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Contrasting growth and mortality responses to climate warming of two pine species in a continental Mediterranean ecosystem

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ABSTRACT

The long lifespan of trees makes them sensitive to climate warming, particularly when abrupt changes in climatic conditions occur and when trees are already growing near to their climatic tolerance thresholds. In many Mediterranean pine forests, drought stress induced by warmer temperatures and increased aridification compromise tree survival, causing growth decline and, eventually, triggering tree mortality. We evaluated the effect of climate on radial growth and mortality comparing dead and living trees of two pine species, *Pinus sylvestris* and *Pinus nigra* subsp. *salzmannii*, in a continental Mediterranean area over a 50-year long period. We used linear mixed models and correlations to evaluate the effect of climate on basal area increment (BAI) and on ring-width indices, respectively. In *P. nigra*, growth was enhanced by wet and cold conditions, whilst growth increased with temperatures in *P. sylvestris*. A gradual BAI reduction was detected in *P. nigra* trees since the late 1970s, becoming more pronounced in recently dead trees. Contrarily, *P. sylvestris* growth did not show such decline, whilst death events in this species were linked to severe and punctual droughts. Our findings show that warming and drought stress trigger contrasting responses in functionally and phylogenetically similar tree species, and suggest climate-mediated important changes on competitive dominance in Mediterranean forests.

1. Introduction

Many cases of forest dieback and tree mortality attributed to drought- or heat-induced stress have been described worldwide over the last decades (Allen et al., 2010, 2015). The long lifespan of trees prevents quick adaptation responses to environmental changes (Lindner et al., 2010), making forests especially vulnerable to climate-warming effects. In the Mediterranean Basin, a decrease of over 25–30% in annual precipitations is expected by the end of the 21st century, together with an increase in the frequency and intensity of dry spells (Beniston et al., 2007). The increase in the variability of precipitations will be likely accompanied by a rise of 4–5 °C in average annual temperatures (Christensen et al., 2007; Giorgi and Lionello, 2008) that could be even higher in mountainous areas (Meehl et al., 2007). Circum-Mediterranean tree populations located at the species' southernmost distribution limits and inhabiting areas prone to drought are particularly susceptible to drought-induced dieback (Sánchez-Salguero et al., 2012). Therefore, drought-induced dieback is expected to affect Mediterranean populations of many tree species, especially conifers showing a high vulnerability to drought-induced embolism such as Scots pine (Camarero et al., 2015b).

Variation in climatic conditions may lead to important changes in tree growth and survival thus altering forest structure and composition (Allen et al., 2010, 2015; Granda et al., 2013). Warm temperatures and reduced precipitation leading to drought stress can trigger tree defoliation and rise mortality rates of dominant trees above basal or background levels (McDowell et al., 2008). Moreover, the differential vulnerability of tree species to climate warming may amplify the changes in composition of forest communities (Valladares, 2008). As a consequence, there is a need to

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increase our understanding on forest dieback processes, and to identify which growth and climatic conditions lead to tree death (Bigler and Bugmann, 2004). This would allow promoting a more sustainable forest management under the ongoing climate change.

A decline in radial growth is a symptom usually associated to forest dieback that can be noticed either immediately during a drought period or several years later (McDowell et al., 2008), and such decline usually precedes tree death (Bigler et al., 2006, 2007). In fact, several studies have reported increases of death risk following a previous period characterized by reduced growth rates (Ogle et al., 2000; Suarez et al., 2004; Bigler et al., 2006). When drought is gradual and maintained over time, it can act in the long term (predisposing factor *sensu* Manion, 1981), progressively weakening the vigor of trees, reducing their growth rates and increasing their vulnerability to recurrent droughts (Tyree and Sperry, 1988; Bigler and Bugmann, 2004). Other factors such as extreme droughts act in the short term (inciting factor *sensu* Manion, 1981) by rapidly reducing the capacity of trees to recover after an acute reduction in water availability. These two types of factors interact with the so-called contribution factors, which are usually opportunistic or secondary pathogens affecting previously weakened trees (Gil Pelegrín et al., 2008; Hereş et al., 2014). Therefore, both long- and short-term reductions in tree growth as a consequence of climate warming and drought stress worsen the capacity of trees to cope with additional stress, increasing the death risk.

There is still a large degree of uncertainty on the patterns behind dieback processes in forests (Allen et al., 2015), including how this phenomenon differently affects tree species along environmental gradients. This is, among other reasons, because climate change induces physiological stress in different ways depending on functional traits like leaf phenology and wood type, and on the phenotypic plasticity of each tree species (Camarero et al., 2015a). For instance, pines are known to close stomata during drought periods to avoid water losses and embolism in the xylem, leading to a decrease in carbon assimilation and, thus, reducing growth and carbon availability (Tyree and Sperry, 1988). However, closely related pine species also respond in different ways to drought, with Scots pine (*Pinus sylvestris* L.) being identified among one of the most susceptible tree species to drought-induced dieback in Western Europe (Martínez-Vilalta and Piñol, 2002). In contrast, Mediterranean pine species as black pine (*Pinus nigra* Arn. subsp. *salzmannii* (Dunal) Franco) are better able to withstand drought stress (Sánchez-Salguero et al., 2012, 2015a), although cumulative water deficit constrains their growth in the long term (Linares and Tíscar, 2010). In addition, tree growth in continental Mediterranean areas is limited not only by summer drought, but also by winter coldness (Mitrakos, 1980; Camarero et al., 2010), which delays the start of the growing season and shortens the optimal period for tree growth in contrast with milder Mediterranean or wetter areas. Thus, the positive effect of increasing winter temperatures on growth in continental Mediterranean regions (Granda et al., 2013) could be counteracted or canceled out due to rising evapotranspiration rates during the growing season in spring and early summer leading to an exacerbated drought stress (Linares and Tíscar, 2010).

Here we evaluate the response of radial-growth patterns to climatic conditions of living and asymptomatic trees (*i.e.* not showing symptoms indicating they are prone to die such as severe defoliation) together with nearby, recently dead trees in two major pine species of Iberian forests showing dieback, namely Scots and black pine (*P. sylvestris* and *P. nigra* subsp. *salzmannii*, respectively). Since climatic factors determining growth shift along altitudinal gradients (Babst et al., 2013) we also evaluated radial growth patterns at different altitudes in the most widely distributed black pine. We aimed at answering three questions: (1) do growth patterns differ between asymptomatic living trees from those of recently dead trees? (2) How sensitive are the two pine species studied to drought? And (3) do growth patterns vary with altitude? We expected dead trees to show lower growth rates than asymptomatic trees for several years prior to death, since a diminishing growth in response to drought in a given year can affect growth of the following years due to legacy effects (Anderegg et al., 2013) including reduced conductivity and photosynthetic rates. Further, recurrent droughts could also deteriorate the hydraulic capacity of trees and cumulate stress over time. Given that the Iberian Peninsula represents the southernmost distribution limit of Scots pine, we also expected higher growth sensitivity to drought in Scots pine as compared to the Mediterranean black pine. Finally, since climatic conditions are colder and more humid at higher than at lower elevations in Mediterranean inland sites, we expected higher growth rates at higher elevations due to a reduced drought stress, and therefore a less evident growth decline prior to tree death.

2. Materials and methods

2.1. Study area and species

The study area is located in the "Alto Tajo" Natural Park (Guadalajara province, central Spain) (see Appendix 1). Soils are poorly developed on limestone and dolomite substrates, and the bedrock frequently outcrops (Carcavilla et al., 2008). Climate is continental Mediterranean, with warm and dry summers and cold winters (Table 1). This area is largely covered by pine, oak and juniper forests. Spanish black pine (*P. nigra* Arn. subsp. *salzmannii* (Dunal) Franco) covers a total of 21,826 ha, representing 11.9% of the Natural Park area (data obtained from the Spanish Forest Map on scale 1:50,000, MFE50; Banco de Datos de la Naturaleza, 2006). It is replaced by Scots pine (*P. sylvestris* L.) in colder and more humid places (25,161 ha, 13.7% of the area) and by Spanish juniper (*Juniperus thurifera* L.) in the most continental ones. The most abundant oak species are holm oak (*Quercus ilex* L. subsp. *ballota* (Desf.) Samp.) and Portuguese oak (*Quercus faginea* Lam.) (Ferrero et al., 2006). We selected two study sites, Peñalén and Buenafuente del Sistal, dominated respectively by Scots pine and black pine (Table 1). Additionally, we sampled at three different elevations in Buenafuente del Sistal to cover an altitudinal gradient for black pine.

In the Iberian Peninsula, the Scots pine appears in mesic and mountainous areas due to its relatively high water requirements (Richardson, 1998), whereas black pine dominates in Circum-Mediterranean mountainous areas and it is more drought tolerant than the Scots pine (Sánchez-Salguero et al., 2012).

2.2. Climatic data

To characterize the climatic conditions of the two study sites we used the Climatic Atlas of the Iberian Peninsula containing mean data for the 1951–1999 period (Ninyerola et al., 2005). Climatic characteristics at the different elevations at Buenafuente del Sistal site were also described by recording meteorological data *in situ* between 2007 and 2009 using three HOBO weather stations (model H21-001; Onset Computer Corporation, USA) (Table 1).

Monthly mean temperatures and total precipitation for the whole study area from 1951 to 2010 were obtained from the nearby Molina de Aragón meteorological station located at 28 km from the study sites (40°50′40″N, 1°53′07″W, 1063 m a.s.l., Spanish National Meteorological Agency, AEMET). Mean and total annual precipitations were calculated for the whole available period from August of the previous year (year $t-1$) to September of the