



# Reduced growth sensitivity to climate in bark-beetle infested Aleppo pines: Connecting climatic and biotic drivers of forest dieback



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## ARTICLE INFO

### Article history:

Received 30 May 2015

Received in revised form 13 August 2015

Accepted 14 August 2015

### Keywords:

Drought stress

Bark beetles

Dendroecology

Carbon isotopes

*Pinus halepensis*

## ABSTRACT

Drought and bark-beetle infestation are major and often interconnected drivers of forest dieback and tree death. These two stressors may interact and accelerate forest mortality, since warmer and drier conditions boost beetle attacks and reduce tree growth. However, the way in which drought and bark-beetle infestation interact and affect declining or dying trees is still poorly understood. To disentangle the long-term interaction between the two stressors, we quantified radial growth (basal area increment), resin production, mortality and intrinsic water-use efficiency (iWUE) inferred from wood-carbon isotope discrimination. We compared trees infested and recently killed by two abundant bark beetle species (*Orthotomicus erosus* and *Tomicus piniperda*) with non-infested living trees in a drought-prone Aleppo pine plantation. Growth and iWUE showed similar values in infested and non-infested trees. Since bark-beetle-infested trees did not grow less than non-infested trees, our results did not support the hypothesis of higher costs of resin production at the expense of stem-wood formation. Radial growth was enhanced by cool and wet winter conditions prior to the growing season. However, infested trees showed lower growth responsiveness than did non-infested trees with respect to this climatic driver of growth. Infested trees also showed a lower resin-duct production two years prior to death than non-infested trees. The growth responsiveness to climate should be characterized in bark-beetle-infested trees, since a weak correlation between climate and growth can be regarded as a predisposing factor of infestation-induced tree death. Such reduced responsiveness to climate stress could be linked to the tree vulnerability to beetle attacks in drought-prone forests.

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## 1. Introduction

Drought frequency, intensity, and duration have increased in many semi-arid areas during the past fifty years (IPCC, 2014). Such aridification trends may trigger recurrent forest dieback and widespread tree-mortality events (Allen et al., 2010). Warmer conditions and extreme droughts have been related to cumulative stress in trees (e.g. cumulative hydraulic failure) causing growth decline, vigor loss, and tree death (Camarero et al., 2015). Nonetheless, rising temperatures could also alter tree-insect interactions, making stressed trees more vulnerable to insect infestation, thereby increasing the extent and intensity of insect-attack damage (Bale et al., 2002; Bentz et al., 2010; Carnicer et al., 2011; Krams et al., 2012). For instance, tree-ring records have revealed that drought stress reduces tree resistance to bark-beetle infestation in some conifer species (Berg et al., 2006). Moreover, different

mortality events of conifer species, usually pines, have been related to bark-beetle attacks in drought-prone areas (Krams et al., 2012; Negrón et al., 2009; Wermelinger et al., 2008). Therefore, combined drought and heat stress presumably act as inciting factors (*sensu* Manion, 1991) by weakening host trees and exacerbating damage due to subsequent biotic stressors, such as bark-beetle infestations (Gaylord et al., 2013).

Drought and heat stress are assumed to cause forest dieback through two physiological mechanisms, which are probably related, namely hydraulic failure and carbon starvation (McDowell et al., 2008, 2011). A reduction in photosynthesis, hydraulic conductivity, and wood production could reduce tree resistance to bark-beetle attacks by altering the tree's secondary metabolism and reducing the production of active defenses, such as resins, which are the main resistance factor to prevent bark-beetle infestation (Ferrenberg et al., 2014; Netherer et al., 2015). In addition, drought stress may alter the biochemical composition of tree tissues, making stressed trees more attractive to bark beetles (Mattson and Haack, 1987). Previous studies have quantified

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the likelihood of bark-beetle infestation in some species at different spatial and temporal scales (Negrón et al., 2009; Kane and Kolb, 2010). Nevertheless, there are still many research gaps regarding the patterns and mechanisms underlying tree susceptibility or predisposition to insect infestation after droughts at the tree level (Raffa et al., 2008). These questions are relevant, since climate-tree-insect relationships affect the global carbon cycle, alter atmosphere forest feedbacks, and influence forest dynamics (Edburg et al., 2012; McDowell et al., 2011; Reed et al., 2014). For instance, recent studies show that forests severely disturbed by bark beetle outbreaks become large carbon sources (Hansen et al., 2015; Kurz et al., 2008). In addition, an increasing recurrence of insect outbreaks could also alter the way in which forests provide ecosystem services from aesthetic concerns to carbon and water regulation (Ayres and Lombardero, 2000).

Furthermore, climate warming could also directly determine the development and survival of insects, due to their physiological sensitivity to temperature (Hicke et al., 2006; Logan et al., 2003), or indirectly through a mismatch of the tree performance (e.g. growth, resin production) and subsequent insect dynamics (Ayres and Lombardero, 2000; Bentz et al., 2010). In summary, increasing warming and drought stress could lead to a vigor loss of infested trees by weakening tree defenses, increasing insect reproduction, and then facilitating the development of outbreaks and ultimately causing tree death (Krams et al., 2012; Loehle, 1988).

In this study, we focus on forest dieback, here characterized by growth decline and rising mortality rates of planted Aleppo pines. These trees grow under semi-arid conditions and have been recently infested by two bark beetle species with different dynamics (*Tomicus piniperda*, a primary beetle species, and *Orthotomicus erosus*, a secondary beetle species). Bark beetles are highly relevant for the forestry sector in Europe, where the estimated average wood volume lost to their infestations was about 2.9 million m<sup>3</sup> per year in the last half of the 20th century (Schelhaas et al., 2003). While the decline model of Manion (1991) considers bark beetles to be a contributing factor of dieback, acting mainly in the final stages of tree death, here we extend this model in order to test whether drought-stressed trees are particularly vulnerable (predisposed) to bark-beetle infestations. We study Aleppo pine plantations experiencing recent dieback because plantations are structurally and genetically less heterogeneous than natural stands, and they are subjected to more homogeneous site conditions and fewer disturbances than comparable unmanaged forests (Sánchez-Salguero et al., 2012). Here we evaluate the interactions between drought stress and bark-beetle infestation and how they affect radial growth, water-use efficiency (iWUE) and mortality in Aleppo pine, which is a species well adapted to seasonal drought (Ne'eman and Trabaud, 2000). We also explore whether there are specific traits (diameter, growth rate, growth responsiveness to climate, resin production, iWUE) that predispose trees to bark-beetle infestations.

## 2. Material and methods

### 2.1. Study area, tree and bark beetle species

The Aleppo pine (*Pinus halepensis* Mill.), a drought-tolerant evergreen conifer species, is widely distributed in areas subjected to seasonal water deficit, mainly low-elevation sites under Mediterranean and semi-arid conditions, across the Western Mediterranean Basin (Ne'eman and Trabaud, 2000). This species has been widely planted in land restoration for forest productivity at xeric sites as a fast-growing pioneer conifer able to rapidly regenerate after fires due to its precocity and abundant seed production (Maestre and Cortina, 2004). Aleppo pine produces

abundant resin ducts and it is able to show high radial-growth rates, irrespective of the cone crop amount, in response to wet conditions in winter to spring (Alfaro-Sánchez et al., 2015).

The study site is an almost flat area covered by planted Aleppo pines occupying ca. 400 ha near the city of Zaragoza (north-eastern Spain) at 340 m.a.s.l. (Supporting Information, Fig. S1). The density and basal area range between 162 and 542 stems ha<sup>-1</sup>, and 4.12 and 20.82 m<sup>2</sup> ha<sup>-1</sup>, respectively. The understory vegetation is dominated by shrubs (*Helianthemum* sp., *Genista scorpius*, *Thymus vulgaris*, and *Rosmarinus officinalis*). The soils are cambisols poorly developed over gypsum outcrops.

*T. piniperda* L. (the common pine-shoot beetle) is a primary beetle species considered to be one of the most important bark beetles in Europe, causing an estimated 20–45% timber losses (Langström and Hellqvist, 1991, 1993; Poland et al., 2003). Disturbances such as forest fires, extreme droughts or windstorms can create favorable conditions for breeding. When these disturbance sites accumulate large populations of beetles, living trees or weakened trees are attacked (Martikainen et al., 2006; Morgan et al., 2004). Contrastingly, *O. erosus* (Woll.) (Mediterranean pine-engraver beetle) is considered a secondary pest infesting recently fallen and already stressed trees and coexisting with other bark beetle species (Haack, 2004; Morgan et al., 2004).

### 2.2. Climate data

According to data from the nearby Zaragoza-airport meteorological station (41°39'38"N, 1°0'15"W, 263 m), located at 12 km from the study site, the climate of the study area is Mediterranean of semi-arid type (Supporting Information, Fig. S2). During the 1950–2012 period, the mean annual temperature was 14.8 °C (the coldest and warmest months were January and July, respectively) and the total annual precipitation was 325 mm (the wettest and driest months were May and July, respectively). To differentiate two climatically different sub-periods with wet (1971–1990) and dry (1991–2010) conditions, we estimated the potential evapotranspiration (PET) using monthly values of mean temperature, daily temperature range, and solar radiation following the Hargreaves–Samani method (Hargreaves and Samani, 1982). Then, we calculated the water balance as the difference between precipitation and PET (P–PET). We also calculated the cumulative water deficit from January through July as the sum of the monthly water-balance values from January to July since Aleppo pine has most of its radial stem growth during that period in the study area (Camarero et al., 2010).

### 2.3. Field sampling and dendrochronological methods

Sampling was conducted in winter 2011–2012. Sampled trees were randomly distributed across the plantation and field sampling followed standard dendrochronological methods (Fritts, 2001). In the case of non-infested trees, two 5-mm-wide cores were taken at 1.3 m using a Pressler increment borer. Most dead Aleppo pines were recently infested by *Tomicus* or *Orthotomicus* (see Table 1). We identified the bark beetle species by the form and size of the galleries excavated in the bark or engraved in the sapwood (Muñoz et al., 2011). We took slices from the two types of infested trees.

The collected wood samples were air-dried and polished with a series of successively finer sand-paper grits until rings were clearly visible. Tree rings were measured to the nearest 0.01 mm using a binocular scope and a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating of the tree rings was checked using the program COFECHA (Holmes, 1983). Tree age at 1.3 m was estimated by counting rings along wood sections or in the oldest core,

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