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Tree vigour influences secondary growth but not responsiveness to climatic variability in Holm oak

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ABSTRACT

Many tree species from Mediterranean regions have started to show increased rates of crown defoliation, reduced growth, and dieback associated with the increase in temperatures and changes in the frequency and intensity of drought events experienced during the last decades. In this regard, *Quercus ilex* L. *subsp. ballota* [Desf.] (Holm oak), despite being a drought-tolerant species widely distributed in the Mediterranean basin, it has recently started to show acute signs of decline, extended areas from Spain being affected. However, few studies have assessed the role of climatic variability (i.e., temperature, precipitation, and drought) on the decline and resilience of Holm oak. Here, we measured secondary growth of seventy Holm oaks from a coppice stand located in central Spain. Sampled trees had different stages of decline, so they were classified into four vigour groups considering their crown foliar lost: healthy (0%), low defoliated (< 25%), highly defoliated (25–70%), and dying (70–100%). Our results showed that during the study period (1980–2009) the highly defoliated and dying Holm oaks grew significantly less than their healthy and low defoliated neighbours, suggesting permanent growth reduction in the less vigorous individuals. Despite these differences, all four vigour groups showed similar responses to climatic variations, especially during winter and late spring – early summer seasons, and similar resilience after severe drought events, managing to significantly recover to pre-drought growth rates after only two years. Our findings, hence, illustrate that tree vigour influences secondary growth but not responsiveness to climatic variability in Holm oak. Still, as reduced growth rates are frequently associated with the process of tree mortality, we conclude that the less vigorous Holm oaks might not be able to cope with future water stress conditions, leading to increased mortality rates among this emblematic Mediterranean species.

1. Introduction

Tree decline is currently one of the main worrisome and studied issues in forest ecology worldwide (Allen et al., 2010; Carnicer et al., 2011), being mainly associated with increasing temperatures and changes in precipitation intensity and frequency (IPCC, 2014). In the last decades this phenomenon has affected all major forest biome types, and thus many conifer and broadleaf species, both evergreen and deciduous, independent of their sensitivity or tolerance to stressful climatic conditions (e.g., droughts) (see Allen et al., 2010). Tree decline leads to low ecosystem productivity, changes in species distribution, and altered forest succession, finally affecting all forest ecosystem services (Anderegg et al., 2013). Thus, to minimize and prevent such changes, identifying the causes that underlie forest vulnerability and decline (e.g., defoliation, growth reduction, dieback), and how these ecosystems respond to changes in climatic conditions, have become of upmost importance.

Tree rings have been recognized as good predictors of increased vulnerability, decline, and stress-induced mortality events. For instance, studies like Hereş et al. (2012) or Cailleret et al. (2017) have identified that long-term decreases in radial growth rates precede tree mortality events. However, in Cailleret et al. (2017) the authors also

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highlighted that mortality can be preceded by quick growth declines, or even by increased growth rates, with different patterns varying among tree species and drought tolerance-strategies. As a consequence, species-specific studies are needed to better identify the causes that underlie forest vulnerability and decline.

Mediterranean regions, where water availability is the main limiting factor for plant growth (Cherubini et al., 2003; Martínez-Vilalta et al., 2008), are considered to be especially vulnerable to increased temperature and changes in the frequency and intensity of drought events (Giorgi and Lionello, 2008; IPCC, 2014). In the Iberian Peninsula, where predicted climatic conditions are already felt (Kovats et al., 2014), many tree species have started to show alarming signs of decline and dieback in the last decades (Peñuelas et al., 2000; Martínez-Vilalta and Piñol, 2002; Camarero et al., 2015a; Hereş et al., 2012; Natalini et al., 2016). Affected tree species include those that reach their southernmost distribution limits in the Iberian Peninsula (e.g., *Pinus sylvestris* L.), and that are considered to be particularly vulnerable to conditions induced by climate change (e.g., droughts), but also species well adapted to dry conditions and widely distributed in the Iberian Peninsula such as the Holm oak (*Quercus ilex* L. *subsp. ballota* [Desf.]).

Holm oak is an evergreen tree species, usually retaining its leaves up to three years (Montserrat-Martí et al., 2009). Its distribution covers western Iberia and North Africa (Rodá et al., 1999), dominating areas with continental Mediterranean conditions (Blanco et al., 1997). Almost 60% of all Holm oak areas are located in Spain (Corcuera et al., 2004), where this species forms natural forests or dehesa ecosystems, playing thus an important role from an environmental and socio-economic point of view (Patón et al., 2009). From all areas covered by Holm oak in Spain, it is estimated that almost 44% of them are coppice stands (see Corcuera et al., 2004 and references therein). Holm oaks tolerate thermal stress and precipitation variability (Gratani, 1996), conditions that are characteristic for the continental Mediterranean climate, being considered a species that can endure both winter frost and summer drought (Terradas and Savé, 1992; Martínez-Vilalta et al., 2002; Montserrat-Martí et al., 2009). Despite the drought-tolerant strategy provided by evergreenness and narrow vessels in the diffuse-to semi-ring-porous wood (Corcuera et al., 2004), this species has recently started to show acute signs of decline (i.e., wilting of leaves, defoliation, growth reduction, dieback, etc.), with extensive affected areas (Brasier, 1996; Gea-Izquierdo et al., 2011; Navarro, 2011; Natalini et al., 2016). Climatic stress (e.g., drought) plays an important role in the decline of this tree species (Gea-Izquierdo et al., 2011; Granda et al., 2013; Camarero et al., 2015b; Camarero et al., 2016; Natalini et al., 2016), as well as other factors such as the pathogenic oomycete *Phytophthora cinnamomi*, and intense management practices (see Natalini et al., 2016 and references therein).

The main objective of this study was to assess the role of climatic variability (i.e., temperature, precipitation, and drought) on the decline and resilience of Holm oak trees growing in a coppice stand located in central Spain. We used tree-ring chronologies that provide retrospective precise temporal insights into the climate-growth relationships of woody plants (Fritts, 1976), and allow comparison on long-term growth rates between trees at different stages of decline. Specifically, we studied Holm oak trees growing in a coppice stand that were classified into four vigour groups depending on their level of defoliation (% of crown foliar lost; used here as a proxy to define the level of decline of the studied trees), with the aim to: *i*) study potential differences in historical growth rates between trees of contrasting defoliation levels; ii) assess whether early signs of growth decline or abrupt growth changes may be identified in less vigorous trees; *iii*) analyse the annual and seasonal climatic influence on the growth of these Holm oaks growing in a coppice stand; and *iv*) evaluate the response of these trees during and after severe drought events.

2. Materials and methods

2.1. Study area

The study area hosts Holm oaks at varying stages of defoliation (between 0 and 100% of crown foliar lost). Tree-ring samples and site data were collected from two coppice stands separated by < 5 km, situated between two localities from the centre of the Iberian Peninsula (Spain, Community of Madrid): Chapinería (40°23′03.4″N 4°11′37.8″W, ≈650 m a.s.l.) and Navas del Rey (40°23′55.80″N 4°14′26.70″W, ≈675 m a.s.l.). Holm oaks from Chapinería and Navas del Rey were treated as a single database as the two coppice stands are close, have similar abiotic and stand conditions, and no significant growth differences were found between the trees sampled in each of them (W = 1330, p = 0.433). The study area is characterized by a low tree density (≈180 trees ha^{-1}; Rodríguez et al., 2016). The overstory is dominated by Holm oak trees, with scarce *Juniperus oxycedrus* (Sibth. and Sm) present, while the understory is represented by shrubs (*Retama* sp., *Lavandula* sp., etc.) and herbaceous species (*Vulpia* sp., *Bromus* sp., *Xolantha* sp., etc.) (Rodríguez et al., 2016). The study area has been traditionally used for pasturage, hunting and logging, although in the last decades human use has been considerably reduced, and no signs of recent logging are observed. The soils have a pH of 6, are sandy upon fractured bedrock mainly formed by biotite granites (8% of estimated superficial stoniness) (García-Angulo et al., unpublished data), and belong to the Cambisols type group (Monturiol Rodríguez and Alcalá del Olmo Bobadilla, 1990). The steepness of the terrain is low, with an estimated slope average of 8%. The climate of the study area is continental Mediterranean, characterized by hot and dry summers and cold winters (Cuatro Vientos meteorological station; Spanish State Agency of Meteorology).

2.2. Field sampling and tree ring analysis

Tree-ring widths were used to reconstruct past growth rates (Fritts, 1976) of adult Holm oak trees showing variable rates of crown defoliation. Seventy Holm oak trees of similar age (years) (Table 1), with no signs of attack by biotic factors (e.g., insects, fungi), were selected and classified into four vigour groups, according to their crown foliar percentage lost: healthy (0% of defoliation), low defoliated (< 25% of

Table 1
Main characteristics of the four Holm oak vigour groups: healthy, low defoliated, highly defoliated, and dying. Age comparisons between the four vigour groups are based on one-way ANOVA analyses followed by a Tukey's Honest Significant Difference (HSD) *post hoc* test. BAI and DBH comparisons between vigour groups are based on Kruskal Wallis analyses followed by a pairwise Wilcoxon test with a Bonferroni correction.

Vigour group	Defoliation (%)	No. of trees	Mean no. of stems per tree	Mean age (years)	Mean BAI (cm^2) 1980–2009	Mean DBH (cm)
Healthy	0	14	5 (4.31)	44 (9.79)^{a}	8.23 (5.73)^{a}	22.61 (4.65)^{a}
Low defoliated	< 25	21	4 (4.12)	47 (11.08)^{a}	8.84 (7.78)^{a}	22.35 (6.32)^{ab}
Highly defoliated	25–70	19	4 (3.72)	40 (8.20)^{a}	5.41 (3.89)^{b}	17.30 (4.47)^{c}
Dying	70–100	16	3 (2.05)	39 (9.11)^{a}	5.59 (3.29)^{b}	17.84 (3.47)^{bc}

Values in brackets represent standard deviations.
Different letters indicate significant differences between vigour groups.
DBH, diameter at breast height; *BAI*, basal area increment.