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Aleppo pine forests from across Spain show drought-induced growth decline and partial recovery

Antonio Gazol [a,*], Montserrat Ribas [b], Emilia Gutiérrez [b], J. Julio Camarero [a]

[a] Instituto Pirenaico de Ecología (IPE-CSIC), Avda Montañana 1005,E-50059 Zaragoza, Spain
[b] Dept. d'Ecologia, Universitat de Barcelona, Avda. Diagonal 645, E-08028 Barcelona, Spain

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ABSTRACT

Drought-induced growth decline is a phenomenon widely described in forests growing in regions subjected to seasonal water shortage such as the Mediterranean Basin. However, how tree species react to drought by modifying their growth pattern across the species distribution range is a question that remains to be answered.

We investigate this question using a network of 27 Aleppo pine forests distributed across the eastern Spain and encompassing diverse site characteristics and climatic conditions. Using dendrochronology we quantify the radial growth responses of this Mediterranean tree species in 1994–1995, when the most severe drought after 1950 affected the study area. We quantify the variation between trees and sites in terms of growth resilience to drought, i.e. the resistance to the drought event and the recovery after it. Then, we quantify the relationship of these responses to tree traits (tree diameter and height, tree age, sapwood area) at the individual tree level, and to site characteristics (climate conditions, stand structure–tree density, basal area and the presence of co-dominant tree species) at the site level.

We found that 1994–95 dry spell strongly impacted tree growth since 25 out of 27 sites and about 88% of trees showed a marked growth reduction of around 60% in radial growth. Climatic conditions were by far more important than tree traits on explaining resilience indices. In particular, the resistance to drought decreased with the increase in drought intensity, whereas the post-drought recovery was linked to site precipitation. Trees from dry sites were less resistant but recovered faster than trees from wet sites.

We demonstrate that the reaction of different tree populations to drought is structured according to local climate conditions. If droughts become more severe and frequent as predicted in the Mediterranean region where climate warming is forecasted, Aleppo pine stands growing in the driest regions will be increasingly more sensitive to intense dry spells.

1. Introduction

There is a consensus that drought is one of the most important factors triggering forest growth decline (Allen et al., 2010; Anderegg et al., 2013). The predicted climate warming will exacerbate the effects of droughts on Mediterranean forest ecosystems by making them more severe and frequent (Giorgi and Lionello, 2008). How these forests will respond to the projected temperature rising is an ongoing challenge. In this sense, it is expected that the forecasted aridification trend will translate into growth decline in drought-prone Mediterranean pine forests (Sarris et al., 2007). Hence, discovering how forests tree species resist drought events and recover after drought is becoming a major ecological issue (Cavin et al., 2013; Pretzsch et al., 2013; Valladares et al., 2015; Gazol and Camarero, 2016). Recently, it has been recognized that growth decline due to water shortage can be considered an early-warning signal of forest dieback (Camarero et al., 2015). Deciphering which factors determine growth resilience to drought, i.e. the resistance to a drought event and the recovery after it, could thus be fundamental to manage and preserve forests ecosystems in dry areas and to forecast their vulnerability to more arid conditions.

The response of a tree species to drought may depend on climatic and site characteristics (geographical location, topography, soils) across the species' distribution area (Pasho et al., 2011; Grossiord et al., 2014; Mölder and Leuschner, 2014; Gazol et al., 2015). However, forest responses to drought may also depend on

* Corresponding author.
E-mail addresses: agazol@ipe.csic.es, agazolbu@gmail.com (A. Gazol).

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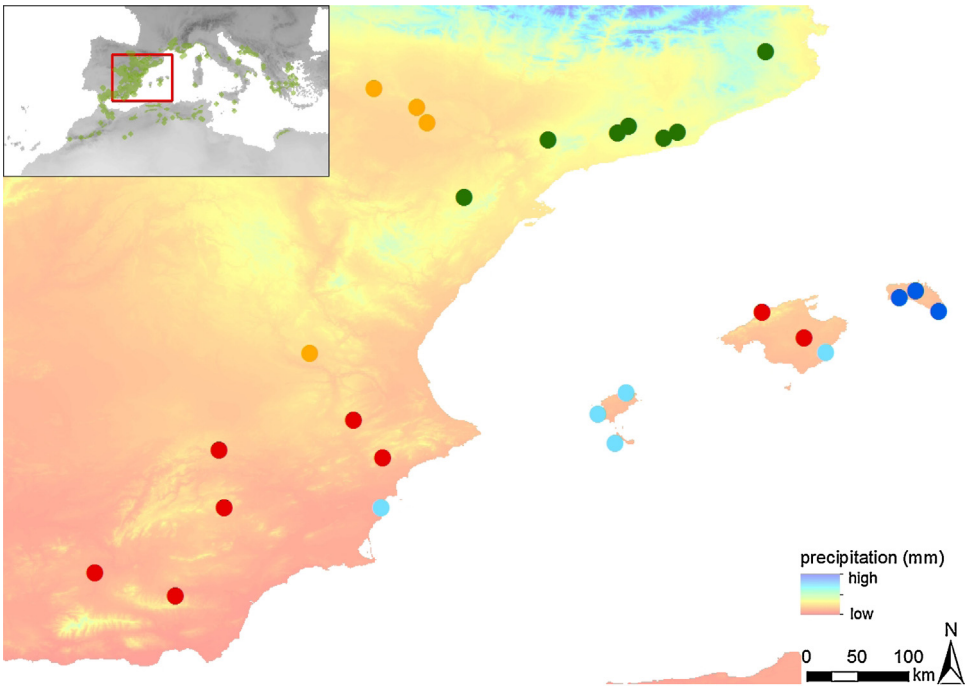

Fig. 1. Geographical distribution of the Aleppo pine populations studied in eastern Spain. A map showing the distribution of Aleppo pine in the Mediterranean Basin is also shown (upper inset, green area) with a square (red box) indicating the study area. The background color key of the map shows the precipitation of the driest quarter (Hijmans et al., 2005). Different colors indicate similarity in growth between the studied populations based on a cluster analyses calculated on the series of ring-width indexes for the 1949–1999 period. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

biotic characteristics such as intraspecific variability (including tree traits as size, age, etc.) and interspecific interactions between coexisting tree species (Lebourgeois et al., 2013; Delzon, 2015; Metz et al., 2015; Gazol and Camarero, 2016). In this sense, the hypothesis that more diverse (in terms of structure, age or composition) stands tolerate drought better than less diverse stands has been repeatedly tested during the last years (Grossiord et al., 2014). Nevertheless, few studies have considered Mediterranean pine forests where tree species diversity is low (Valladares et al., 2015). How forests respond to droughts across a species distribution range and which site factors and tree traits influence these responses can be a fundamental question to mitigate the consequences of aridification on Mediterranean pine forests (De Luis et al., 2013).

Pine woodlands cover at least 13 million hectares in the Mediterranean Basin, which represent about 5% of the forested area in the region (Barbéro et al., 1998). Aleppo pine (*Pinus halepensis* Mill.) is the most important tree species in the western Mediterranean Basin where it is dominant in the driest and warmest sites covering ca. 3.5 million hectares as reforestations and as natural stands (Ne'eman and Trabaud, 2000). Half of the natural coverage of Aleppo pine in the Mediterranean Basin corresponds to eastern Spanish forests which makes this species very important in providing ecosystem services in that area such as regulation of the carbon and water cycles (Gil et al., 1996). Aleppo pine can grow at different elevations and on different soil substrates leading to diverse water availabilities, but it usually displays several strategies to withstand drought, for instance by reducing wood-formation rates as water availability decreases (Ribas, 2006; De Luis et al., 2007; Camarero et al., 2010).

Evidence coming from dendrochronological studies indicates that Aleppo pine forests growth and productivity are sensitive to changes in water availability (Pasho et al., 2011; Novak et al., 2013; Del Castillo et al., 2015; Dorman et al., 2015a). This species is able to maximize carbon gain during the wet late winter and early spring before needle and stem growth start (Schiller, 2000; Maseyk et al., 2008). Particularly, cumulative precipitation from previous winter to spring of the growth year is a very important factor driving Aleppo pine secondary growth (Pasho et al., 2011). In this sense, severe drought events may result in widespread growth decline and local mortality episodes, the latter being usually observed in planted Aleppo pine stands of dry regions or in marginal populations under semi-arid conditions (Sánchez-Salguero et al., 2010; Dorman et al., 2015b,a). For instance, the drought which started in 1994 and ended in 1995 resulted in growth decline, widespread defoliation and a sharp reduction of productivity in many forests from eastern Spain (Peñuelas et al., 2001; Corcuera et al., 2004). This drought is considered as the most severe dry spell affecting eastern Spain during the second half of the 20th century (Peñuelas et al., 2001). Despite it is well known that growth and performance of Aleppo pine varies across the species distribution area (De Luis et al., 2013; Del Castillo et al., 2015), how tree individuals from different populations responded to an extreme drought as the 1994–1995 dry spell is not so clear.

Several studies have demonstrated that Aleppo pine growth sensitivity in response to water shortage varies across its distribution range (Pasho et al., 2011; De Luis et al., 2013). However, other studies suggest that despite important variations between tree populations and across regions, water shortage is the main constrain of Aleppo pine forests growth and productivity (Del Río et al., 2014). Given that this species presents a great plasticity in its growth responses to climate it is plausible to consider that it will display different responses to a severe drought event across its distribution range. Recently, Lloret et al. (2011) proposed three indexes to quantify the resilience of tree growth to drought based on the differences in growth before, during and after the drought event. These indexes decompose growth resilience to drought in three components: resistance to drought, recovery after drought and resilience.

In this study, we investigate how trees in 27 Aleppo pine populations distributed across the species distribution range in Spain responded to the 1994–1995 drought. In each site, we quantified annual basal area increment of dominant trees by using