Large-scale atmospheric circulation enhances the Mediterranean East-West tree growth contrast at rear-edge deciduous forests

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Highlights

- General growth reduction in rear-edge Mediterranean deciduous populations.
- Western populations display a stronger growth decrease than eastern populations.
- Summer climate has gained importance for growth during the last three decades.
- The recent strengthening of the SNAO imparts an east-west dipole to summer climate
- Atmospheric circulation patterns may be determinant in future forest persistence

Abstract

Overlaid to a general reduction of European beech and sessile oak tree growth over the recent decades in the Mediterranean Basin, tree-ring records from western Mediterranean populations display a stronger growth decrease than eastern populations. We investigate here to what extent the impact of sustained atmospheric circulation patterns in summertime can explain the observed spatial patterns of tree growth. We use Canonical Correlation Analysis, a statistical method that identifies the coupled patterns that are optimally correlated between two multivariate data sets. A general change in growth trends, shifting from a general increase during the period 1950-1981 to a decrease during the last three decades, can be attributed to increasing summer temperatures, which exert a dominant and negative influence on growth in both tree species across sites. However, summer precipitation has gained importance for growth, coinciding with the intensification of the geographical polarity in climate conditions across the Mediterranean Basin. This intensification during the last three decades can be traced back to a strengthening of the Summer North Atlantic Oscillation (SNAO), which imparts an east-west dipole to summer climate in this region. Under predicted persistent stronger SNAO in the future, western populations would face harsher summer conditions than central and eastern rear-edge populations, due to decreasing precipitation and increasing temperatures in the west Mediterranean Basin. These results evidence the determinant role that changes in the atmospheric circulation patterns may play in the persistence of rear-edge temperate deciduous forests in the near future.

1. Introduction

The Mediterranean Basin (MB) constitutes a major ecotone between dry and wet climates where most of the European boreal and temperate tree species meet their southern distribution limit (the so-called rear-edge; Ellenberg, 1996; Hampe and Petit, 2005). At these latitudes, summer is usually the most challenging period for tree growth due to the combination of high temperatures and low precipitation, leading to xeric conditions and high evaporative demands (Mitrakos, 1980). Populations located at the rear edges are more exposed to the negative effects of forthcoming climate change since the conditions for tree growth are currently at the limit of species' tolerance (Hampe and Petit, 2005).

A large number of dendroecological studies have addressed the impact of changes in climate on tree growth of temperate species at the rear edge of their natural distribution in Europe. Some of those studies reported growth increases during the last decades (e.g., Bascietto et al., 2004; Tegel et al., 2014), while others described growth declines associated to summer drought stress (Peñuelas and Boada, 2003; Jump et al., 2006; Macias et al., 2006; Granier et al., 2007; Piovesan et al., 2008, Chen et al., 2015), despite evidences of a positive impact of rising CO_2 concentrations on intrinsic water use efficiency in Mediterranean tree populations (Andreu-Hayles et al., 2011; Peñuelas et al., 2011; Saurer et al., 2014; Camarero et al., 2015). The variety of results obtained so far might be partly due to the different time spans covered by the different studies, the diverse sources of climate data used (i.e. stations versus gridded products), the influence of micro-environmental conditions and land use changes (Motta et al., 2006). Furthermore, climate variations associated with geographical features such as elevation, lead to substantial differences in terms of radial growth (Cailleret and Davi, 2011; Gea-Izquierdo et al., 2014) and climate signal (Gutiérrez, 1988; Piovesan et al., 2005; Di Filippo et al., 2007) in Mediterranean mountains. Thus, an accurate selection of forests at the limits of the specie's tolerance becomes crucial when aiming at assessing climate impacts on rear-edge populations.

The ensemble of climate change projections from the Coupled Model Intercomparison Project Phase 3 and Phase 5 (CMIP3 and CMIP5) mostly agree that during the next century the MB will experience drying, particularly during summer (Christensen et al., 2007; Giorgi and Lionello, 2008; Kirtman et al., 2013) as well as increases in frequency and severity of extreme droughts, hot extremes, and heat waves (Fink et al., 2004; Pal et al., 2004; Schär et al., 2004; Seneviratne et al., 2006). This may trigger forest die-back at rear-edge populations and force temperate and boreal species to migrate to higher altitudes or latitudes in order to cope with the increase in temperatures and changes in precipitation (Gates, 1993; Allen and Breshears, 1998; Thuiller et al., 2005; Lenoir et al., 2008; Falk and Hempelmann, 2013).

Recent changes in climate may be related to internal dynamics of the system, particularly at regional scales (Deser et al., 2012), or may be a response to changes in natural or anthropogenic external forcings (Ottera et al., 2010; Myhre et al., 2013), or a combination of both (i.e., atmospheric patterns of internal variability could also be influenced by external forcing; Miller et al., 2006). The link between climate, direct external forcing (e.g., volcanism, increase in atmospheric concentration of CO_2) and tree growth has been investigated at regional scales (e.g., Saurer et al., 2014). However, the association between climate, atmospheric circulation patterns and tree growth at the MB has been mostly analysed at local scales (e.g., Piovesan and Schirone, 2000; Camarero, 2011; Piraino and Roig-Juñet, 2014; Esper et al., 2015; Rozas et al., 2015).

Understanding the link between tree growth, climate and the atmospheric circulation may lead to untapped sources of predictability of tree growth under forthcoming climate change scenarios. This is particularly relevant on areas of heightened susceptibility to climate change such as the MB. Therefore, this paper addresses the relative role of internal variability on the increasing harshness in summer conditions affecting tree growth of two rear-edge temperate broadleaf deciduous species in the MB during the last decades.

We present a statistical analysis of tree-ring width chronologies and meteorological data based on Canonical Correlation Analysis (CCA). CCA allows extracting pairs of spatial patterns of tree-growth variability and summer climate that have an optimal time correlation. The use of this multivariate technique helps to separate the systematic variations from noise, thus favoring the minimization of local-effects (i.e., forest management) and smaller scale processes that may obscure the common climate signal. The geographical patterns of tree sensitivity to summer climate identified by the CCA were then used to infer atmospheric circulation patterns that give rise to the observed patterns in tree growth during the last six decades.

2. Methods

2.1 Study sites

The study was conducted using a newly developed network composed by 12 European beech (*Fagus sylvatica* L., beech hereafter) and nine Sessile oak (*Quercus petraea* (Matt.) Liebl; oak hereafter) sites distributed across the southernmost limit of their natural distribution area in Europe (see details in Supplementary Table1). Beech is a shade-tolerant species with a low tolerance to drought and requires a certain degree of atmospheric humidity to survive. Oak is considered a warmth- and medium light-demanding species in the context of temperate forests and assumed to be more resistant to drought than beech (Aranda et al., 2005). The studied forests were carefully selected in areas where summer conditions (high temperature and relatively low precipitation) are potentially limiting tree growth. Differences in macroclimatic conditions can be recognized in Figure 1: the Iberian Peninsula (western populations) and the Italian Peninsula (central populations) are generally drier than the sites located in eastern MB, which are wetter and milder. Overall, the two sites located in Slovenia (B_Sl1 and O_Sl1) have the mildest summer, while the forests in the Iberian Peninsula endure the driest and hottest summers among the 21 sites.

Beech and oak were dominant or co-dominant species in all sampled forests. Most of the beech sites were pure stands and only B_Sp1 and B_Sl1 were mixed beech-oak forests. In B_Sp1 beech was mixed with *Q. pyrenaica* Willd. and *Q. petraea*, whereas B_Sl1 was mixed with *Q. petraea* in the latter. Similarly, the majority of oak forests were pure stands, or mixed with other oaks species in O_Sp2 (*Q. pubescens* Willd.) and in Q_It2 and Q_It3 (*Q. cerris* L.). Although all sites suffered from logging in the past, there were no logging activities in the selected forests for the last 40-50 years (many of them are protected areas nowadays) except for B_Sl1 and O_Sl1 where logging still sparsely takes place.

2.2 Sampling

A field campaign was carried out during summers of 2013 and 2014 across Spain, Italy, Slovenia, Bulgaria and Romania in order to develop a homogeneous and up-to-date tree-ring network of marginal forests (Supplementary Table1). From each of the 21 sites sampled, 20 dominant or isolated trees of different adult age classes (i.e., individuals at least 80 years old to avoid the juvenile effect, except for O_sp2, where the minimum age was 65) were selected and two cores per tree were extracted with an increment borer. Samples were visually cross-dated and measured with an accuracy of 0.01 using a Linntab 6 (RINNTECH) measuring device. Tree-ring width series were processed using dplR (Bunn, 2008) and according to standard dendrochronological procedures described in Cook and Kairiukstis (1990). Individual tree-ring series were standardized by fitting a negative exponential function to the raw series in order to remove age-related trends (Cook, 1987). This relatively stiff standardization emphasizes inter-annual variations but also keeps multi-decadal scale wavelengths in the final chronology (Cook et al., 1995). A master chronology using a bi-weight robust mean which reduces bias caused by extreme values was built for each site. This set of chronologies is called standard chronologies (*std*). Additionally, a second set of chronologies (*res*) was generated by subtracting the long-term linear trends from the standard chronologies using a linear regression.

2.3 Climate data

Climate data from local stations were not available for all sampled sites and therefore, a high-resolution and homogenized gridded daily data set of climate variables over Europe (termed E-OBS, Haylock et al., 2008) was used for investigating the climate-growth relationships. Monthly summer (June, July and August) temperature means and mean daily precipitation were downloaded for the 1ºx1º grid-cells surrounding every sampled site. Additionally, the 850mb geopotential height field of the NCEP/NCAR meteorological reanalysis and the Summer NAO index based on the NCEP/NCAR reanalysis sea-level pressure reconstruction were used to identify the summer circulation anomalies linked to tree growth.

The strength and temporal stability of the influence of climate on tree growth over the last six decades was investigated by splitting the records into two equally long sub-periods: 1950-1981 and 1982-2012. This split approximately matches the described periods of prominent global changes in climate which may have enhanced regime shifts (Reid et al., 2016)

2.4 Statistical analysis: PCA and CCA

For computational reasons, it is advisable to prefilter the data with a Principal Component Analysis (PCA) prior to the Canonical Correlation Analysis (CCA) (Bretherton et al., 1992;

not to be confused with Canonical Correspondence Analysis, also frequently applied in ecology). The PCA was applied to extract the main patterns of variability from the set of tree-ring width chronologies (TRW) and summer meteorological variables at the sampling sites: June-to-August mean temperature (Ts) and June-to-August total precipitation (Ps).

The calculated principal components of the tree-ring chronologies were linked to the climate variables by using CCA. CCA, similarly to PCA, decomposes multivariate variables as a sum of patterns whose amplitude is described by an associated time series. Given two multivariate variables, in this case two sets of PCs derived from chronologies and meteorological records, CCA identifies pairs of patterns (one pattern for each multivariate variable) for which the associated canonical time series have the highest possible correlation. The statistical interpretation of CCA is, therefore, that one pair of canonical patterns tend to appear simultaneously in each set of variables, i.e. they tend to co-variate. This co-variability is summarized by the canonical correlation coefficient, which is the correlation between the corresponding canonical time series (von Storch and Zwiers, 1999).

In this analysis, the CCA is applied to the principal components (PCs) of the TRW and the climate variables (Ts, Ps) previously calculated. There is no theoretical rule to establish the optimal number of PCs per variable to be included in the CCA. Here, following von Storch and Zwiers (1999), we explored the spectrum of explained variances of PCs of each variable. Usually, this spectrum quickly flattens after a certain number of PCs, after which the cumulative explained variance grows much more slowly. This was the level of PCA-truncation chosen here and the number of PCs included ranged from 2 to 5 (Supplementary Table2)

In order to disentangle the connection between tree growth and summer climate that is due to long-term trends from that due to the coherent interannual-to-decadal variability, we have considered different CCA cases. In one case, we use the standard series (std_CCA), whereas in the second case we used the residuals after subtracting the long-term trend of the original time series (res_CCA). For the latter case, the long-term linear trends of the climate data and of the tree-ring chronologies were subtracted using a linear regression for the period 1950-2012. The CCA were carried out in two periods (1950-1981 and 1982-2012) to investigate whether the links between these variables may have changed through time. The choice of a linear detrending in time versus more complicated functional forms is dictated by the length of the records, which does not allow to clearly discriminate between a linear fit and non-linear fit. The residual records after linearly detrending do not display clear or significant long-term autocorrelations at decadal lags, as it should be expected if the underlying long-term trends could be represented by higher order polynomials in time.

To identify the atmospheric circulation anomalies that may explain the temperature and precipitation variations linked to TRW, we calculated the correlation pattern between the TRW canonical time series and the NCEP/NCAR 850mb geopotential height field. The residual canonical axes (res_CCA) were chosen since the long-term trend is generally weak compared to the interannual and decadal variations in geopotential height.

3. Results

3.1Growth trends and temporal patterns

Tree growth has generally decreased in the rear-edge beech forest since 1950s, whereas in rear-edge oak forests changes in growth have been more variable (Figure 2; Supplementary Figure 3). A closer look at the two equally long periods covering the last six decades considered in this study, revealed differences in growth trends between the two(Fig. 2; Supplementary Table1). For the period 1950-1981, most of the beech and oak chronologies displayed positive growth trends, though not all of them were significant ($p<0.05$). In the case of beech, 67% of the trends were positive (33% significant) and 33% were negative (17% significant), whereas for oak, 67% of the trend were positive (44% significant) and no significant negative growth trends were observed.

During the period 1981-2012, concurrent with a general increase in temperature (Supplementary Figure 1), most of the sites displayed negative growth trends (83% and 67% for beech and oak, respectively) though not all of them were significant. For beech, 83% of the trends were negative (42% significant), while for oak 67% of the trends were negative (22% significant) (Fig. 2). Remarkably, no significant positive growth trends were found during this period, either in beech or in oak sites.

Overall, the Eastern sites of both species displayed a lower amount of significant negative growth trends during recent decades than western and central MB stands (Supplementary Table 1, Supplementary Figure 3). This geographical pattern of tree growth was further supported by the results of the PCA performed with the 21 chronologies for the period 1950-2012 (Supplementary Figure 2), which did not reveal a clear species-specific or altitudinal pattern but rather displayed east-west gradients for both PC1 and PC2.

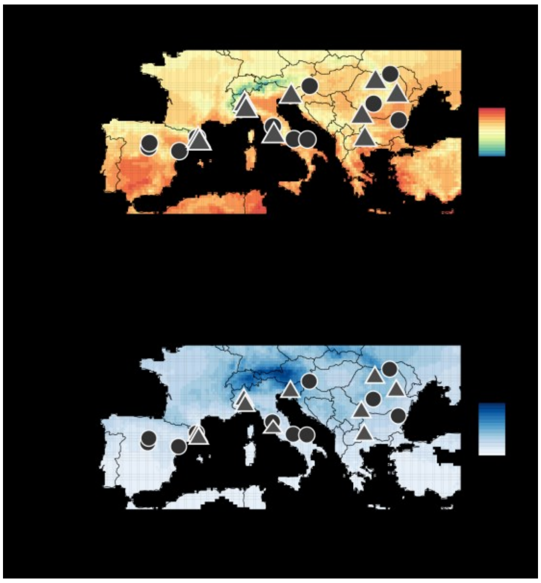

Figure 1 *Location of the 12 European beech (black circles) and nine Sessile Oak (black triangles) rear-edge forests. Symbols are superimposed to the mean summer temperature for the period 1950-2012 (upper map) and mean daily summer precipitation for the same period (bottom map).*

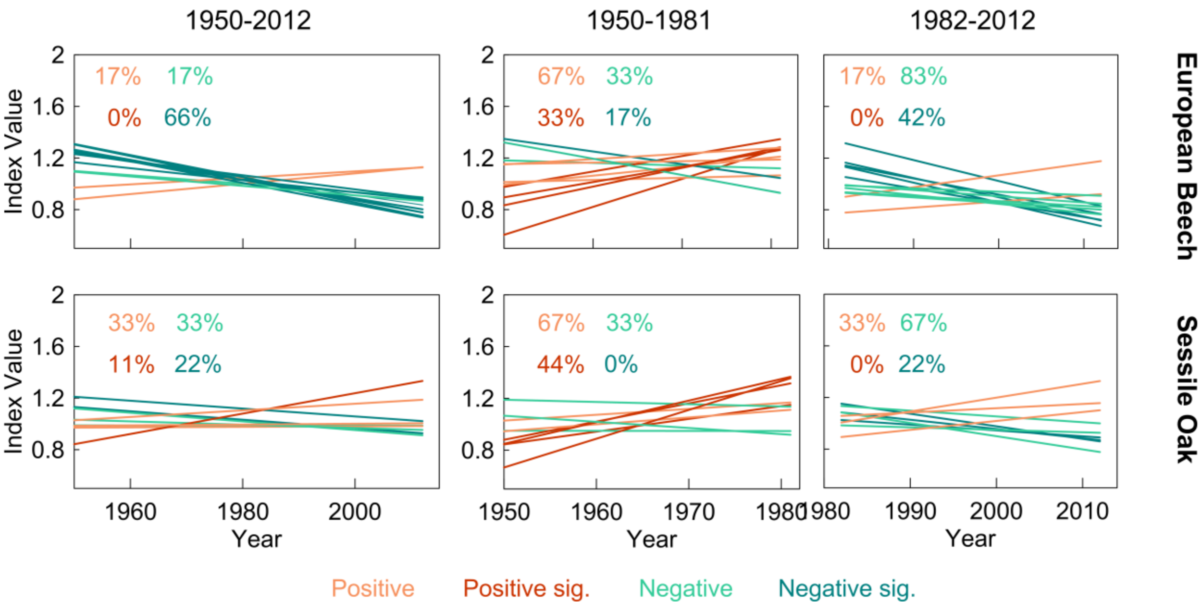

Figure 2*. Growth trends during the full period 1950-2012 (left panel) and the two subperiods 1950-1981 (middle panel) and 1982-2012 (right panel) for European beech and Sessile Oak. Colours indicate sign and significance of the growth trends: positive non-significant (light orange), positive significant (dark orange), negative non-significant (light green), negative significant (dark green).*

Percentage of chronologies in each growth-trend group is also shown. Linear trends were fitted on the std chronologies.

3.2 CCA with and without long-term trends

The results of the CCA are interpreted in pairs of canonical axes (Table 1). Each pair is composed of one spatial pattern of each of the variables included in the analysis. For the analysis with TRW and summer temperature, each canonical pair consist of one pattern of TRW chronologies and one pattern of summer temperature. Analogously, for the analysis of tree-ring width and summer precipitation each canonical pattern consist of a TRW pattern and a precipitation pattern. These paired patterns are those that have the highest possible temporal correlation, which measures the degree of co-variability between the patterns of the variables.

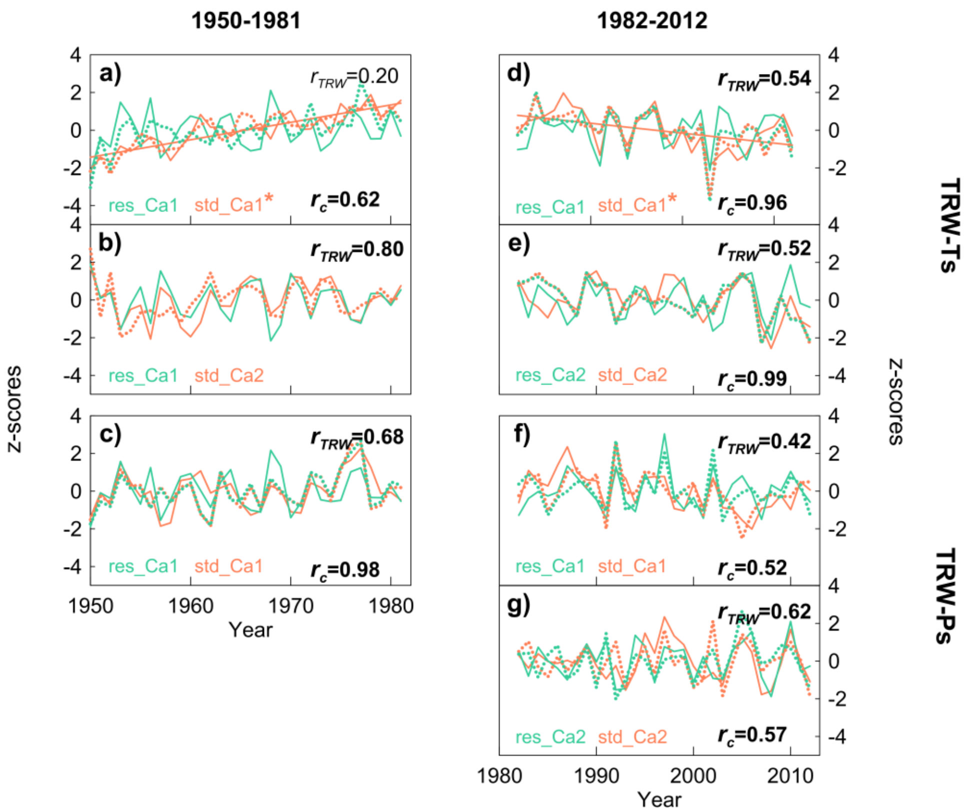

Figure 3. *Comparison of the significant pairs of canonical axes derived from the std_CCA and res_CCA for the two periods 1950-1981 (left panel) and 1982-2012 (right panel). Tree-ring width (continuous lines) and climate-variable (dashed lines) significant canonical axes (Ca) derived from the analysis with summer temperature (TRW-Ts; panels a-b, d-e) and summer precipitation (TRW-Ps; panels c, f-g) are shown. Pearson's correlation values between the tree-ring canonical axes (r_{TRW}) and the climate canonical axes (r_c) derived from res and std analysis are shown. Bold numbers indicate significance at 95% level. Linear trends are superimposed to the canonical axis when significant.* indicates significant trend at 99% level.*

The CCA was performed for the early period 1950-1981 between summer temperature (Ts) or precipitation (Ps) and the set of TRW in two settings: with and without long-term trends (std_CCA and res_CCA, respectively). These analyses revealed three canonical pairs (two pairs related to summer temperature and one pair related to summer precipitation) and two pairs (one related summer temperature and one related to summer precipitation), respectively(Table 1). The canonical correlations and the percentage of explained variance were similar in the analyses with summer precipitation (TRW-Ps) when including or excluding the long-term trends. In contrast, for the analysis with summer temperature (TRW-Ts), the amount of explained variance by the std_CCA was much larger (44%) than the same analysis without long-term trends res_CCA (17%). The canonical correlations were also higher for the std_CCA pairs ($r_{\_Ca1}$=0.83 and $r_{\_Ca2}$=0.46, respectively) than for res_CCA pair ($r_{\_Ca1}$=0.48).

The visual comparison of the canonical time series derived from std_CCA and res_CCA, showed a clear difference in trend for the leading mode TRW-Ts (significant for std_CCA but not for res_CCA) (Figure 3a), whereas the rest of canonical time series were similar in trend (Figure 3b-c). Thus, long-term trends were confined into the leading canonical mode TRW-Ts of std_CCA, being the rest of significant pairs of canonical axes similar to those of res_CCA. All correlation values between significant axes can be found in the Supporting material (Supplementary Table 3 for TRW axes and Supplementary Table 4 for climate variable axes).

The same analysis conducted for the period 1982-2012 revealed four significant pairs of canonical axes for both std_CCA and res_CCA: two related summer temperature and one related to summer precipitation. The amounts of explained variance were higher than in the previous period. The two significant pairs of axes TRW-Ts explained 39% and 27% of variance for std_CCA and res_CCA, respectively, whereas the two TRW-Ps explained 32% and 27% of variance, respectively (Table 1). In contrast to the previous period, where the std_CCA and res_CCA analysis revealed a different behavior regarding the long-term trends of the leading TRW-Ts mode, all canonical time series in std_CCA and res_CCA displayed high similarities (Figure 3). This can be seen in the significant correlations between the tree-ring axes derived from both analyses (r_{TRW} in Fig. 3) and the correlation between the climate axes derived from both analyses (r_C in Fig. 3).

3.3 Linking tree growth and summer climate during 1950-1981

The statistical similarities and differences found among the canonical time series were also visible in the canonical patterns of Figure 4. A canonical pattern is composed by the correlation between the canonical time series and the time series of each variable at one particular site. The comparison of a pair of canonical patterns (i.e., TRW and summer temperature) reveals the sign of the climate influence on tree growth and the geographical gradient of such influence.

CCA pair	1950-1981				1982-2012			
	TRW-Ts		TRW-Ps		TRW-Ts		TRW-Ps	
	std	res	std	res	std	res	std	res
*r*_Ca1	0.83**	0.48*	0.57*	0.50*	0.70**	0.62**	0.73**	0.72**
*r*_Ca2	0.46*	0.32	0.41	0.41	0.54*	0.46*	0.56*	0.60**
r^2(%)	44%	17%	17%	14%	39%	27%	32%	27%

Table 1 *Output of the canonical correlation analysis (CCA) performed for each subperiod. Analyses performed using the PCs derived from tree-ring chronologies (TRW) and summer temperature (Ts) or summer precipitation (Ps) for the standard (std) and residual series (res). The correlations of each canonical pair of axis are shown (r_Ca1, r_Ca2) as well as the total explained variance (r^2). (*) and (**) indicates significance at 95% and 99% level, respectively.*

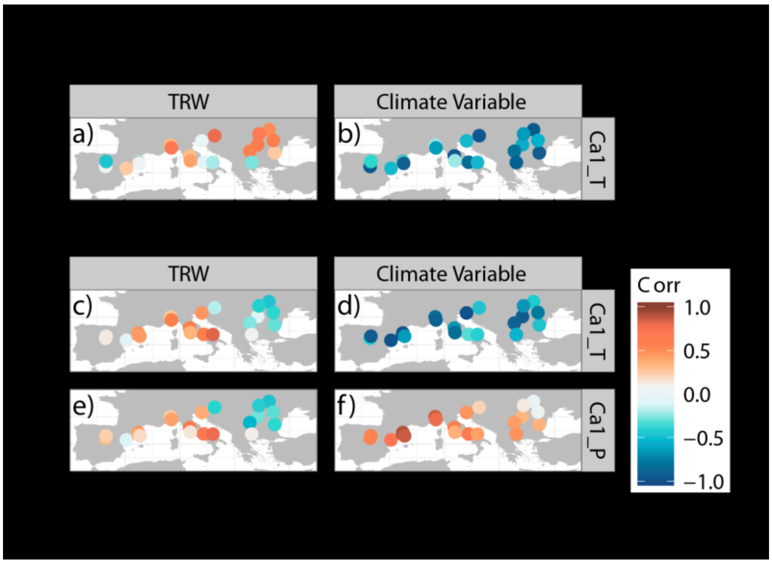

Figure 4. *Canonical patterns corresponding to the period 1950-1981 for every significant pair of canonical axes.* ***a-b)*** *leading significant pair of tree-ring width (TRW) and summer temperature (Ts) from the std_CCA;* ***c-d)*** *significant pair of TRW-Ts from the res_CCA;* ***e-f)*** *significant pair of TRW-Ps from the res_CCA. The rest of canonical patterns corresponding to the significant axes of the std_CCA can be found in Supplementary Figure 4.*

In line with the differences found in the canonical axes in Fig 3a, the leading mode of the std_CCA and res_CCA related to summer temperature (Fig. 4a-b and c-d, respectively) displayed different canonical patterns. The tree-ring patterns derived from the leading mode of std_CCA (Fig. 4a) showed a positive sign at eastern and most of the central MB sites and the corresponding canonical patterns for temperature (Fig. 4b) displayed a negative sign at all sites. The interpretation of these pair of patterns is that higher temperatures were generally detrimental to tree growth in eastern and central MB. In contrast, the leading tree-ring canonical pattern of the res_CCA (Fig. 4c) encapsulated a gradient in the east-west direction, with a positive sign particularly in the central MB and negative sign in the eastern MB, whereas the canonical patterns for temperature (Fig. 4d) displayed a negative sign at all sites. The interpretation is that tree growth at the western and central (eastern) MB was negatively (positively) influenced by higher temperatures at interannual-to-decadal timescales. This gradient is similar to that described by the second tree-ring canonical pattern of std_CCA (see Supplementary Figure 4c-d). Therefore, the impact of summer temperature on tree growth was generally negative for all sites in a multidecadal perspective but at interannual time scales the influence of summer temperature was positive at the eastern sites and negative at the central and western sites.

Concerning the link between the TRW and precipitation, the canonical TRW pattern was characterized by high positive values in the Central Mediterranean, low positive values in the West and negative values in the East (Fig. 4e) The associated precipitation pattern displayed a similar structure, with the same sign (Fig. 4f), indicating that higher precipitation was linked to stronger tree growth particularly at the central MB, whereas summer rain is linked to reduced growth in eastern MB. Since the canonical patterns related to precipitation derived from std_CCA and res_CCA are very similar, only the patterns derived from the res_CCA are shown in Fig. 4.

3.4 Linking tree growth and summer climate during 1982-2012

In accordance with the correlation between the time series described above, the leading pattern of the std_CCA (Fig 5a-b) presented similar information as the leading pattern of the analysis without long-term trends (res_CCA; Fig 5c-d).

Both patterns of TRW related to temperature (Fig 5c-d) illustrated similar negative impact of summer temperature in the Italian Peninsula, whereas in the case of res_CCA, they differed in the sign of the summer temperature effect in the western Mediterranean. Since the canonical patterns are very similar, only the ones derived from res_CCA are shown. The rest of the patterns derived from std_CCA can be found in the Supplementary Figure 5. The second canonical pattern related to summer temperature describes a geographical dipole of tree growth, evident in the res_CCA (Fig. 5 e-f).

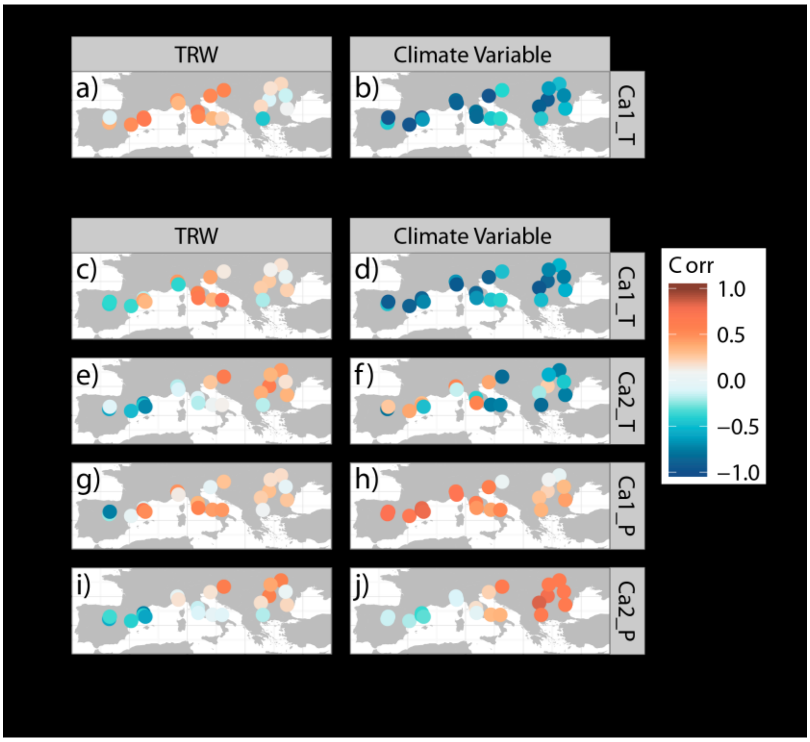

Figure 5. *Canonical patterns corresponding to the period 1982-2012 for every significant pair of canonical axes.* ***a-b)*** *leading significant pair of tree-ring width (TRW) and summer temperature (Ts) from the std_CCA;* ***c-d)*** *first significant pair of TRW-Ts derived from res_CCA;* ***e-f)*** *second significant pair of TRW-Ts derived from res_CCA;* ***g-h)*** *first significant pair of TRW and summer precipitation (Ps);* ***i-j)*** *second significant pair of TRW_Ps. The rest of canonical patterns corresponding to the significant axes of the std_CCA can be found in Supplementary Figure 5.*

The canonical axes related to summer precipitation reproduced similar canonical patterns as those described by the analysis with summer temperature. The first pair (Fig. 5g-h) encapsulated a gradient similar to the first pattern related to summer temperature (Fig. 5 c-d), with values of TRW anomalies stronger in the central Mediterranean. The second pair of canonical patterns related to summer precipitation (Fig. 5i-j), which only appeared significant in the later period, described the same geographical dipole pattern as the second mode related to temperature (Fig. 5e-f). According to this canonical pattern, summer precipitation positively influenced tree growth at eastern and western sites and no clear effect is observed on the central MB populations. In this climatic configuration, dry summers (detrimental to tree-growth) in the west correspond to favorable years in the east and vice versa.

3.5 Links to atmospheric circulation

The correlation between the TRW canonical time series and the field of geopotential height allowed identifying the atmospheric circulation linked to the canonical patterns of summer temperature and summer precipitation, which are almost identical in most of cases. The link between tree growth and summer climate in the MB was essentially explained by a single mode of atmospheric cyclonic circulation during the first period of study and by two modes during the second period. During the period 1950-81, the leading circulation mode was centred on the MB and linked to higher precipitation and lower temperatures in the Italian peninsula, to northerly advection in the Western Mediterranean and to southerly advection in the Eastern Mediterranean (Fig. 6a). The leading pattern related to summer precipitation represented the same cyclonic circulation as the pattern related to summer temperature (Supplementary Figure 6a). This leading pattern of cyclonic circulation became more pronounced and displaced towards the western MB basin during the period 1982-2012 (Fig. 6b; Supplementary Figure 6b). The new (second) geopotential height pattern in the latter period represents cyclonic circulation centered in the eastern half of the basin and linked to higher summer precipitation and lower summer temperatures (Fig. 6c; Supplementary Figure 6c).

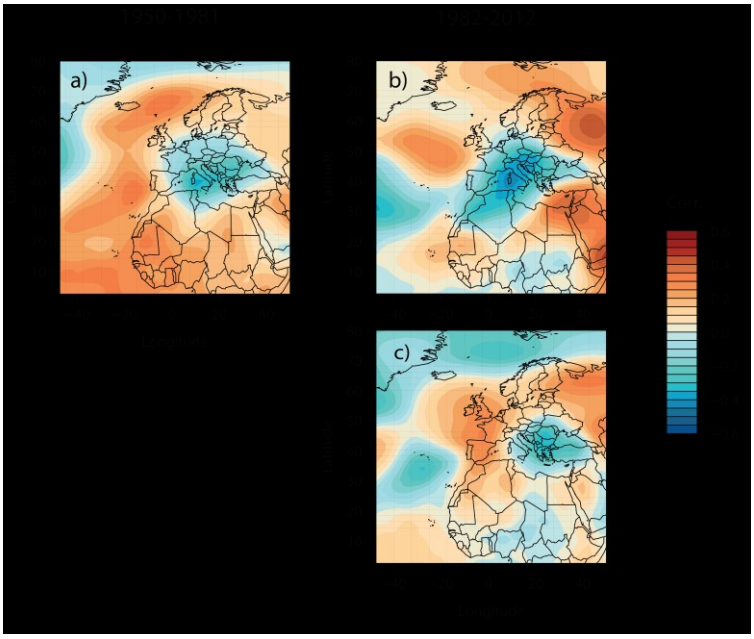

__Figure 6.__ Spatial patterns of correlations of significant canonical axes with the field of 850mb geopotential height (NCEP/NCAR). The canonical axes related to tree ring-width (TRW) derived from the residual analysis (res_CCA) with summer temperature are used. __a)__ field correlation of the leading canonical mode of TRW and summer temperature for the period 1950-1981; __b-c)__ field correlation of the first and second significant canonical modes of TRW and summer temperature for the period 1982-2012, respectively. The spatial patterns of correlations of the significant canonical axes derived from TRW and summer precipitation can be found in Supporting Information.

4. Discussion

4.1Growth of rear-edge deciduous forests at the MB is not increasing

In temperate and boreal forests, rising temperatures and the increasing concentration of atmospheric CO_2 have been found to stimulate growth (e.g., Salzer et al., 2009; Pretzsch et al., 2014), most likely due to the lengthening of the growing season (Menzel and Fabian, 1999; Menzel et al., 2006) and the CO_2 fertilization effect (Luo et al., 2006; Huang et al., 2007; Bonan, 2008; Guiot et al., 2010). However, the potential positive effects of climate change on tree growth are not so evident at the MB (Andreu-Hayles et al., 2011; Peñuelas et al., 2011). The 21 marginal deciduous populations considered in the present study show a general reduction in growth during the last three decades. Beech stands displayed a decrease in growth more often than oak stands, which can be related to the lower drought tolerance of beech: under drought stress, since oak usually maintains higher stomatal conductance and higher photosynthetic rates than beech (Raftoyannis and Radoglou, 2002; Aranda et al., 2005; Pretzsch et al., 2012). However, and despite these species-specific ecophysiological particularities, the sensitivity of the studied populations to summer climate was found here to be more related to their geographical location than to the tree species.

Thus, the results of this study support the hypothesis that site effects prevail over the phylogenetic determinism at the rear-edge populations (see Cook et al., 2001). The position in the east-west gradient within the rear-edge network seemed to be more determinant for tree growth than other geographical features such as altitude. Overall, western populations displayed more significant negative growth trends than eastern populations and these growth trends were mainly confined to the leading mode related to temperature. This indicates that summer temperature might be the main contributor to decreasing long-term growth trends, whereas the contribution of summer precipitation was restricted to interannual-to-decadal variations. However, differences observed in the sign of correlation when comparing canonical patterns with and without long-term trends revealed that some trends were likely not related to summer temperature (i.e., eastern MB populations during the period 1950-1981) and might result from climate variations in a slightly different season from the one considered in this study (i.e., early summer; Piovesan et al., 2005; Di Filippo et al., 2010; Rozas, 2015), or from management activities (growth release as a consequence of tree harvesting).

4.2 Increasing relevance of summer climate for tree growth

The increase in the variance explained by the canonical analysis between the two subperiods evidenced the enhancement of the summer climate influence on tree growth during recent decades (Anderegg et al., 2012; Allen et al., 2015).

Summer temperature has been a dominant driver of tree growth during the last six decades, whereas summer precipitation gained a more prominent role since 1980s, as shown by the increase in the explained variance. Furthermore, the similarity of the significant canonical axes obtained from the std_CCA and res_CCA also revealed an increased (decreased) relevance of interannual and decadal (multidecadal) variations of summer climate in tree growth. However, the effect of summer climate at the different locations has changed through time. Summer temperature exerted an opposite effect in eastern (positive) and western (negative) MB until the 1980s, pointing to high temperature-induced growth limitation in the western (Rebetez et al., 2006; Williams et al., 2013; Allen et al., 2015) but not in the eastern sites. From 1980 onwards, summer temperature has generally been detrimental for tree-growth in the rear-edge deciduous forests, concurrent with the higher amount of negative growth trends discussed above. Similarly, summer precipitation has also exerted a polarized influence on tree growth until the 1980s, positive (negative) on western and central (eastern) MB populations. The positive effect of summer precipitation on growth at the central and western populations most likely relates to the alleviation effect produced by an increased water availability under high summer air temperatures (Farquhar, 1978). However, under a non-moisture or temperature limiting context (i.e., eastern MB during 1950-1981), a surplus of water can be even counterproductive for tree growth due to the waterlogging-induced soil anoxic conditions that affects the mineral nutrition of trees in multiple ways (Kreuzwieser et al., 2004; Kreuzwieser and Gessler, 2010) or because several consecutive days of cloudy weather can reduce the amount of sunlight available for photosynthesis (Alton, 2008).

The effect of summer precipitation on tree growth has been more spatially variable since 1980s, including non-significant effects for some populations. Higher temperatures and more intense drought are known to induce stomata closure at all canopy levels (Sp_1, Aranda et al., 2000), and they may also have forced trees to modify their phenology and start growing earlier in spring (Piovesan et al., 2005; Di Filippo et al., 2010; Shestakova et al., 2016). High temperatures are known to even promote a summer quiescent period in other tree species at the MB (i.e., Gutiérrez et al., 2011), which could explain the unresponsiveness of some sites to summer precipitation.

4.3 SNAO-like patterns have enhanced geographical differences in summer climate during recent decades

According to our results, the link between summer climate and tree growth during the last six decades at rear-edge populations in the MB can be largely explained by the main cyclonic circulation patterns related to summer temperature variability described by Xoplaki et al. (2003). The leading pattern correspond to the first canonical mode of Xoplaki et al. (2003) who reported a positive phase of summer air temperature variability associated with blocking conditions, subsidence and stability related to warm Mediterranean summers. A cooling phase pattern was dominant during the period 1950-81 and exerted a prevailing influence on broadleaf forests in Italy, where cyclonic conditions lead to more rain and lower summer temperatures that positively influenced tree growth, and opposite effects in eastern and in western MB forests. In addition, the synoptic maps of correlations of the first significant canonical axes with geopotential height show a spatial coherence with the long-term reconstruction of Mediterranean drought variability (cf. Fig. 6b with Figs. 6-7 in Cook et al. 2016), with a north-south antiphasing in the eastern basin that becomes more pronounced in the recent period. This leading pattern of cyclonic circulation became more pronounced in recent decades, but displaced towards the central-western MB basin during the period 1982-2012 where the impact of climate variation was most severe also in terms of forest dieback (e.g. Di Filippo et al. 2010).

During recent decades, a new significant geopotential height pattern of North Mediterranean summer climate has appeared, consisting of an east-west seesaw that show a strong similarity to the second circulation pattern described by Xoplaki et al. (2003). This second pattern is linked to lower temperatures and higher precipitation in the eastern MB and northerly air advection in the western Europe including the MB. The east-west polarity observed in tree growth is not due to different climate drivers governing tree growth on eastern and on western MB (e.g., Seim et al., 2015) but to an east-west climate dipole (i.e., when the summer climate is harsher in the western MB, conditions are cooler in the eastern and vice versa). This pattern bears some resemblance to the spatial pattern usually ascribed to the Summer North Atlantic Oscillation (SNAO; Hurrel and Folland, 2002; Folland et al., 2009; see also Supplementary Figure 7) although in our analysis we considered the three summer months and not only July and August as in Folland et al. (2009). However, since the west sector of this dipole includes the Mediterranean SW Europe, an area not reported in other studies (e.g. Trouet et al. 2012), further studies are needed to fully evaluate the role of the SNAO.

High SNAO is generally associated with positive (negative) summer temperature anomalies in western (eastern) MB (Folland et al., 2009, see also Supplementary Figure 8) and wetter conditions over southern Europe, particularly in the central and eastern MB (Folland et al., 2009; Bladé et al., 2012a). Thus, under the global warming and during high phases of SNAO, tree growth may be less limited in the eastern than in western MB due to cooler summer temperatures and higher precipitation. Such a dipole pattern might be further enhanced during negative phases of the East-Atlantic pattern (Bastos et al., 2015). The net effect of the SNAO on the central MB (Italian Peninsula) is less distinct, probably due to its location at the interface between western and eastern MB.

The strengthening of the relationships between interannual variations of the SNAO-like pattern and tree growth during the last decades is consistent with the reported higher values of the SNAO index since the 1970s compared to previous decades (Folland et al., 2009, Supplementary Figure 8). In fact, the SNAO has become a dominant atmospheric dynamical pattern for summer precipitation during the last three decades, particularly over eastern MB (Bladé et al., 2012a).

4.4 Implications for forest modelling

Our results show that variability linked to SNAO has gained a larger relevance in regional summer climate leading to an east-west see-saw summer climatic gradient mirrored by the tree response to climate. Although the predicted SNAO trend sign over the 21st century is being debated (Bladé et al., 2012b; Cattiaux et al. 2013; Hanna et al., 2015), the spatially heterogeneous impact of the SNAO implies that under more frequent high SNAO phases, the persistence and survival of marginal deciduous forests may diverge in the future between the western and the central/eastern MB. While western MB may suffer from the combined effect of higher summer temperatures and no increase in summer precipitation, eastern MB forests may benefit from temperatures cooler than in the west and from sustained summer rain that alleviates the evaporative demand. The geographical location of the Italian peninsula in the transition between eastern-western MB hampers an evaluation of SNAO net effects on the forests of this region. Distinguishing the effects due to vapor pressure deficit from those due to drought (water potentials) is difficult, but trees growing under both drought and high temperatures are more prone to die (Adams et al., 2009). Therefore, if the frequency of higher SNAO phases continue in the future as in the recent decades, forests on western MB could be more susceptible to dieback phenomena than forest in eastern MB. Indeed, forest dieback has been more often reported in western and central than eastern MB in recent decades (i.e., Allen et al., 2010).

An accurate prognosis of how the forests will respond to changes in climate at the MB depends to a great extent on the ability of the climate models to simulate future climate trends. However, climate models from the CMIP3 do not reproduce the east-west geographical polarity described by the observational records (Bladé et al., 2012a, 2012b; Kelley et al., 2012; Barkhordarian et al., 2013) and also visible in some long-term paleorecords (i.e., Dermody et al., 2012; Roberts et al., 2012; Mensing et al., 2016). The latest generation of climate models (CMIP5) did not show improvements in this regard (Baker and Huang, 2014). As a consequence, the MB is generally simulated as a homogenous domain instead of showing an east-west pattern of summer climate. The reasons for this contrast of simulations *versus* observations is unclear (i.e., whether climate trends are a result of anthropogenic forcing or multidecadal internal variations). However, the shortcoming in the projections of summer climate changes may propagate into simulations of future species distribution or tree growth that use simulated climate data (i.e., Keenan et al., 2011).

Our results also revealed that multidecadal variations were not only related to changes in summer climate and, thus, other factors potentially giving rise to multidecadal variations and long-term growth trends such as climate variation in other seasons or competition among trees, should eventually also be taken into account.

Future projections of tree growth and species distribution models in the MB should take into consideration the differences in the regional climate trends as well as the underlying causes. Accurate projections of forest growth are relevant not only as a climate impact but also as a factor contributing to climate change, since changes in forest coverage and species composition may also feed-back onto further altering circulation and precipitation patterns by contributing to changes in temperature and energy gradients (Swann et al., 2012).

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