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Tree growth-climate relationships in a forest-plot network on Mediterranean mountains

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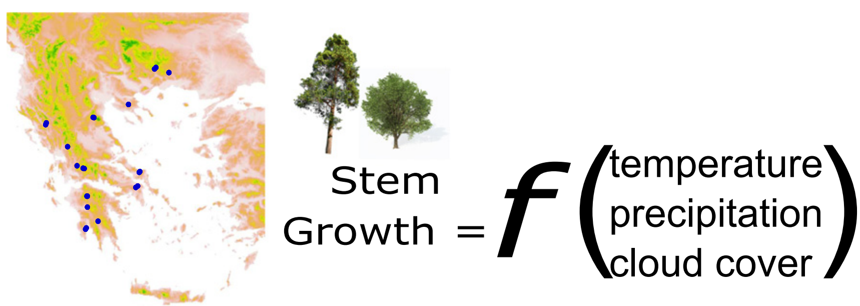
HIGHLIGHTS

- We explored tree-growth climate relationships for seven dominant tree species in 20 mountainous forests in Greece
- Water availability during May-August was a key determinant of tree-growth
- Species specific responses were related to measurements instantaneous water use efficiency

GRAPHICAL ABSTRACT



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ABSTRACT

In this study we analysed a novel tree-growth dataset, inferred from annual ring-width measurements, of 7 forest tree species from 12 mountain regions in Greece, in order to identify tree growth – climate relationships. The tree species of interest were: *Abies cephalonica*, *Abies borisii-regis*, *Picea abies*, *Pinus nigra*, *Pinus sylvestris*, *Fagus sylvatica* and *Quercus frainetto* growing across a gradient of climate conditions with mean annual temperature ranging from 5.7 to 12.6 °C and total annual precipitation from 500 to 950 mm. In total, 344 tree cores (one per tree) were analysed across a network of 20 study sites. We found that water availability during the summer period (May–August) was a strong predictor of interannual variation in tree growth for all study species. Across species and sites, annual tree growth was positively related to summer season precipitation (P_{SP}). The responsiveness of annual growth to P_{SP} was tightly related to species and site specific measurements of instantaneous photosynthetic water use efficiency (WUE), suggesting that the growth of species with efficient water use is more responsive to variations in precipitation during the dry months of the year. Our findings support the importance of water availability for the growth of mountainous Mediterranean tree species and highlight that future reductions in precipitation are likely to lead to reduced tree-growth under climate change conditions.

1. Introduction

Forests are sensitive to climatic variation, as tree longevity does not allow for rapid adaptation to environmental changes (Kramer et al.,

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2000; Lindner et al., 2010). Shifts in climatic drivers can control independently or synergistically forest dynamics. For example, changes in intensity, duration and frequency of drought events have significant consequences for tree growth and forest dieback (Peñuelas et al., 2001; Allen, 2009; Granda et al., 2013). Alterations of fire regime associated with climatic shifts have been documented in different world regions (Flannigan et al., 2000; Bowman et al., 2009), including areas where wildfires are considered an integral part of natural ecosystems (Bond et al., 2005; Pausas and Fernández-Muñoz, 2011). At the same time, forest ecosystems play a crucial role in regulating climate through the global carbon cycle (Pan et al., 2011). Understanding the potential effects of climate change on forest function is thus a long-standing goal of the forest ecological and ecophysiological research agenda.

Across the Mediterranean basin forests cover around 80 million hectares and provide various supportive, regulatory, provisional and cultural ecosystem services (FAO, 2013). Mediterranean forests have a rich floral and faunal diversity with a relatively high genetic variability (Scarascia-Mugnozza et al., 2000). Projections of various global and regional climate models, suggest that Mediterranean forests are likely to experience severe climatic conditions in the upcoming decades, including longer and more intense drought periods (Giorgi and Lionello, 2008), extreme drought events (Gao et al., 2006) as well as temporal and spatial extensions of the fire risk season (Bedia et al., 2013; Fréjaville and Curt, 2015). Driven with such climate scenarios, dynamic vegetation models project many forest areas in the Mediterranean to be replaced by shrublands (Hickler et al., 2012) and highlight potential shifts in species distributions and drought-wildfire interactions (Fyllas and Troumbis, 2009; Fyllas et al., 2017). Although during the last decades our knowledge regarding the potential impacts of climate change on forest ecosystems has considerably increased, large uncertainties still remain around the impacts in European forests, particularly in areas where the most adverse effects are expected, such as the Mediterranean region (Lindner et al., 2014).

Interannual tree-ring width variability has been widely used for climate reconstruction (Fritts and Swetnam, 1989). A network of sites located in the eastern part of the Mediterranean Basin has revealed synchronicity of tree-ring response over large geographic areas and has been used to identify drivers of climatic variation on regional to global spatial scales (Touchan et al., 2014). Using tree-ring chronologies, Cook et al. (2015, 2016) reconstructed drought variability over the last 900 years across the Mediterranean basin. Various dendroclimatological studies have been made in Greece (e.g. Kuniholm and Striker, 1983; Fazan et al., 2012; Katsavou and Ganatsas, 2012; Touchan et al., 2012) but there are still relatively few dendroecological studies that specifically analyze the relationships between tree-growth and climate variability in the eastern part of the Mediterranean. Understanding tree growth-climate relationships can help us to infer the potential response of forests to climate change and to inform prognostic vegetation models. In general, dendroecological studies in the northeastern part of the Mediterranean suggest that annual tree growth is positively associated with spring and summer water availability (Griggs et al., 2007; Klesse et al., 2015; Papadopoulos, 2009, 2016; Koutavas, 2013) as well as annual precipitation (Sarris et al., 2007; Sarris et al., 2010), while late spring and summer temperature have a negative effect on the growth of various tree species (Hughes et al., 2001; Klesse et al., 2015). However, few studies have explored how tree growth - climate relationships vary between populations of species across sites (de Luis et al., 2013; Papadopoulos, 2016; Manrique-Alba et al., 2017).

In parallel with climatic shifts, the long-term increase in atmospheric CO_2 concentration (Canadell et al., 2007) can control forest productivity through increased photosynthesis and reduced stomatal conductance (Keenan et al., 2013), although there are still some uncertainties regarding the processes and environmental constraints that modulate these two fundamental gas-exchange functions (Ainsworth and Rogers, 2007; Battipaglia et al., 2013). Tree-ring data from forest grown under enhanced CO_2 concentrations suggest that the intrinsic water use efficiency of trees increases under elevated CO_2 (Battipaglia et al., 2013). Photosynthetic water use efficiency (WUE), the ratio of carbon acquired per unit of water lost, is an adaptive trait (Ehleringer, 1993) and improved WUE is usually achieved by reduced stomatal opening for a given carbon assimilation rate (Medrano et al., 2008). Mediterranean plant species are characterized by a relatively high WUE (Gulías et al., 2003; Peñuelas et al., 2011) although variation does exist between different growth-forms (Medrano et al., 2008). Long-term increases in WUE have been observed in Mediterranean forest (Maseyk et al., 2011; Peñuelas et al., 2011) with some studies suggesting that this does not translate into enhanced tree growth (Peñuelas et al., 2011) while others supporting a significant WUE effect on tree growth (Koutavas, 2013). However forest response to elevated CO_2 could depend on species composition and in particular the species-specific WUE (Battipaglia et al., 2013).

In this study we analysed a novel tree ring-width dataset of seven dominant tree species in Greece, across a network of 20 sites in 12 mountainous regions growing along a gradient of climatic conditions. At 15 of those sites we have also measured the instantaneous WUE of each study species. Based on their ecological characteristics and geographical distribution we hypothesized i) that the study species will present different responses to various climatic drivers, with water availability being particularly important in these water-limited ecosystems. Furthermore ii) we expected that species with a high WUE will respond more promptly to inter-annual variation in water availability. To test the above hypotheses we initially analysed climate-growth relationships for each species and site combination. We then explored if for a given species the key climate-growth drivers are consistent across sites. Finally, we explored whether estimates of instantaneous WUE are good predictors of the species annual growth responsiveness to water availability.

2. Materials and methods

2.1. Study sites and study species

All study sites are part of the Mediterranean Forests in Transition (MEDIT) forest plots network, where stand structural, tree functional, tree growth and environmental data were systematically collected during the summer months of 2012 to 2015. The MEDIT forest plots network spans Greece (Fig. 1), covering the most dominant forest tree species and forest types. We note that the criteria for selecting the plots was to sample the most representative forest types along a range of environmental conditions (climatic and edaphic) and not to "maximize" individual-tree response to climate. In this study we analysed tree ring-width data of seven tree species from 20 sites, with a mean annual temperature range from 5.7 to 12.6 °C and a total annual precipitation range from 500 to 950 mm (Table 1).

The study species are the dominant tree species in Greece, covering >30% of total forest area of the country (National Inventory of Greece, 1992). These are: *Abies cephalonica* Loudon, *Abies borisii-regis* Mattf., *Picea abies* (L.) H. Karst., *Pinus nigra* J.F. Arnold, *Pinus sylvestris* L., *Fagus sylvatica* L. and *Quercus frainetto* Ten. *Abies cephalonica* (Greek fir) is an endemic tree species to southern continental Greece and the islands of Cephalonia and Evia. *A. borisii-regis* (Bulgarian fir), an endemic of the southern Balkan Peninsula, is found mainly in the northern and central part of the country and is considered a hybrid of *Abies alba* and *A. cephalonica*. Following a drought avoidance strategy (Aussenac, 2002), *A. cephalonica* copes better with long droughts than *A. borisii-regis* (Papadopoulos, 2016) and thus can be found in a greater variety of substrates, including dry hard limestones. In contrast, *A. borisii-regis* occurs in more humid sites and at higher latitudes (Korakis, 2015). *P. nigra* (European black pine) is a circum-Mediterranean pine species extending from Spain and north Morocco to Austria, Turkey and Cyprus. *P. nigra* is a drought-sensitive species,