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Contrasting vulnerability and resilience to drought-induced decline of densely planted vs. natural rear-edge *Pinus nigra* forests

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ABSTRACT

The southernmost European natural and planted pine forests are among the most vulnerable areas to warming-induced drought decline. Both drought stress and management factors (e.g., stand origin or reduced thinning) may induce decline by reducing the water available to trees but their relative importances have not been properly assessed. The role of stand origin – densely planted vs. naturally regenerated stands – as a decline driver can be assessed by comparing the growth and vigor responses to drought of similar natural vs. planted stands. Here, we compare these responses in natural and planted Black pine (*Pinus nigra*) stands located in southern Spain. We analyze how environmental factors – climatic (temperature and precipitation anomalies) and site conditions – and biotic factors – stand structure (age, tree size, density) and defoliation by the pine processionary moth – drive radial growth and crown condition at stand and tree levels. We also assess the climatic trends in the study area over the last 60 years. We use dendrochronology, linear mixed-effects models of basal area increment and structural equation models to determine how natural and planted stands respond to drought and current competition intensity. We observed that a temperature rise and a decrease in precipitation during the growing period led to increasing drought stress during the late 20th century. Trees from planted stands experienced stronger growth reductions and displayed more severe crown defoliation after severe droughts than those from natural stands. High stand density negatively drove growth and enhanced crown dieback, particularly in planted stands. Also pine processionary moth defoliation was more severe in the growth of natural than in planted stands but affected tree crown condition similarly in both stand types. In response to drought, sharp growth reduction and widespread defoliation of planted Mediterranean pine stands indicate that they are more vulnerable and less resilient to drought stress than natural stands. To mitigate forest decline of planted stands in xeric areas such as the Mediterranean Basin, less dense and more diverse stands should be created through selective thinning or by selecting species or provenances that are more drought tolerant.

1. Introduction

According to climatic models a generalized rise in temperature and related aridification trends is expected in the Circum-Mediterranean area within the current century (IPCC, 2007). Drought stress is probably among the main drivers of the current forest decline of conifer woodlands in the Mediterranean Basin, particularly in southern Europe (Linares et al., 2009; Allen et al., 2010; Sarris et al., 2010; Carnicer et al., 2011). Rear-edge tree populations located near the southernmost or dry limits of the species distribution area serve as valuable models for assessing tree sensitivity to drought stress (see Macias et al., 2006; Sánchez-Salguero et al., 2012a). Southernmost European mountain conifer forests located in southeastern Spain (Andalusia) are considered to be among the most vulnerable areas for the loss of endemic tree

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species and relict populations due to warming-induced drying trends (Bakkenes et al., 2002; Sánchez-Salguero et al., 2012a).

The processes leading to forest decline and the subsequent responses in tree vigor (vulnerability, resilience) are still poorly understood because several stress factors in addition to drought interact at different spatial and temporal scales leading to lagged cause-effect relationships (Manion, 2003; Camarero et al., 2011). According to the Manion (1981) conceptual model stress factors act successively leading to a progressive loss in tree vigor. The model starts by considering predisposing factors (e.g., site conditions), followed by inciting factors (e.g., drought) and finally ending with contributing factors (e.g., secondary insects and pathogens). However, few studies have assessed the role of past management on forest decline (but see Camarero et al., 2011; Vilà-Cabrera et al., 2013). Specifically, stand origin – planted vs. naturally regenerated stands – may act as a predisposing factor which can be incorporated into Manion (1981) conceptual framework.

Here we evaluate growth and vigor change (crown condition) in response to drought stress in both naturally regenerated stands and similar nearby plantations of the same species. Pine plantations in Spain present a series of characteristics that might make them more vulnerable and less resilient to climate change, chiefly higher density, lower biological diversity and lack of local adaptation due to unknown seed origin (e.g., Benito Garzón et al., 2011; Ruiz-Benito et al., 2012). Thus pine plantations near the rear-edge of the species distribution constitute valuable monitors of drought and past management effects on impending decline, yet the effects of drought-induced decline episodes and management on vulnerability and resilience at the stand and individual tree levels in these systems are poorly documented (Martínez-Vilalta et al., 2012). This information is however desperately needed to establish adaptation guidelines to increase the resilience of similar rear-edge forests subjected to drought-induced decline process.

The Mediterranean Basin is one of the world regions with the largest proportion of planted pine forests and a long history of planned management (FAO, 2006). For instance, the Spanish Reforestation Plan of 1939 involved planting more than 3.5 million ha of forests, mainly pine species, but reduced post-plantation thinning has often resulted in high-density stands (Montero, 1997). These dense and potentially drought-vulnerable pine plantations have shown a high vulnerabilty (elevated defoliation and mortality rates) to recent drought stress since they were often planted under favorable climatic conditions during past wet decades as the 1970s (Ruiz-Benito et al., 2012; Sánchez-Salguero et al., 2012b).

Black pine (*Pinus nigra* Arn.) is widely distributed in southern Europe, where it covers a wide latitudinal and longitudinal gradient from Austria to Algeria and from Turkey to Spain (Barbero et al., 1998). The subspecies *P. nigra* subsp. *salzmannii* (Dunal) Franco covers an area over 350,000 ha in Spain (Fig. 1a). The Iberian *P. nigra* forests represent the southwestern limit of distribution of the species and some stands in SE Spain include some of the driest sites where *P. nigra* grows. Dendrochronological studies have revealed that recurrent and severe droughts have negatively affected Iberian *P. nigra* radial growth during the second half of the 20th century (Andreu et al., 2007; Linares and Tíscar, 2010; Martín-Benito et al., 2010a; Camarero et al., 2013). Further, these declining growth patterns have been observed in natural stands and also in planted populations (Sánchez-Salguero et al., 2012a,b).

Many decline studies are based on the assumption of established relationships between growth, vigor status (defoliation, mortality) and the stress factor (Wunder et al., 2006). Yet, establishing these relationships is difficult because of the highly variable nature of decline over space and time (Hawkes, 2000). Thus, long-term permanent monitoring plots represent valuable tools to accurately assess climate–growth–vigor associations and changes in vulnerability and resilience in response to drought. Here, we analyze how environmental, structural and climatic variables modulate the effects of warming-induced drought stress and management on vigor and growth in natural vs. planted *P. nigra* stands and trees. We use a retrospective approach based on assessments of crown condition, here considered as a surrogate of tree vigor, measured in long-term monitoring plots of the regional Andalusian Forest Monitoring Network (hereafter abbreviated as AFMN). Previous studies suggest that crown condition is an accurate descriptor of tree vigor and well correlated with tree growth (Dobbertin, 2005). The intensity of defoliation by *Thaumetopoea pytiocampa* Schiff., the pine processionary moth (hereafter abbreviated as PPM), was also considered since this is the major defoliator of Mediterranean pine stands and reduces tree growth (Hódar et al., 2003). We define vulnerability as relative loss in growth after a drought, whereas resilience is defined as the capacity of trees to recover levels similar to those previous to the drought (Lloret et al., 2011).

Our specific aims are: (1) to examine if naturally regenerated and planted *P. nigra* stands exhibit contrasting growth responses to drought, (2) to investigate the relationships among growth patterns and sensitivity to drought as predictors of recent crown condition at the tree level, and (3) to determine if stand and tree variables (age, size, competition), biotic factors (PPM outbreaks) and drought stress act synergistically causing differential forest decline in natural vs. planted stands. We hypothesize that planted *P. nigra* stands would show a higher vulnerability and less resilience in response to drought than natural stands.

2. Materials and methods

The study area is located in eastern Andalusia, southeastern Spain (Fig. 1), and includes the southern limit of distribution of *P. nigra* subsp. *salzmanii* which comprises declining forests (Linares and Tíscar, 2010; Sánchez-Salguero et al., 2012a). In this area 44,000 km^2 are currently forested (REDIAM, 2009). Mountain systems surround the region and lie on both sides of the Guadalquivir River Basin, with palaeozoic and siliceous materials dominant in the north, and limestone and sandstone substrates prevailing in the south. The climate is Mediterranean, with mean annual precipitation varying between 140 and 2153 mm. Dry and warm summers (average July temperature is within the range 15–31 °C; precipitation varies from 0 to 39 mm) are followed by cold winters (average January temperature varies from −2 to 12 °C). The natural *P. nigra* forests in eastern Andalusia are dominant in north-oriented and high-elevation sites (1500–2270 m a.s.l) and occupy ca. 107,000 ha. Plantations cover ca. 40,000 ha and they were mostly planted in mid to high-elevation sites (1200–2150 m) between the 1960s and 1970s using seeds mostly collected in southern Spain (Alía et al., 2005).

The data used in this study are from the Andalusia adaptation (AFMN) of the "Pan-European Programme for Intensive and Continuous Monitoring of Forest Ecosystems" within the context of the International Cooperative Programme (ICP) on Assessment and Monitoring of Air Pollution Effects on Forests (Dobbertin, 2004). These intensive monitoring plots have been established since 1985 based on a 16-km grid covering Europe. In addition, the Andalusian government established in 2000 a regional forest monitoring network (AFMN) with the same harmonized criteria, but based on a 8-km grid covering the forested surface of Andalusia (2,106,252 ha) (for more details see Appendix A). The AFMN comprised data from 408 circular plots distributed systematically and each plot had a variable radius but always included 24 trees (Fig. 1b).

2.1. Climate data

We used monthly climatic data (mean temperature, total precipitation) for the period from 1950 to 2010 provided by the