Forest Ecology and Management 425 (2018) 126–137

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Earlywood vessels and latewood width explain the role of climate on wood formation of *Quercus pyrenaica* Willd. across the Atlantic-Mediterranean boundary in NW Iberia

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ARTICLE INFO

Keywords:
Climate-growth relationships
Dendrochronology
Distribution boundary
Earlywood vessels
Quantitative wood anatomy
Quercus pyrenaica

ABSTRACT

Quercus pyrenaica is one of the most widespread species in pure or mixed stands across the Iberian Peninsula. It mostly occurs in mountain areas within the Mediterranean region, but also dominates forests along the boundary to the Atlantic northern Iberia. Given this role as a transitional species, the understanding of its behavior is of great relevance in a context of climate change.

We analyzed five *Q. pyrenaica* stands in northwestern Iberia, located along a transect of increasing elevation in the Atlantic/Mediterranean biogeographical boundary. Tree-ring chronologies were obtained by measuring the earlywood vessel size, and the radial increment on a representative number of trees. Three variables were used, namely (i) the hydraulically-weighted diameter for the earlywood vessels in the first row (D_H-r1), (ii) for vessels outside this row (D_H-nr1), and (iii) the latewood width (LW). Variable chronologies were compared to monthly meteorological records, and to the North Atlantic Oscillation index (NAO).

LW variation was controlled by water availability during late spring-early summer all throughout the study area, but differences among sites were mostly driven by the presence of abrupt growth changes linked to forest disturbance regime. In contrast, earlywood responses were modulated by the topographic position. The three low-elevation sites, located at windward of a central mountain range, were related to environmental conditions during quiescence, whereas the two others responded at the moment of wood formation; D_H-r1 was more controlled by climate than D_H-nr1. The close association between NAO and vessel size was in accordance with the elevation gradient.

Our results showed relevant signals related to micro-, meso-, and macroclimatic conditions, and pointed out to the existence of cause-effect relationships. Therefore, the combined time-series analysis of earlywood vessels and latewood increment is a powerful tool to understand the ecological behavior of marcescent oaks in marginal populations, which often dominate transitional areas.

1. Introduction

The deciduous oak species *Quercus pyrenaica* has its natural distribution area in the Iberian Peninsula, southwestern France, and northern Morocco (Amaral Franco, 1990). In Iberia, it is one of the most widespread tree species, and mainly occurs on siliceous soils within western mountain regions (Sánchez-de-Dios et al., 2009). This species usually dominates areas with a subhumid to humid precipitation regime, but supports a considerable summer water deficit (Hernández-Santana et al., 2008). It is the most abundant deciduous tree under continental Mediterranean climate (Hernández-Santana et al., 2009), and it usually forms monospecific stands, which have been traditionally managed as coppice or silvopastoral systems (Gea-Izquierdo and Cañellas, 2014).

The short growing season is one of the main ecophysiological adaptations of *Q. pyrenaica*, which can span for less than six months, because it is well-adapted to avoid late frosts, and therefore most of the early phenological events are delayed. This length of the growing season can limit its geographic distribution area (Rico et al., 1996). Furthermore, it belongs to the so-called ‘marcescent’ oaks, i.e., deciduous oaks that maintain their dry leaves for most of the winter, which constitutes an ecological adaptation to the special conditions of sub-Mediterranean areas (Sánchez-de-Dios et al., 2009). These are boundary territories between the Eurosiberian and Mediterranean

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https://doi.org/10.1016/j.foreco.2018.05.042
Received 5 April 2018; Received in revised form 16 May 2018; Accepted 17 May 2018

vegetation (Rivas-Martínez et al., 2001). Due to this transitional position, *Q. pyrenaica* is one of the species whose distribution area could be potentially modified under a climate change scenario as it could replace other temperate oaks if summer drought increases (Sánchez-de-Dios et al., 2009).

Understanding its ecophysiological requirements is essential to anticipate the future performance of Iberian forests, as it could affect the distribution of other tree species. Despite its abundance, *Q. pyrenaica* has been poorly studied, with only a few investigations about stomatal responses and water use efficiency (Hernández-Santana et al., 2009; Rico et al., 1996), floristic studies (Díaz-Maroto and Vila-Lameiro, 2007), or dendrochronological analyses (Gea-Izquierdo and Cañellas, 2014; González-González et al., 2014; González-González et al., 2015).

The use of quantitative anatomical parameters measured annually across sequences of tree rings is one of the most promising tools to study the potential effects of global change on tree performance (Fonti et al., 2010). Among these, the size of the earlywood vessels of ring-porous trees proved to have a strong and reliable relationship to climate (Fonti et al., 2007; Gea-Izquierdo and Cañellas, 2014), even in areas where 'classic' dendrochronology does not perform well, such as mesic regions (Fonti and García-González, 2008). Thus, time series of earlywood vessels of *Q. pyrenaica* were successfully used to study climatic responses (González-González et al., 2014; González-González et al., 2015), as well as those of other sub-Mediterranean oaks such as *Q. canariensis* Willd. (Gea-Izquierdo et al., 2012) or *Q. faginea* Lam. (Corcuera et al., 2004). In a comparative study in the Cantabrian Mountains, González-González et al. (2014) found that the earlywood vessels of *Q. pyrenaica* appeared to be very plastic at adapting to environmental conditions, and hypothesized that this should be an advantage to cope with climate change, as compared to other oaks such as *Q. petraea* (Matt.) Liebl. Pérez-de-Lis et al. (2016b) confirmed the delayed phenology of *Q. pyrenaica* in regard to *Q. robur* along a gradient in northwestern Spain, and also found differences in wood formation dynamics, whereby growing season length was shorter for *Q. pyrenaica*, and unrelated to vessel size.

Q. pyrenaica has ecophysiological strategies that are different from those of temperate oaks, which indicate more drought stress-tolerance. For example, Pardos et al. (2004) showed that *Q. pyrenaica* seedlings had a much more efficient osmoregulation than those of *Q. petraea*, and Rodríguez-Calcerrada et al. (2008) observed that it performed more efficiently in environments with a high light availability.

In this paper, we use dendrochronology to analyze the earlywood vessels and radial increment of *Q. pyrenaica*, along an altitudinal transect in northwestern Iberia. We study five stands on the boundary between the Atlantic and Mediterranean regions, which involve most of the altitudinal range of the species, as well as different climatic characteristics and disturbance regimes. Our main objective is to identify the most relevant environmental factors that influence radial growth across this transitional area.

2. Materials and methods

2.1. Study area and sites

We sampled five *Q. pyrenaica* stands at its northern distribution boundary in the Mediterranean region in NW Spain. The study sites are located along a NW-E increasing elevation transect, within a mountain range between 42.04–42.48°N and 7.10–7.63°W (Fig. 1a), which covers the whole altitudinal range of this oak in the area. The stands represent a wide range of environmental conditions and disturbance regimes, so they should not be considered as a proper gradient. The lowest sites, A-1 and A-2, are respectively located within and at the edge of a Tertiary basin, not exceeding 350 m asl., dominated by fluvial sedimentary materials. A-3 lies on the northern slope of a mountain range facing the basin, and these three sites are separated from B-4 and B-5 by a granitic massif with peaks reaching 2000 m asl.

Climate is dominated by an Atlantic precipitation regime, but with a remarkable seasonality that leads to Mediterranean conditions during summer (Fig. 1b). Thus, rainfall is abundant (900–1200 mm), and mainly concentrated in autumn and winter, but there is a remarkable summer drought, especially towards the lowland Tertiary basin, where temperature considerably raises. The inland location of the stands involves continentality, whereas altitude and orography are responsible for significant differences in rainfall and temperature patterns among stands (Table 1).

Sites are close to the boundary between the Eurosiberian and Mediterranean biogeographical regions, with all but A-3 clearly located within the latter (Rivas-Martínez et al., 2001). Most sampled woodlands are humid oak forests dominated by *Q. pyrenaica* occurring at the transition to the Mediterranean region, and only B-4 bears more xeric characteristics. The lower stands were traditionally coppiced in the past, or replaced by farmlands and recent conifer reforestations. Consequently, the only natural forests available nowadays at these locations originate from land abandonment, and are often young.

A-1 and A-2 are mixed woodlands of *Q. pyrenaica* and *Q. robur* L. on a gentle slope facing south, and a deep and fertile soil. Human pressure is notable, so that the understory includes species such as *Cytisus scoparius* (L.) Link, and thermophile species as *Ruscus aculeatus* L. A-1 is a young and dense forest on a fluvial terrace, with few old trees on the deepest area. A-2 is a small and sparse woodland with medium-sized trees, and old oaks on the edges, surrounded by younger oak forests from natural regeneration and meadows, on a soil prone to flooding.

The mid-elevation site A-3 is located on a slope facing north-east at windward of a mountain range, which causes a high local rainfall, and considerably moister conditions than at the other sites. Local microtopography facilitates the occurrence of seasonal watercourses with abundance of *Q. robur*, and old chestnuts (*Castanea sativa* Mill.), silviculturally managed in the past. However, sampling was restricted to the least moist area of the hillside, a managed monospecific forest of medium-sized *Q. pyrenaica* trees on a deep soil, with thermophile species as *Ruscus aculeatus* or *Genista falcata* Brot.

B-4 is situated on a moderate east-facing slope, close to a river reservoir, which increases the frequency of fogs. It is a high-density monospecific woodland, with understory of *Prunus avium* L., *Crataegus monogyna* Jacq. and *Genista falcata*. A few old *Castanea sativa* trees for a former plantation and stumps from occasional fuelwood extraction are the only evidences of recent human activity.

The highest site B-5 faces north on a moderate slope of a narrow and elongated valley; despite a watercourse at the valley bottom, there is no evidence of soil water accumulation. The woodland is monospecific, with medium-sized trees, and a shrub understory of *Erica australis* L. It is not managed at present, but logging and occasional fires occurred in the recent past.

2.2. Sampling, processing, and anatomical measurements

We sampled 15 to 20 dominant trees at each site, extracting at least two 5-mm increment cores at breast height per tree. Cores were air-dried, glued onto wooden supports, and prepared for an optimal visualization of tree rings and vessels. Samples were first surfaced using a WSL sliding microtome (Gärtner and Nievergelt, 2010), but a further polishing with progressively finer sandpaper (grain sizes from P220 to P1200, FEPA Abrasives) was necessary to completely remove knife spurs. Tyloses and wood dust inside vessel lumina were removed using high-pressure water blast, dry samples stained with black printer ink, and earlywood vessels filled with chalk, thus achieving an optimal contrast for image analysis (Fig. 2).

We measured earlywood width (EW) and latewood width (LW) to the nearest 0.001 mm in each tree ring, using a tree-ring measuring linear stage (Velmex TA UniSlide, Velmex Inc., Bloomfield NY, USA) coupled to a binocular microscope (Olympus SZ60) at 20–40× magnification. The boundary between earlywood and latewood was set