



Increased growth and reduced summer drought limitation at the southern limit of *Fagus sylvatica* L., despite regionally warmer and drier conditions



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ABSTRACT

Tree populations at the equatorward edge of their distribution are predicted to respond to increased temperature and drought with declining performance. Empirical studies of *Fagus sylvatica* L., one of the most studied tree species in Europe, have broadly supported these predictions. Using a network of tree ring chronologies from northern Greece, we showed that growth in populations of this species at their southeast distribution limit was limited by summer temperature and precipitation, particularly at low elevations. Furthermore, decadal periods of lower precipitation and higher temperature in the twentieth century were associated with multi-year growth depressions. However, since 1990, growth trends were positive across the network, despite continued dry and hot summer conditions. Growth trends were not correlated with either elevation or tree age. Additionally, correlations between growth and temperature and precipitation were weaker in recent decades. These results are consistent with another recent report from the Balkan Peninsula, and indicate that forests in this region may be more resistant to regional climate change than previously considered.

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1. Introduction

Populations at the equator-ward or low-elevation edge of their species distribution are expected to respond to increased temperatures and drought with a reduction in performance (Woodward, 1987). In tree species, this response is expected to be evident in declining growth, increased mortality and reduced recruitment (Jump et al., 2010). Changes in demographic and subsequent distribution shifts have already been observed at the trailing edge of many tree species distributions in response to recent climate change (e.g. Beckage et al., 2008). *Fagus sylvatica* L. (European beech) is a widely distributed species in Europe, with great economic and biodiversity value (Gessler et al., 2007), and has often been used as a model species for investigating the current and future impact of climate change on forest ecosystems (e.g. Kramer et al., 2010). It is widely considered to have high sensitivity to growing season drought, based on evidence from experimental and physiological studies (Robson et al., 2012), forest inventory

data (Seynave et al., 2008), dendrochronological studies (Piovesan et al., 2005) and statistical and process-based models of distribution (Kramer et al., 2010). Furthermore, drought stress is widely considered to limit the distribution of *F. sylvatica* at its southern distribution limit, and subsequently the increase in temperature and summer drought in southern Europe over the last half century (Giorgi, 2002) are expected to have led to reduced performance in many of these southern populations (Fyllas and Troumbis, 2009). In contrast, in northern Europe, beech is expected to have increased in competitiveness and expanded into areas currently occupied by boreo-nemoral species as a consequence of increasing survival and seed maturation success, and higher growth rates (Koca et al., 2006). These trends are expected to continue over the next century as climate continues to warm. It is important to test these predictions as they are key to predicting future range shifts, and if species responses to climate change differ from expectations this will have far-reaching consequences for forest carbon cycling, biodiversity and forest-based economic activities.

Until recently, empirical studies have broadly supported predictions, with evidence of increased growth and competitiveness reported in northern Europe (Bascietto et al., 2004; Bolte et al., 2010) and growth declines and increased mortality reported at the southern distribution edge (Jump et al., 2006; Piovesan et al.,

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2008). Recently however, the picture has become more complex, with climate warming in northern Europe linked with evidence of negative impacts of climate change on forest growth, including declines in growth (Aertsen et al., 2014; Latte et al., 2015). Additionally, a recent study has reported increased tree growth in southern European beech forests, during the ongoing period of regional warming (Tegel et al., 2014). There is therefore a pressing need to improve understanding of the relationships between tree growth and climate in this species, particularly at the southern distribution margin where beech forests are understudied in comparison to central and northern Europe. Furthermore, we require additional understanding of the response of growth in this region to recent changes in climate, which have been characterised by increasing temperatures and summer drought stress (Giorgi, 2002). Tree rings provide a valuable way to investigate such growth responses, allowing reliable assessment of annual aboveground net primary production (Bascietto et al., 2004). However, tree-rings contain multiple biological and environmental signals necessitating careful analysis and interpretation (e.g. Bowman et al., 2013).

This study uses a new network of 21 ring chronologies from across northern Greece to investigate evidence of the impacts of recent climate change on tree growth at the southeast distribution limit of this species. We specifically address the following research questions:

1. What is the relationship between tree growth (ring width) and climate at the southeast distribution limit of beech?
2. How have interannual and decadal variations in growth in beech responded to recent changes in climate?
3. What do growth-climate relationships and growth trends within the network tell us about ongoing and likely future response of this species to climate change?

2. Material and methods

2.1. Study area

The study was conducted in northern Greece, in forests which represent the most south-easterly populations of beech in Europe. Beech forms the treeline on many mountains (~1900 m a.s.l.), and at lower elevations beech is typically replaced by mixed deciduous oak-dominated woodland (~800 m a.s.l.) (Tsiripidis et al., 2007). Research focused on an intensively sampled elevation transect on Mt. Vermio (40.64°N, 21.95°E), with eleven sampled sites extending from the high elevation treeline at ~1950 m a.s.l. to the lowest elevation site at 880 m a.s.l. (Table 1 and Fig. 1). Additionally, 10 further sites were sampled across northern Greece to test the regional consistency of results (Table 1 and Fig. 1). This additional network of sites included a stand on Mt. Oxia (38.78°N, 21.97°E), the most extreme southeast population of beech in Europe, and the most southerly occurrence in the Balkan peninsula (Tsiripidis et al., 2007).

Climate in this region is typically Mediterranean, with warm dry summers and cold wet winters, although there is geographical and elevational variation (Figure S 1 and S 2). Changes in climate over the last century are consistent with other regions in the Mediterranean, with warming during the first half of the 20th century, followed by a trend of cooling temperature from 1950 to 1970. Since the 1970s temperatures have risen. Annual precipitation has no significant long-term trend, but summer precipitation was lower during the 1940s and 1950s, and during the decade centred on 2000.

2.2. Tree ring sampling

At each site increment cores were extracted from 20 to 31 canopy dominant trees with two (occasionally three) cores taken per tree from opposite directions and parallel to any slope. Sample preparation followed standard dendrochronological methods, involving the mounting of cores, and then surface sanding until individual ring boundaries were clearly visible. Cores were scanned at either 1600 or 2400 dpi (the latter when rings were particularly narrow), and ring widths for each core was measured using the software *CooRecorder* v7.3 (Larsson, 2003). Initial cross-dating was conducted in *CDendro* v7.3 (Larsson, 2010), and then checked for each individual site using the standard dendrochronological software *COFECHA* (Grissino-Mayer, 2001). Some cores could not be successfully measured or cross-dated and these were excluded from subsequent analysis. Commonly used chronology statistics were used to confirm the suitability of our chronologies for dendrochronological analysis (Grissino-Mayer, 2001) (Table 2), and PCA analysis was used to quantify the common signal between sites in the network.

2.3. Tree ring processing

Raw ring width chronologies typically contain low-frequency signals (i.e. decadal and longer), associated with changes in tree age and size, canopy position and long-term changes in the abiotic environment. We used two techniques in order to account for these effects. In the first, we removed low-frequency variance from each individual tree chronology by detrending the ring width time-series using the R package *dplR* (Bunn, 2008), individually fitting the raw ring width series from each core with a 32-year cubic spline with a 50% frequency cut off. Dimensionless ring width indices were created for each core by dividing the observed ring width by the spline, with individual indices then averaged to produce a mean ring width index (RWI) for each sampled site, with a prewhitening procedure applied to account for autocorrelation in the RWI time-series. The RWI captures high frequency (i.e. interannual) variation in tree growth. In the second technique we converted raw ring width measurements into basal area increment (BAI) using the formula:

$$BAI_t = \pi(r_t^2 - r_{t-1}^2)$$

where r is the radius of the tree in year t . BAI chronologies account for the geometric effect (increasing cambium area as tree size increases), but retain low frequency variation due to changes in growing conditions (e.g. climate, canopy position). A mean site BAI chronology is expected to show a long-term positive trend during the juvenile phase, partly due to stand dynamics and changes in tree size. The early parts of a mean BAI chronology represent suppressed growth only, with increasing BAI in the mean site chronology as sampled trees increase in size and gain access to the canopy (Bowman et al., 2013). In order to account for this potential bias, individual tree BAI chronologies were truncated to include only mature-phase growth. The cut-off was determined as either the end of the most recent canopy release event, or the transition to mature growth (following the method of Jump et al. (2006), applied to individual trees) (see Figure S 3 for more details). Individual chronologies were averaged for each site to create mature BAI (mBAI) chronologies, and then scaled and centred for plotting and analysis. BAI chronologies created without the removal of juvenile phase growth are included in the supplementary information.

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