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Drought induced decline could portend widespread pine mortality at the xeric ecotone in managed mediterranean pine-oak woodlands

Guillermo Gea-Izquierdo [a,b,*], Bárbara Viguera [a], Miguel Cabrera [c], Isabel Cañellas [a]

[a] INIA-CIFOR, Crta. La Coruña km 7.5, 28040 Madrid, Spain
[b] CEREGE UMR 7330, CNRS/Aix-Marseille Université, Europole de l'Arbois, BP 8013545, Aix-en-Provence cedex 4, France
[c] Aranzada Gestión Forestal S.L.P., C/Alonso Heredia, 31, 28028 Madrid, Spain

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ABSTRACT

There is a need to better understand how different biotic and abiotic factors interact to determine climate change enhanced tree mortality. Here, we investigated whether rising water stress determined enhanced *Pinus sylvestris* L. mortality at the species low-elevation limit in Central Spain. We analyzed the factors determining the health status of pines and compared with co-occurring and more drought-tolerant *Quercus pyrenaica* Willd along one transect following an elevation gradient. We used ordinal logistic regression to model the susceptibility of a tree to decline in relation to variability in stand competition and individual growth-patterns. The mortality pattern differed with local site conditions. Pine growth was faster but life-span shorter at drier and warmer low-elevations than at high-elevations. However, within stands, healthy trees exhibited less abrupt growth reductions and higher growth-rates but not as a consequence of lower competition, which under present stand conditions did not seem to increase adult mortality risk. Low moisture availability reduced tree-growth and, although *P. sylvestris* is less tolerant to drought, *Q. pyrenaica* was more sensitive to year-to-year moisture variability. Previous growth of dead trees from both species declined with rising water stress after the 1970s at low-elevations, which suggests that water stress intensity limited particularly tree-growth of dead trees in the long-term. For pines, widespread symptoms of crown decline (expressed by mistletoe infestation and defoliation) were only observed at low-elevation stands where, in opposition to oaks, weakened and healthy pines also exhibited recent negative growth-trends parallel to those of dead trees. The pervasive growth decline with enhanced water stress in pines from all health status at the species sampled xeric ecotone combined with the abundant crown decline symptoms observed, suggest pine vulnerability and could portend widespread mortality at its current low-elevation limit.

1. Introduction

Climate change related increases in drought frequency and severity have a negative impact on forest ecosystem productivity and tree performance (Boisvenue and Running, 2006; Lenoir et al., 2008; Choat et al., 2012). Therefore it is crucial to better describe the underlying processes governing forest acclimation to water stress (Bréda et al., 2006; Niinemets, 2010; McDowell et al., 2011) particularly at those ecosystems where sustainability is threatened by enhanced mortality caused by recent climatic changes (Adams et al., 2009; Van Mantgem et al., 2009; Allen et al., 2010). Accurate prediction of tree vulnerability to increasing water stress is challenging because many biotic and abiotic factors interact at different time scales and trees with symptoms of low vitality can recover from stress provided they do not fall below thresholds where irreversible damage occurs (Suárez et al., 2004; Dobbertin, 2005; Breshears et al., 2009). In addition, it can be particularly complex to isolate the long-term effect of climate at those sites where land-use has shaped the current state of forests and determine forest dynamics (Gimmi et al., 2010; Van Bogaert et al., 2011; Wischnewski et al., 2011).

The interdependent factors that determine species-specific susceptibility to drought induced decline and mortality must be investigated at different temporal scales in order to understand forest vulnerability. Growth can be used as a direct proxy to the tree net carbon pool. Using dendrochronological methods it is possible to analyze long-term environmental stressors (like water stress) predisposing trees to decline and short-term agents or events inciting posterior death of individuals (Suárez et al., 2004;

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* Corresponding author at: CEREGE UMR 7330, CNRS/Aix-Marseille Université, Europole de l'Arbois, BP 8013545, Aix-en-Provence cedex 4, France. Tel.: +33 (0) 442971532.

E-mail addresses: gea-izquierdo@cerege.fr, guigeiz@gmail.com (G. Gea-Izquierdo).

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McDowell et al., 2010; Linares and Camarero, 2012). The size-dependent mortality risk of trees increases under more resource stressful conditions when stand competition is intense (Zahner et al., 1989; Voelker et al., 2008; Luo and Chen, 2011) and within stands the trees with a higher likelihood to die are generally those with slow growth and negative growth-trends (Bigler and Bugmann, 2004; Suárez et al., 2004; Bigler et al., 2006).

Plants co-regulate different functional traits to cope with water stress (Bréda et al., 2006; Niinemets, 2010; McDowell et al., 2011) and complementary functionalities between species can help them to optimize environmental resources in mixed stands (Cavard et al., 2011; Luo and Chen, 2011). A widespread example in the Northern Hemisphere is that of oak-pine forests (Brose and Waldrop, 2010; Wischnewski et al., 2011; Sheffer, 2012). There is variability in drought tolerance among oak and pine species. Often pines behave as isohydric species (i.e. plant maintain relatively constant leaf water potential through stomatal control and reduced conductance despite declining soil and root water potentials) whereas oaks as anisohydric, which means they developed different strategies to cope with water stress (Abrams, 1990; Eilmann et al., 2009). Submediterranean oak species are expected to endure water stress further than less drought tolerant boreal conifers such as *P. sylvestris* and there could exist already an ongoing shift in species composition in mountain oak-pine forests, e.g. in the Alps (Bigler et al., 2006; Gimmi et al., 2010; Rigling et al., 2013) and the Pyrenees (Galiano et al., 2010; Heres et al., 2012; Vilá-Cabrera et al., 2013).

In this study we analyzed how climate and stand related factors determined the health status of two functionally different co-occurring species (*Q. pyrenaica*, a deciduous submediterranean oak, and *P. sylvestris*, an evergreen boreal pine) along an altitudinal gradient in Central Spain where pine stands at low-elevations seem to express symptoms of decline and enhanced mortality. The response to climate and the long-term growth-trends of dead, weakened and healthy trees were compared in relation to recent enhancement in water stress. The likelihood for a tree of being within a given health status was modeled to describe variability in the mortality pattern along the altitudinal gradient. By comparing the growth trends of trees with different health status we specifically analyzed whether the growth pattern of live trees resembled that of dead trees to analyze stand vulnerability to climate change. We hypothesize that the two species will exhibit different growth-trends in relation to recent water stress increase, particularly: (1) within stands, dead trees of both species will exhibit slower growth with recent negative trends; (2) weakened trees will show similar growth-trends to those of dead trees, which will portend near mortality; (3) the growth-trends of non-healthy trees at low elevations will match the recent regional increase in water stress, suggesting that long-term drought severity enhancement predisposed trees to decline only at xeric sites; (4) recent growth-trends of healthy trees resembling those of dead trees will express species-specific vulnerability to climate change.

2. Material and methods

2.1. Study site and data

Trees were sampled at four locations in Central Spain along one transect following an altitudinal gradient of increasing rainfall and decreasing temperature with increasing altitude (Table 1). Low-elevation stands (i.e. Sites #0 and #1) were an open oak woodland with some clusters of adult pines at an altitude around 1075 m subjected to typical silvopastoral management in Mediterranean oak woodlands, i.e. thinning to convert open woodland, grazing livestock and copicing for firewood. Clusters of adult trees were monospecific within stands: Site #0 corresponds to stands with adult pine overstory whereas Site #1 to stands with oak overstory. Low-elevation Site #2 (altitude around 1180 m) was dominated by pine with an irregularly mixed oak saplings understory. High-elevation Site #3 (altitude above 1400 m) was monospecific *P. sylvestris* forest. Sites #2 and #3 presented higher stand density but generally not full canopy cover. Sites #1 and #2 are within the current local low-elevation xeric ecotone for pine (Table 1), but the distribution of the two species has been likely modified by management in history (López-Sáez et al., 2014). Low elevation stands (Sites #0, #1 and #2) presented low pine regeneration (likely partly as a result of higher grazing pressure and differences in management between stands (Donés and Cabrera, 2009)), widespread symptoms of crown dieback, defoliation and abundant mistletoe infestation, which has been shown to be one of the several agents (with drought) involved in *P. sylvestris* decline (Dobbertin and Rigling, 2006; Sangüesa-Barreda et al., 2013; Zweifel et al., 2012).

To analyze the relationship between climate and tree health and characterize the mortality pattern under different ecological conditions we sampled trees within three health status classes at the four different elevations: (1) *'dead'* when trees presented 100% crown dieback; (2) *'weakened or declining'* were considered those oaks with stem basal rot and partial canopy dieback, and those pines with a certain level of crown defoliation (over 20% compared to neighboring healthy trees) and infested by the semiparasite plant *Viscum album* L. (mistletoe) in at least one third of the canopy (Sangüesa-Barreda et al., 2012, 2013); (3) '*healthy*' were those trees without the symptoms described in the previous two categories. It must be noted that trees with canopy decline presented both defoliation and mistletoe infestation. We sampled dominant adult trees (dbh > 25 cm) to analyze the growth trends in the longest possible interval and avoid oak resprouts of 40–70 years old likely established after last logging for firewood in the mid 1900s. We sampled neighboring trees of different health classes subject to similar stand competition conditions. However, this was not possible in all cases, the reason why we report a different number of plots for the different sites and health status (see below for definition of sampled plot).

2.2. Dendrochronological methods

At each site we searched for target individuals of the two species with different health status. Trees were bored twice at

Table 1
Mean site characteristics. Ps = *P. sylvestris*; Qp = *Q. pyrenaica*. dbh = diameter at 1.30 m; BA = basal area; Dd = stand density. DBH, BA and Dd are plot values calculated from the characteristics of the neighbor trees (either the closest 10 of dbh over 7.5 cm if they are closer than 10 m or those included within a radius of 10 m) of those cored. Different letters correspond to significant differences using the LSD test on a one-way ANOVA comparing the four sites. Standard deviations are between parentheses.

Site	Name	Sp.	# Plots	Altitude (m)	Coordinates		Slope	Climate			Competition		
							(°)	Ppt (mm)	T_{mean} (°C)	T_{min} (°C)	dbh (cm)	BA (m^2/ha)	Dd (n/ha)
0	$QUPY_0$	Qp	28	1056 (57)	40.86°N	4.02°W	0–15	660.3	10.3	5.35	29.1 (15.4)^a	12.0 (11.0)^b	213.5 (281.4)^a
1	$PISY_{1\text{-low}}$	Ps	17	1077 (17)	40.86°N	4.01°W	15–25	660.3	10.3	5.35	14.6 (9.1)^b	5.5 (8.5)^c	155.9 (222.1)^a
2	$PISY_{2\text{-medium}}$	Ps	20	1179 (92)	40.90°N	4.02°W	0–15	731.4	9.9	5.15	36.2 (15.6)^a	22.4 (13.2)^a	197.8 (80.9)^a
3	$PISY_{3\text{-high}}$	Ps	17	1596 (105)	40.84°N	4.06°W	0–45	944.4	7.9	2.95	35.9 (18.7)^a	22.0 (11.7)^a	263.2 (286.4)^a