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Summer drought and ENSO-related cloudiness distinctly drive *Fagus sylvatica* growth near the species rear-edge in northern Spain

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A B S T R A C T

The ample distribution of common beech (*Fagus sylvatica*) across Europe implies that this key tree species occurs under a broad variety of climatic conditions despite its sensitivity to drought stress. Iberian beech rear-edge (southernmost) forests are located along the boundary between the Eurosiberian and Mediterranean biogeographical regions. Therefore, those forests are considered to be sensitive monitors of the effects of warming-induced drought stress on marginal tree populations. We evaluate if the radial growth of Iberian beech populations is mainly constrained by drought. Since previous findings indicated that El Niño-Southern Oscillation (ENSO) teleconnections may influence the rainfall regime in northern Spain, we also assessed if beech response to drought and water availability is modulated by this large-scale climatic pattern. We compared the recent growth patterns and responses to climate across a network of 30 tree-ring site chronologies established throughout northern Spain where beech forests are subjected to contrasting climatic conditions. Iberian beech populations located near or within the Mediterranean biogeographical region were the most sensitive to June water deficit. However, the dependency of beech growth on drought stress near the rear-edge of the species was mitigated where cloudy conditions prevail in summer, namely in mesic stands located in the Eurosiberian region. Drought stress in the latter populations was alleviated by cloudiness, which in turn depended on ENSO, and this effect on growth has been intensifying for the last decades. We prove that the sensitivity of rear-edge populations to drought, in terms of growth reduction, is greatly modulated by local or regional environmental gradients, but also by the influence of large-scale climatic variation.

1. Introduction

Common beech (*Fagus sylvatica* L.) is one of the most widely distributed tree species over European forests. This highly-competitive, late-successional, deciduous hardwood tree species shows a wide tolerance to climatic conditions, growing under continental, sub-boreal, oceanic and sub-Mediterranean climates, but usually requires a humid atmosphere and a well-drained soil (Fang and Lechowicz, 2006). *F. sylvatica* forms pure or mixed stands over large areas, and therefore it is considered a key species since its forests contain a high biodiversity and they encompass a wide range of habitat types at elevations ranging from sea level to the upper tree line (von Wuehlisch, 2008; Packham et al., 2012).

Beech is also known to be sensitive to water deficit mainly due to its vulnerability to xylem cavitation leading to a loss in hydraulic conductivity and enhanced tree mortality under severe drought conditions (Herbette et al., 2010; Barigah et al., 2013). In fact, the geographical distribution of this species depends on its low tolerance to summer drought, being therefore abundant at sites with sub-oceanic and temperate climates, i.e. subjected to cool and mesic conditions (Giesecke et al., 2007; Bradshaw et al., 2010). In the Mediterranean Basin, *F. sylvatica* grows in mountain areas where rainfall is high enough, just barely within the limit of its requirements (Fotelli et al., 2009). On the other hand, low temperatures that induce late frosts and shorten the length of the growing season determine the upper altitudinal, northern latitudinal and eastern longitudinal limits of distribution of the species (Bolte et al., 2007; Maxime and Hendrik, 2011).

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Much research has recently focused on the mechanisms of *F. sylvatica* drought tolerance either by studying saplings in provenance trials or by sampling adults living in rear-edge populations, i.e. stands forming the southernmost or xeric limit of distribution (Aranda et al., 2000; Nahm et al., 2006; Jump et al., 2007; Meier and Leuschner, 2008; Rose et al., 2009; Pluess and Weber, 2012; Robson et al., 2013). This research has stimulated an active debate on the future performance of rear-edge *F. sylvatica* forests under the prospect of a drier and warmer climate (e.g., Gessler et al., 2007; Kramer et al., 2010; Meier et al., 2011).

From a dendrochronological perspective, adult *F. sylvatica* trees have been relatively well studied with networks of tree-ring chronologies developed in central, southern, western and northern European forests (Dittmar et al., 2003; Lebourgeois et al., 2005; Piovesan et al., 2005; Di Filippo et al., 2007; Friedrichs et al., 2009; Drobyshev et al., 2010; Babst et al., 2013; Tegel et al., 2014). Several studies showed coherent geographic patterns in the tree-ring growth response to climate, but these also depend upon local environmental gradients modulated by altitude or latitude (Piovesan et al., 2005; Di Filippo et al., 2007). For instance, analyses of *F. sylvatica* tree-ring width chronologies from southwestern Europe have shown that May temperature and water availability in summer, together with the amount of winter precipitation, are the major drivers of radial growth (Biondi, 1993; Piovesan et al., 2005; Lebourgeois et al., 2005). On the other side, drought is the major constraint of growth near the *F. sylvatica* southwestern range boundary in northern Spain (Gutiérrez, 1988; Rozas, 2001; Jump et al., 2007).

Growth dynamics of western European *F. sylvatica* forests may also reflect large-scale atmospheric circulation patterns, as was the case for the Northern Atlantic Oscillation (NAO) in Italy (Piovesan and Schirone, 2000). In the Iberian Peninsula, climate and hydrological conditions are transitional between Atlantic influences westwards and Mediterranean influences eastwards, being therefore not only influenced by the NAO but also by other atmospheric dynamics operating at large distances (teleconnection) like the El Niño-Southern Oscillation (ENSO) (Rodó et al., 1997; Knippertz et al., 2003; Pozo-Vázquez et al., 2005). In fact, ENSO represents the strongest interannual variation of Earth's climate affecting a wide range of geographic areas (Stenseth et al., 2003), but we still do not know how ENSO affects the long-term growth of rear-edge Iberian *F. sylvatica* forests. We hypothesize that *F. sylvatica* growth in the Iberian Peninsula is (i) mainly constrained by water scarcity across regional and local geographical gradients, and (ii) such drought response is modulated by the ENSO variability, as it has been recently found for other tree species in Spain (Rozas and García-González, 2012a, Rozas and García-González, 2012b). In this work, we tested both hypotheses by comparing growth responses to climate across a network of tree-ring chronologies established throughout northern Spain where *F. sylvatica* forests are subjected to diverse climatic conditions. These rear-edge populations represent the southwestern distribution limit of the species, being located along the boundary between the Eurosiberian and Mediterranean biogeographical regions. Therefore, they are considered sensitive forests potentially recording the effects of ongoing warming and drying trends on tree populations.

2. Materials and methods

2.1. Study area

We sampled 30 forest stands located along a wide area in northern Spain, at the southwestern boundary of the species range (Fig. 1a), ranging from 42.10°N to 43.43°N, and from 0.37°W to 7.07°W. Sites were distributed along a broad elevation range between 140 and 1400 m a.s.l. (Table 1), which covers the complete elevation range of *F. sylvatica* in the study region, even if the upper forest limit is mainly due to historical deforestation of mountain areas for pasture. Sampled stands were more abundant in the central Cantabrian area, including lowland mixed deciduous stands (Supplementary material, Fig. S1a), as well as monospecific stands on littoral mountains and on the Cantabrian Range (Fig. S1b). In addition, pure or mixed stands were also sampled on the western Cantabrian Range, Galician mountains, mountains of Álava and Navarra, Iberian Range, pre-Pyrenean mountains, and the western Pyrenees including sites located in the Eurosiberian and Mediterranean regions, and also in transitional areas (Fig. 1b). Associated tree species in the Cantabrian area were mainly deciduous oaks (*Quercus robur*, *Q. petraea*, *Q. pyrenaica*), and other species such as *Fraxinus excelsior*, *Acer campestre*, *Acer pseudoplatanus* or *Taxus baccata* (Table 1). In the pre-Pyrenees, however, the main co-dominant species was *Pinus sylvestris* (Fig. S1c), and *Abies alba* in the Pyrenees (Fig. S1d). A considerable diversity of habitats occupied by *F. sylvatica* in northern Spain were included in our sampling, with abundant representation of western Cantabrian acidofilous, sub-humid neutrophilous oro-Cantabrian, and sub-Mediterranean calcicolous *F. sylvatica* forests (Table 1).

F. sylvatica forests in the Cantabrian area are mainly associated with foggy conditions, under the influence of wet winds from the Cantabrian Sea. These stands occur in lowland hilly areas (Fig. S1e), and on northern-faced mountain slopes (Fig. S1f). There, soils were mainly deep brown on slightly acidic, neutral or basic bedrock, even if some study stands were located on calcium-rich karst plateaus (e.g., sites CUE and URB).

The climate in the study area is diverse, varying from temperate humid Atlantic conditions without a dry period westwards or northwards, to sub-humid Mediterranean conditions with a marked summer drought eastwards or southwards (Fig. 1). The majority of stands were located within the Eurosiberian biogeographical region, but eleven stands were near the Eurosiberian-Mediterranean boundary (FON, LIN, SIS, ZAN, VAL, HIJ, IZK, URB, LUE, PEI, MON), and one stand from the Iberian Range (DIU) was located well within the Mediterranean Region (Fig. 1b). This referred boundary between Eurosiberian and Mediterranean biogeographical regions in the northern Iberian Peninsula is based on both bioclimatic and botanical criteria (Rivas-Martínez et al., 2002). The climate in the Cantabrian and Pyrenean Ranges is humid temperate, with a mean annual precipitation ranging from 930 to 1945 mm, and a mean annual temperature of 8.3 to 10.2 °C. In the mountains of Álava and Navarra, there are transitional conditions between Atlantic and Mediterranean climates, with mean annual precipitation of over 900 mm and around 9.8 °C in mean annual temperature. A dry period in summer, mainly in July and August, was evident in the Galician mountains and the western Cantabrian Range (Fig. 1). Dry summer was more remarkable under Mediterranean climate conditions in the pre-Pyrenees, but also in the Iberian Range (site DIU) where the climate is continental Mediterranean, with a mean annual precipitation of over 660–670 mm, and a mean annual temperature of 10.6 to 11.9 °C.

2.2. Field sampling, sample processing and tree-ring measuring

Most of the sampled stands were selected in protected areas (e.g., Regional and National Parks) preferentially without signs of recent human disturbance. Latitude and longitude, elevation, dominant tree species, and European Nature Information System (EUNIS) habitat type (Davies et al., 2004; http://eunis.eea.europa.eu/habitats.jsp) were recorded for every sampled stand. We randomly chose six to 43 dominant or co-dominant trees at each stand, separated by at least 10 m, for sampling between 1998 and 2012. We collected two wood cores per tree, along