variation in the pace of xylem formation (De Micco et al., 2007), thus providing information on environmental cues on the cambial activity at intra-annual scale (Olano et al., 2015; Zalloni et al., 2016).

In this work, we explored the climatic factors constraining *Pinus pinaster* Ait. cambial activity along a 300 km latitudinal climatic (precipitation and temperature) gradient comprising a significant portion of this species environmental range. *P. pinaster* is a species of interest, since it inhabits a wide diversity of climatic and environmental conditions, from nearly frost-free areas under Atlantic climates with high water availability to Mediterranean continental climates with strong summer drought and long frost periods.

We analyzed the effect of climatic factors through multiple anatomical proxies of cambial activity. We included tree-ring width at annual (ring) and intra-annual (earlywood and latewood) time scales. We also evaluated the climatic control of wood density, including not only the commonly studied maximum wood density (Vaganov et al., 2011), but also minimum density that may have a strong climatic signal of spring conditions in drought-constrained environments (Camarero et al., 2014; Cleaveland, 1986). Finally, we evaluated the occurrence of different types of IADFs (Rozas et al., 2011; Zalloni et al., 2016), reflecting the potential of *P. pinaster* to adjust its cambial activity to changing climatic conditions at both inter- and intra-annual levels.

We hypothesized that water availability would be the major climatic factor constraining *P. pinaster* cambial activity along the climatic gradient with the effect of water limitation permeating all analyzed tree rings traits (Olano et al., 2014). A plastic response of cambial activity would allow encompass to the range of climatic conditions along the gradient by adjusting its timing to benefit from favorable periods. Finally, we explored the potential of microdensitometric time series as climatic proxies in Atlantic and Mediterranean environments.

2. Materials and methods

2.1. Study area and study species

We sampled four *Pinus pinaster* forest sites along a 300 km North-South gradient of increasing elevation, continentality and summer drought stress in Northern Spain, ranging from oceanic climate conditions at the Spanish Cantabrian Coast to continental climate at the Central Iberian Range (Fig. 1). First site was located at 33 m asl in the Cantabrian Coast (S1, Azkorri, Bizkaia, 43°22'40"N, 3° 0'42"W), with a mean annual temperature of 14.4 °C and a total annual precipitation of 1183 mm, on parent rock of Cretaceous flysch. Second site was located at 750 m asl in the Alto Ebro (S2, Oña, Burgos; 42°45'39"N, 3°25'58"W), with a mean annual temperature of 11.9 °C and a total annual precipitation of 663 mm, on parent rock of Cretaceous sandstone. Third site was located at 1030 m asl in the Alto Duero (S3, Tardelcuende, Soria; 41°36'6"N,2°38'14"W), with a mean annual temperature of 10.7 °C and a total annual precipitation of 519 mm, on parent rock of Cenozoic sandstone. Fourth site was located at 1143 m asl in the Alto Tajo (S4, Corduente, Guadalajara; 40°49'49"N, 2° 0'27"W), with a mean annual temperature of 10.3 °C and a total annual precipitation of 490 mm, on parent rock of Triassic sandstone. Climate data were obtained from the nearest meteorological station to each site for the period 1961–2015 from AEMET (Spanish Meteorological Agency) network (see Supplementary Table 1 for further details).

Pinus pinaster is an evergreen conifer endemic to the Western Mediterranean basin inhabiting humid and sub-humid areas. It prefers acidic soils, but occasionally can grow on basic soils, with a large altitudinal distribution range from sea level to 2000 m asl (Abad Viñas et al., 2016). It is a species of major conservational and productive interest in the Iberian Peninsula that is widely used for forest restoration, wood production and resin extraction (Calama et al., 2010). *P. pinaster* secondary growth is mainly promoted by spring and early summer precipitation (Bogino and Bravo, 2008), while IADF formation is mainly linked to autumn precipitation (Vieira et al., 2010), being IADF occurring mostly in the latewood (Campelo et al., 2007; Vieira et al., 2009).

2.2. Sampling design, tree-ring width measuring and processing

We sampled twenty mature dominant or co-dominant trees (between 45 and 126 years old) at each site in February 2016. Three wood cores were taken at breast height from each stem with a 5-mm diameter increment borer. Cores were labeled and taken to the laboratory. A core per tree was reserved for microdensitometrical analysis and the other two cores were air dried and mounted on wooden supports for their processing using standard dendrochronological techniques. Cores were manually surfaced and polished with a series of progressively finer grades of sandpaper until the xylem cellular structure was clearly visible under magnification.

After visual cross-dating, tree-ring (RW), earlywood (EW) and latewood widths (LW) were measured to the nearest 0.001 mm by using a sliding stage micrometer (Velmex, Inc., USA) interfaced with a computer. Cross-dating accuracy was checked using the software COFECHA (Grissino-Mayer, 2001). Each individual raw series for measured parameter was standardized using the software ARSTAN (Cook and Holmes, 1996). Raw series were fitted to a spline function with a 50% frequency response of 32 years, which was flexible enough to reduce the non-climatic variance while preserving high-frequency climatic information (Cook and Peters, 1981), albeit long-term climatic effects are removed. EW and LW chronologies were highly correlated (reaching a maximum of $r = 0.55$; $P < .001$ in S4) reflecting common constraints and the effect of earlywood conductance on latewood growth (Pérez-de-Lis et al., 2016a; von Arx et al., 2017). Therefore, we removed the dependence of LW on EW (Babst et al., 2016), by extracting the residuals of the regression between LW and EW and dividing them by the predicted value. This procedure provided an adjusted latewood index (LW_{adj}) (Meko and Baisan, 2001) that was independent of EW chronology (Stahle et al., 2009).

2.3. Intra-annual wood density fluctuations (IADFs)

Cross-dated cores were visually analyzed under magnification for IADF identification. In accordance to their position within the tree-ring, IADFs were classified into three types (Fig. 2). IADFs type E were characterized as a latewood-like cells band within the earlywood. IADFs types L and L+ were defined as earlywood-like cells band within the latewood (L) and between latewood and earlywood of the following ring (L+) (Vieira et al., 2009). The relative proportion of IADFs occurrence was estimated as the relative frequency (F) as $F = (n_x/N) \times 100$, where n_x is the total number of cores with IADFs in the year x, and N is the total number of cores in that particular year. The IADFs type E were very scarce in almost all the sites and then were discarded for further analysis.