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Factors driving growth responses to drought in Mediterranean forests

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Abstract We lack information regarding the main factors driving growth responses to drought in tree species with different vulnerability against this stressor and considering sites with contrasting climatic conditions. In this paper, we identify the main drivers controlling growth response to a multi-scalar drought index (Standardized Precipitation Index, SPI) in eight tree species (*Abies alba*, *Pinus halepensis*, *Quercus faginea*, *Pinus sylvestris*, *Quercus ilex*, *Pinus pinea*, *Pinus nigra*, *Juniperus thurifera*). We sampled forests growing across a pronounced climatic gradient under Mediterranean conditions in north-eastern Spain. To summarize the patterns of growth responses to drought, we used principal component analysis (PCA). To determine the main factors affecting growth responses to drought, correlation and regression analyses were carried out using a set of abiotic (climate, topography, soil type) and biotic (Normalized Difference Vegetation Index, Enhanced Vegetation Index, tree-ring width, diameter at breast height) predictors and the PCs loadings as response variables. The PCA analysis detected two patterns of growth responses to drought corresponding to xeric and mesic sites, respectively. The regression analyses indicated that growth responses to drought in xeric forests were mainly driven by the annual precipitation, while in mesic sites the annual water balance was the most important driver. The management of Mediterranean forests under the forecasted warmer and drier conditions should focus on the main local factors modulating the negative impacts of drought on tree growth in xeric and mesic sites.

Keywords Dendrochronology · Drought · Iberian Peninsula · Radial growth · Standardized precipitation index

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Introduction

Warming-related water deficit is one of the major drivers of growth dieback and related mortality episodes in forests affecting selectively tree species, stands, and trees (Allen et al. 2010; Koepke et al. 2010). Drought causes reductions in radial growth and alterations in hydraulic conductivity (McDowell et al. 2008) and decreases productivity due to limitations in water use and photosynthesis (Hsiao 1973; Flexas and Medrano 2002). These effects are enhanced particularly in Mediterranean drought-prone forests where water availability is the main factor constraining growth (Pereira and Chaves 1995; Vicente-Serrano et al. 2006; Sarris et al. 2007, 2011; Linares et al. 2009, 2010).

Different studies evidence that our understanding of the drought impact on growth of tree species at different time scales and across contrasting site conditions is still very limited (Orwig and Abrams 1997; Adams and Kolb 2005).

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Usually, radial growth of tree species and populations growing in xeric sites are more affected by drought than in mesic locations (Abrams et al. 1998). However, other researchers argued that species growing in xeric sites show adaptive features to withstand the negative effects of drought (De Luis et al. 2007; McDowell et al. 2008; Linares et al. 2010). This implies that these drought-adapted species may be less vulnerable against drought stress, in terms of growth, than species inhabiting wet sites.

The lacking information regarding the factors driving the spatial and temporal patterns of growth responses to drought may be partially obtained by quantifying growth trends across environmental and climatic gradients. Growth responses to drought can vary as a function of the species' responsiveness to water deficit (Orwig and Abrams 1997; Bogino and Bravo 2008), site features (Tardif and Bergeron 1997; Macias et al. 2006; Linares and Tíscar 2010), and characteristics of trees (size, age, competition, genetic differences) (De Luis et al. 2009; Kuparinen et al. 2010; Linares et al. 2010).

During the second half of the twentieth century, climate trends in the Western Mediterranean Basin were characterized by remarkably high air temperatures and an increase in both the frequency and severity of droughts (Houghton et al. 2001; García-Ruiz et al. 2011; Xoplaki et al. 2006). These conditions are expected to be intensified in the future under warmer conditions enhancing evapotranspiration and water deficit in many forested areas (Giorgi and Lionello 2008). In Circum-Mediterranean forests, several studies have emphasized that the inter-annual variability of precipitation and drought occurrence are among the main constrains of tree growth (Andreu et al. 2007; Sarris et al. 2011). However, previous works in mountain forests also found that the regional climatic conditions can be greatly modulated by site features such as elevation or topography (Rolland et al. 1999; Tardif et al. 2003). These local factors may impose additional risks exacerbating drought stress (e.g., rocky soils or steep slopes) or they may partially mitigate its negative effects on tree growth (e.g., deep soils or northern aspects). For instance, water deficit has been linked to growth decline of tree populations mainly located in xeric sites (Martínez-Vilalta and Piñol 2002; Camarero et al. 2011).

In this study, we aimed: (i) to describe the spatio-temporal growth responses to drought across a wide climatic gradient in north-eastern Spain and (ii) to detect the main drivers influencing these responses. We studied eight tree species with contrasting sensitivity to drought stress ranging from pine species in semi-arid areas (e.g., *Pinus halepensis*) to fir species dominating wet sites (e.g., *Abies alba*), thus providing a wide ecological gradient representative for many Mediterranean forests.

Materials and methods

Study area

The study area includes forests located in Aragón, north-eastern Spain (Fig. 1; see sites in Table 1 in Pasho et al. 2011). This area is under Mediterranean influence with a strong climatic gradient ranging from semi-arid conditions in the Middle Ebro Basin (mean annual temperature 15.0 °C, total annual precipitation 318 mm) to humid conditions northwards in the Pyrenees (mean annual temperature 8.5 °C, total annual precipitation 1,750 mm). The seasonal variability in precipitation is more pronounced in the Middle Ebro Basin than in the Pyrenees and severe summer droughts (periods of more than 80 days without precipitation) are common in the former area (Vicente-Serrano and Beguería 2003). In the Middle Ebro Basin, the lithology is characterized by millstones and gypsums (Peña
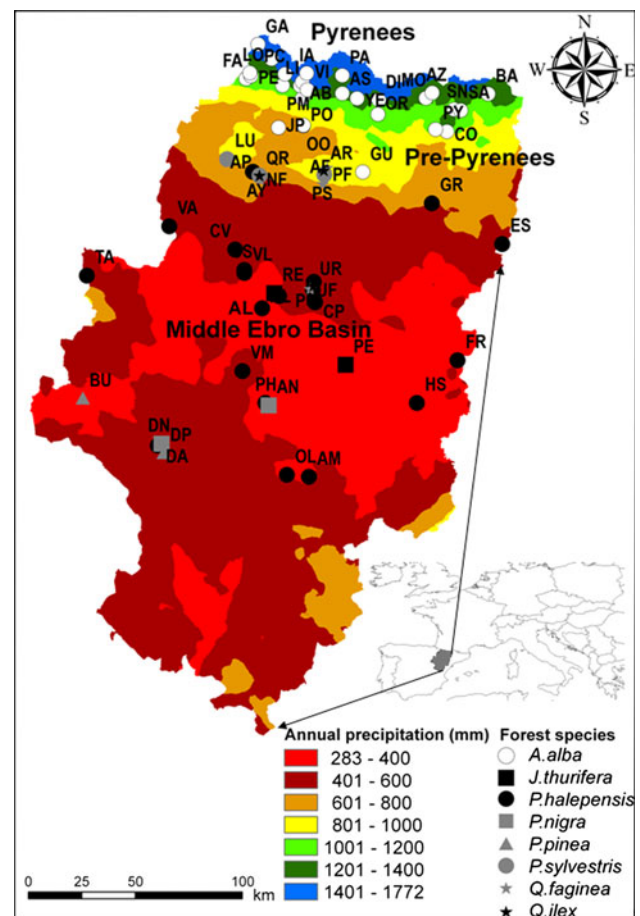

Fig. 1 Location of sampled sites and annual precipitation values in Aragón, north-eastern Spain. *Different symbols* and *colors* represent different tree species and precipitation ranges, respectively. The three sub-areas studied (Pyrenees, Pre-Pyrenees, and Middle Ebro Basin) are also indicated in the map. Sites' codes are as in Table 1 in Pasho et al. 2011

Table 1 Significant ($P < 0.01$) correlations between explanatory variables and the first two principal components (PC1, first component; PC2, second component) summarizing the growth responses to drought

Type of variables	Explanatory variables (abbreviations, units)	PC1	PC2
Tree variables	Diameter at breast height (DBH, cm)	−0.70	0.63
	Tree-ring width (TRW, mm)	−0.46	0.44
Remote sensing variables	Annual NDVI (NDVI)	−0.73	0.64
	Annual EVI (EVI)	−0.66	0.62
	April-June NDVI (AJ NDVI)	−0.78	0.71
	April-June EVI (AJ EVI)	−0.71	0.71
Soil variables	Inceptisol (IS)	−0.72	0.72
Climatic variables	Annual water balance (WB, mm)	−0.85	0.78
	Annual precipitation (AP, mm)	−0.85	0.75
	Annual potential evapotranspiration (PET, mm)	0.64	−0.65
	Mean maximum annual temperature (AMxT, °C)	0.80	−0.70
	Mean minimum annual temperature (AMiT, °C)	0.79	−0.67
	July mean maximum temperature (JMxT, °C)	0.79	−0.70
	January mean minimum temperature (JMiT, °C)	0.74	−0.61
	Incoming solar radiation (R, W m^{-2})	0.38	−0.48
Topographic variables	Elevation (E, m)	−0.78	0.66
	Slope (S, %)	−0.70	0.54

et al. 2002), which contribute to aridity due to their poor ability to retain water (Navas and Machín 1998). In the Pyrenees, soils are usually deep and basic and develop over limestone, sandstones, and granites.

The study area is characterized by a variety of forest types and vegetation communities mostly determined by climate (Costa et al. 2005). Most of the studied sites are located in the mountainous Pyrenean area forming pure stands or mixed conifer-hardwood forests (e.g., silver fir, *Abies alba* Mill.). Southwards, in sub-Mediterranean areas of the Pre-Pyrenees, forested landscapes comprise stands of *Pinus sylvestris* L., *Pinus pinea* L., *Pinus nigra* subsp. *salzmannii* (Dunal) Franco., *Quercus faginea* Lam., and *Quercus ilex* L. subsp. *ballota* (Desf.) Samp. In the semi-arid Middle Ebro Basin, the forests and woodlands are dominated by *Pinus halepensis* Mill., with a few relict populations of *Juniperus thurifera* L. The *P. halepensis* forests in the Middle Ebro Basin commonly occur on plateaus and slopes of structural platforms developed on Miocene carbonate and marl sediments, whereas the valley bottoms have been traditionally used for agriculture and livestock grazing.

Dendrochronological methods

To reconstruct recent growth trends in the studied sites, we used dendrochronological methods. Forests were selected based on: (i) the species dominance in the canopy over at least 1 hectare of fully forested area and (ii) the occurrence of harsh environmental conditions potentially constraining tree

growth such as steep slopes or shallow or rocky soils. The selected sites were considered to capture most of the climatically mediated growth variability of the studied species in north-eastern Spain (see Pasho et al. 2011). In addition, the sampling strategy was adjusted according to the biogeography of the investigated species. In this regard, we only sampled one *A. alba* stand near the southernmost distribution limit of the species because similar populations may be more drought stressed than other located in more mesic sites at higher latitudes. The sampled *A. alba* sites are considered mesic in terms of the species' distribution across Europe since the climatic conditions and the coexisting species (e.g., *Fagus sylvatica* L.) are similar to other mixed silver fir stands in mesic areas from Central Europe. At each of 65 sites visited in the field, 10–35 dominant trees separated by at least 10 m were randomly selected, their diameter at 1.3 m (Dbh) was measured, and they were sampled (see Table 1 in Pasho et al. 2011). Two radial cores per tree were extracted at 1.3 m height using a Pressler increment borer. The cores were prepared following standard dendrochronological methods (Fritts, 2001). They were air dried, mounted, and sanded with sandpapers until tree rings were clearly visible with a binocular microscope. All samples were visually cross-dated and the ring width was measured to a precision of 0.001 mm (accuracy ± 0.0003 mm), using a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating was evaluated using the COFECHA program (Holmes 1983).

To retain the high-frequency variability of growth, each ring-width series was double-detrended using a negative

exponential function and a spline function with a 50 % frequency response of 32 years. Detrending and standardization involved transforming the measured values into dimensionless indices by dividing the raw values by the expected values given by the negative exponential and spline functions. Autoregressive modeling was carried out on each series to remove the temporal autocorrelation. The indexed residual (pre-whitened) series of all trees within each site were then averaged using a biweight robust mean to obtain mean site residual chronologies of ring width which were used in further analyses. We used the program ARSTAN to obtain the residual site chronologies (Cook 1985).

The quality of the chronologies was evaluated for the common period 1970–1999 using several dendrochronological statistics (Briffa and Cook 1990): the mean width and standard deviation (SD) of the raw ring-width series; the first-order autocorrelation (AC1) of raw series, which measures the year-to-year persistence; the mean sensitivity (MSx) of the residual series, which quantifies the relative change in width among consecutive years; the mean correlation (Rbar) among individual series within each site; and the expressed population signal (EPS) of residual series, which indicates to what extent the sample size is representative of a theoretical infinite population. The common period 1970–1999 was selected because all chronologies showed EPS values above the 0.85 threshold for this interval, and such threshold is widely recognized in dendrochronological studies for accepting mean growth series as being well replicated (Wigley et al. 1984).

Drought index calculation

To quantify the impact of drought on forest growth, we employed the Standardized Precipitation Index (SPI). The SPI has the advantage of allowing the determination of duration, magnitude, and intensity of droughts and can be calculated at different time scales (Hayes et al. 1999). The quantification of droughts at different time scales is important in determining their ecological impacts, considering the different physiological strategies of vegetation to deal with water deficit (Hsiao 1973).

The SPI is calculated using precipitation data and it was developed by McKee et al. (1993) to identify the varied times of response of different hydrological systems to precipitation deficits. The precipitation data in the region have been obtained from a homogeneous and spatially dense dataset of local observatories (Vicente-Serrano et al. 2010). Nevertheless, since the available observatories are commonly located near populated areas, few stations are available in mountainous locations where we sampled many of the studied forests. For this reason, the available local precipitation data were interpolated at a spatial

resolution of 1,000 m and converted to monthly data for the period 1950–2006 to have a regular grid with information in each one of the sampled forests. To take into account the effect of elevation on precipitation, the interpolation was done using a Digital Terrain Model (DTM) and a Geographic Information System assisted regression-based approach (Vicente-Serrano et al. 2003, 2007; Ninyerola et al. 2007). The precipitation in each 1,000-m grid point was estimated by means of a stepwise-regression model in which the independent variables were the elevation, the latitude, and the longitude of each site. The residuals, that is, the differences between the observations and the modeled precipitation, were also included in the estimations by means of a local interpolation procedure (splines with tension, see Mitasova and Mitas 1993) to include the local precipitation features which were not well captured by the regression models.

The validation of the gridded monthly layers was done for each layer by a jackknifing method, based on withholding, in turn, one station out of the network, estimating regression coefficients from the remaining observatories and calculating the difference between the predicted and observed value for each withheld observatory (Phillips et al. 1992). The average root mean square error for the different months and years was 15.2 mm, being lower in summer (6.5 mm) than in winter (22.3 mm). The D agreement index (Willmott 1982) showed an average of 0.94 for the different monthly layers, with a range between 0.82 and 0.99, which indicates a high reliability between the observed and the modeled precipitation data.

An average monthly precipitation series was obtained for each one of the 65 sites using the gridded monthly precipitation data. From each series, we obtained the SPI at time scales ranging from 1 to 48 months to obtain a wide range of time scales to be compared with growth. Positive and negative SPI values correspond to wet and dry conditions, respectively. SPI values below -2.0 indicate extreme droughts. The SPI was calculated by adjusting the precipitation series to a given probability distribution. Initially, the SPI was calculated following a Gamma distribution (McKee et al. 1993), but further analyses indicated that the Pearson III distribution was more robust (see Vicente-Serrano 2006).

Factors affecting growth-drought responses: climate, topography, remote sensing data

We used climatologies for different variables obtained from the digital climatic atlas of Aragon at a spatial resolution of 1 km (Cuadrat et al. 2007). The climatic variables used in the study were: annual water balance, annual precipitation, annual potential evapotranspiration, annual mean maximum temperature, annual mean minimum

temperature, July mean maximum temperature, January mean minimum temperature, and solar radiation. The incoming solar radiation, which provides information on the slope aspect, was obtained using a terrain model (Pons and Ninyerola 2008) implemented in the MiraMon Geographical Information System (Pons 2011). For each sampled forest, the average value of these variables was extracted.

The topographic data consisted of the following variables: elevation (m) recorded at each sample plot by using a GPS and slope (%) derived by using a DTM of the area with a spatial resolution of 100 m. The soil types were determined by using the Spanish soil map developed by the Spanish Geographic Institute following the Soil Taxonomy of the USDA (IGN 2006).

To evaluate the potential roles of the differences in leaf activity and leaf-area index in explaining the spatial differences in the growth responses to drought, we used remote sensing data to quantify these variables in each forest. The utility of remote sensing for vegetation monitoring is based on the response of vegetation cover to radiation in the visible and near-infrared regions of the electromagnetic spectrum (Myneni et al. 1995). Visible radiation is mainly absorbed by vegetation in photosynthesis processes while near-infrared radiation is principally reflected, owing to the internal structure of leaves (Knipling 1970). High vegetation activity is characterized by low reflectivity of solar visible radiation and high reflectivity in the near-infrared region of the spectrum.

Different indices have been developed for monitoring and measuring vegetation status using spectral data (Bannari et al. 1995). Among them, the most widely used is the Normalized Difference Vegetation Index (NDVI) (Rouse et al. 1973). Numerous authors have pointed out the close relationship between NDVI and several ecological parameters (e.g., Vicente-Serrano et al. 2010). The NDVI measures the fractional absorbed photosynthetically active radiation (Myneni et al. 1995) and exhibits a strong relationship with vegetation parameters such as green leaf-area index (Carlson and Ripley 1997). In addition, we also used the Enhanced Vegetation Index (EVI) since this index enhances the vegetation signal with improved sensitivity in high biomass regions and allows improved vegetation monitoring through a decoupling of the canopy background signal and a reduction in atmosphere influences (Huete et al. 2002).

Time series of NDVI and EVI covering the period 2000–2010 were used in the study. The data were obtained from the products of Moderate Resolution Imaging Spectro-radiometer (MODIS 13A1 product, 16-day at 500-m resolution; available at http://www.daac.ornl.gov/MODIS/modis.html in HDF format; see Huete et al. 2002). Data processing included images re-projected from a Sinusoidal to a UTM-30 N–S/IGN projection, images stacking to provide a full coverage of the study area, and crossing of the images with forest sites location to extract the NDVI and EVI values at each sampled forest. Subsequently, the mean annual and April-June (period with the highest forest activity; see Vicente-Serrano et al. 2010) NDVI and EVI values were calculated and used in further analysis.

Statistical analyses

The spatial variability of growth responses to the drought index (SPI) was analyzed by using a S-mode principal component analysis (PCA) which enabled common features to be identified and relevant local characteristics to be detected (Richman 1986). The PCA was performed on a covariance matrix calculated from the correlations between the 1–48 time scales SPIs and the residual ring-width chronologies for all sites (Legendre and Legendre 1998). The number of components was selected based on those with eigenvalues greater than 1, and the components were rotated (Varimax) to redistribute the final explained variance and to obtain more stable and robust spatial patterns (Richman 1986). Components were presented in the non-standardized original units to make the interpretation easier. For this purpose, the loadings at each forest site were multiplied by the coefficient scores of each principal component and summed up by rows. In other words, the PC scores were converted to correlation values, summarizing the correlation series at all forest sites. The geographical variability in terms of forest response to drought was identified by mapping the factorial loadings.

To detect the factors which potentially affect the growth responses to drought, correlation and regression analysis were carried out between the PCs loadings and a set of abiotic (climatic and topographic variables, soil type) and biotic (Dbh, mean tree-ring width for the period 1970–1999, NDVI, and EVI) variables. Categorical variables, like the soil type, were converted to binary variables to be included in the regression analyses. The importance of each variable was assessed by using a forward selection method which starts with no variables in the model, trying out the variables one by one, and including them if they were significant ($P \leq 0.05$).

Results

Spatial patterns of the growth responses to drought

The first two components of the PCA accounted for 75.1 % (PC1, 41.3 %; PC2, 33.8 %) of the total amount of the variability of growth responses to drought. The PCs correlation coefficients, summarizing the species' growth responses to drought at xeric and mesic areas, showed that
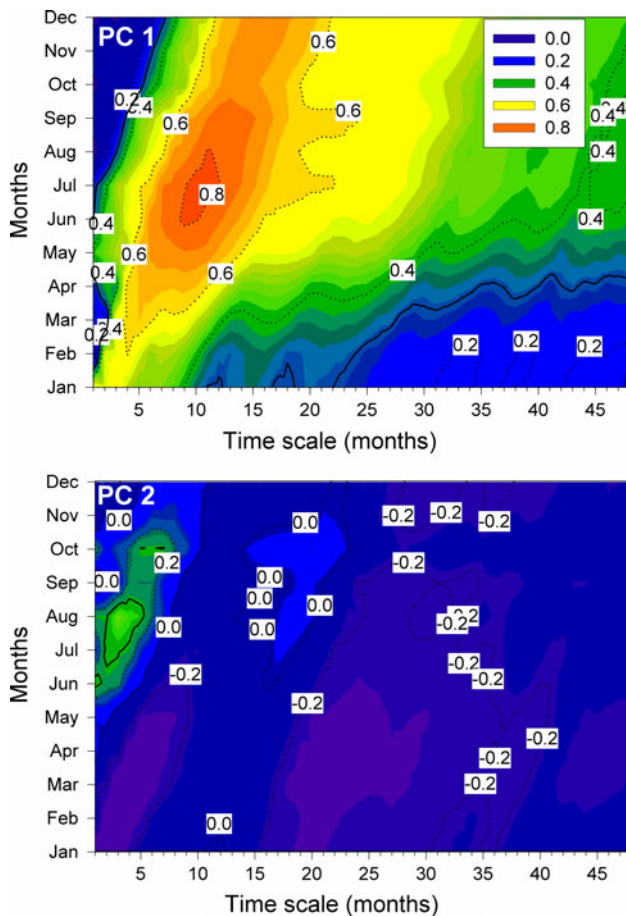
Fig. 2 First (PC1) and second (PC2) principal components summarizing the correlations between all ring-width chronologies and monthly drought (SPI) series at different time scales. *Bold lines* frame significant correlations ($P \leq 0.05$)

tree species associated with the first principal component (PC1) presented significant correlations ($r > 0.29$) at all time scales, with the highest ones ($r > 0.80$) achieved at time scales ranging between 9 and 12 months, during summer months (Fig. 2). The second principal component (PC2) captured significant growth responses to drought at 2–5 month scales, again during summer.

The spatial distribution of the loadings of the PC1 and PC2 components shows two clear spatial patterns of responses to drought across the study area (Fig. 3). The first pattern represented by PC1 was found in the southern study area (Middle Ebro Basin), while the second one described by the PC2 corresponded to the northern study area (Pyrenees). The PC loadings of each forest indicated that the highest contribution to the PC1 variability was accounted for by species growing in xeric locations such as *P. halepensis*, *P. nigra*, *P. pinea*, *J. thurifera*, *Q. faginea*, and *Q. ilex*. On the other hand, the PC2 captured the growth responses to drought expressed by species

located in sub-Mediterranean and mesic sites (*A. alba*, *P. sylvestris*).

Drivers of the growth responses to drought

The associations between abiotic and biotic variables and the two first principal components (PC1, PC2) summarizing the growth responses to drought indicated that tree-related (Dbh, tree-ring width), remote sensing (NDVI, EVI), climatic (water balance, precipitation) and topographic variables were significantly ($P < 0.01$) and inversely correlated with the PC1 (Table 1). Most climatic variables (potential evapotranspiration, mean maximum and minimum temperatures, July mean maximum and January mean minimum temperatures, solar radiation) were negatively related to the PC2. The PC1 was mainly driven by water availability, temperature, and elevation, while the PC2 was also strongly associated to these variables and to NDVI and EVI data.

The regression analysis indicated that four variables (annual precipitation, inceptisol soils, April-June NDVI, and slope) explained 78 % of the total spatial variability accounted for by the PC1 and three variables (annual water balance, April-June EVI, and inceptisol soils) determined 66 % of the variance represented by PC2 (Table 2).

The coefficients of the selected regression models (Table 3) showed that the main variable driving growth responses to drought in xeric sites represented by PC1 was annual precipitation ($P < 0.003$), followed by the soil type (inceptisol), April-June NDVI, and slope. Considering the PC2, the main driver of growth responsiveness to drought was the annual water balance ($P < 0.002$), whereas April-June EVI and soil type (inceptisol) influences were less important.

The partial correlations between the PCs and each predictor of the regression models were significant ($P < 0.05$) when the effect of the other independent variables was controlled, suggesting that the growth responses to drought in xeric and mesic sites were mainly driven by precipitation and the water balance, respectively. In fact, the PC loadings and the most important drivers of growth responses to drought confirmed the high dependence of the growth responsiveness on annual precipitation in xeric sites (Fig. 4). The variability in the responses to drought of mesic forests characterized by the PC2 was driven by the annual water balance.

Discussion

We have evaluated the growth responses to drought and factors driving this responsiveness in eight tree species growing across a wide climatic gradient by means of

Fig. 3 Spatial patterns of species' growth responses to drought as revealed by the loadings of the first (PC1) and second (PC2) principal components (*upper graphs* the size of *circles* is proportional to the loadings) and within-species variability of these responses (*lower graphs* box plots of species loadings in the two principal components, PC1 and PC2, respectively). Species codes: *Aa*, *Abies alba*; *Ph*, *Pinus halepensis*; *Pn*, *Pinus nigra*; *Pp*, *Pinus pinea*; *Ps*, *Pinus sylvestris*; *Jt*, *Juniperus thurifera*; *Qf*, *Quercus faginea*; *Qi*, *Quercus ilex*
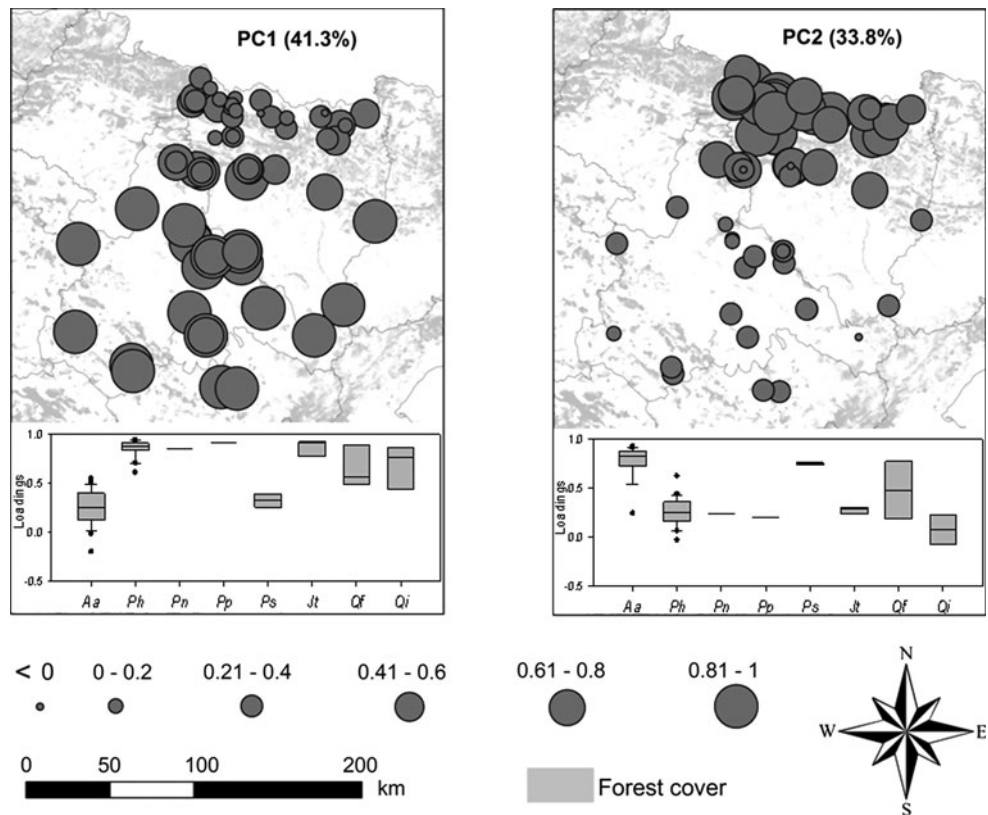

Table 2 Selected regression models explaining the patterns of the first (PC1) and second (PC2) principal components of growth responses to drought for all species and corresponding statistics (R^2adj, adjusted percentage of variability explained by models; F, F-ratio, P, probability level)

Response variables	Explanatory variables	R^2adj (%)	F	P
PC1	$1.240 - 0.001$ AP $- 0.142$ IS $- 0.471$ AJ_NDVI $- 0.002$ S	77.7	58.44	<0.0001
PC2	$0.064 + 0.001$ WB $+ 1.245$ AJ_EVI $+ 0.163$ IS	65.8	43.42	0.0001

The PCs were calculated from the matrix of correlations obtained between the 1–48 months drought index (SPI) and the residual ring-width chronologies. See variables abbreviations in Table 1

dendrochronological methods and a quantitative assessment of drought at different time scales based on the multiscalar Standardized Precipitation Index (SPI). This is the first investigation evaluating the factors responsible for the variable growth responses to drought in diverse Mediterranean forests. Particularly, we evaluated the role of biotic and abiotic variables on modulating the spatial and temporal variability within and among species in the growth responsiveness to drought focusing on contrasting environmental conditions in xeric and mesic sites.

The PCA analyses revealed two distinct spatial patterns in terms of growth response to drought across the study area corresponding to: (i) species growing in the Middle Ebro Basin (represented by PC1) under Mediterranean semi-arid conditions (all *Pinus* species excepting *P. sylvestris*, *Quercus* species, and *J. thurifera*) and (ii) species distributed in mountainous areas, (represented by PC2,

from the Pre-Pyrenees and Pyrenees (*A. alba*, *P. sylvestris*)) characterized by a humid and cold sub-Mediterranean climate.

The regression analyses showed that the annual precipitation is the main driver of forest growth sensitivity to drought in the xeric sites, indicating that in dry Mediterranean forests tree growth is mainly constrained by low water availability (Borghetti et al. 1998; De Luis et al. 2007; Vicente-Serrano 2007; Camarero et al. 2010). This has been also confirmed by additional studies on growth and phenology of pine and oaks species in nearby areas (Corcuera et al. 2004a, b; Andreu et al. 2007; Montserrat-Martí et al. 2009; Gutiérrez et al. 2011; Pasho et al. 2011). In general, these studies found important spatial variations in the growth responses to drought of forests as a function of climate conditions, confirming that forests located in the driest sites are the most sensitive to drought occurrence and

Table 3 Statistics of the coefficients of the selected regression models (see Table 2) explaining the patterns of the first (PC1) and second (PC2) principal components of growth responses to drought for all tree species

	Student t	P	Partial correlation
PC1			
Constant	15.094	<0.0001	
Annual precipitation	−3.038	0.003	−0.360
Inceptisol	−2.620	0.011	−0.316
April–June NDVI	−2.152	0.035	−0.264
Slope	−2.091	0.041	−0.257
PC2			
Constant	0.417	0.678	
Annual water balance	2.452	0.002	0.295
April–June EVI	2.884	0.008	0.341
Inceptisol	2.482	0.017	0.299

Fig. 4 Scattergram of the loadings of the first two principal components and the main predictor variables as revealed by linear regressions (see Table 3). The *different symbols* correspond to different species (see symbols in Fig. 1)
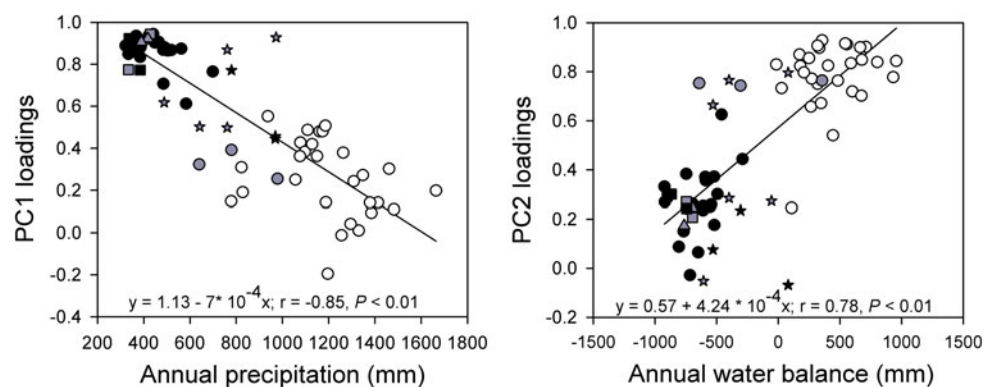
severity. Furthermore, these results suggest that growth declines in xeric areas, and plausibly dieback events and episodes of high mortality as those reported by Allen et al. (2010), will be observed in response to long-term dry conditions greatly reducing the water balance.

Contrastingly, we found that even short-term summer drought, lasting between 2 and 6 months, can affect radial growth of mountain conifers from mesic sites such as *A. alba*. This association may be explained by the low water-use efficiency of *A. alba*, which is a species whose photosynthetic rates are very sensitive to atmospheric drought (Guehl et al. 1991) and its growth rates respond to cumulative water deficit in late summer and to temperature-related drought stress (Rolland et al. 1999; Camarero et al. 2011).

The growth responses to drought of mountain forests from mesic and wet sites such as Pyrenean silver fir forests were also determined by a combined influence of several drivers, with the most significant impact exerted by annual water balance and temperature variables. In mountain conifer forests, the high temperatures in combination with strong radiation can intensify evaporation rates that additionally decrease moisture content in the upper layers of the soil and deplete moisture reserves, influencing so the soil water balance negatively (Pichler and Oberhuber 2007; Vicente-Serrano et al. 2010). Short-term warming-induced water deficits during late summer may cause growth decline and forest dieback of *A. alba* forests (Camarero et al. 2011). Hence, growth declines in silver fir forests located in the less humid sites may be expected in response to warming-induced short-term drought stress (Macias et al. 2006). In addition, the low temperatures in winter also affect growth responses to drought in mesic silver fir forests because they may cause frost-induced xylem embolism and reduce photosynthesis (Rolland et al. 1999, Aussenac 2002).

The contribution of each site to the respective first two principal components was different, indicating a site- and species-dependent variability in terms of growth responses to drought (Orwig and Abrams 1997). The species' responsiveness to drought seems to be conditioned by contrasting climatic conditions and local variability in soil water holding capacity. For example, Sánchez-Salguero et al. (2010) showed a more intense growth reduction of *P. pinaster* and *P. halepensis* in response to extreme droughts in xeric than in wet sites in south-eastern Spain.

This is in line with the findings of Fekedulegn et al. (2003) who stressed that forest responses to drought may be affected by a combination of many factors including precipitation, temperature, inherent species' characteristics, and site topographic features. These factors may impose additional constrains on the growth responses to drought. As revealed in this study, the growth sensitivity to drought was also affected by soil and topographic conditions. For instance, the lithology (millstones and gypsums) that characterize xeric environments in the study area enhance the negative effects of water deficit on growth since soils are generally shallow, characterized by limited ability to hold adequate moisture (Guerrero et al. 1999; Vicente-Serrano 2007), which increase the negative effects of drought on tree growth. In the Pyrenees, the dominant soils (e.g., inceptisol) had an inverse association with the growth responsiveness to drought, suggesting the presence of mitigating effects of the negative impacts of water deficit on growth, most likely due to the high capacity of these soils to hold water in the deeper layers. This is the case of many *A. alba* forests located in valley bottoms of the Pyrenees, characterized by deep soils and humid climatic conditions (Macias et al. 2006; Camarero et al. 2011).

We expected that topographic factors such as elevation and slope would exert contrasting influences on the species responses to drought in xeric and mesic forest sites, respectively. However, we found that the growth responses to drought were only affected by slope in the case of xeric sites (PC1), most likely due to its local influence on surface runoff and water retention by soils. The studied forests in xeric sites, mostly located in low elevation but topographically complex areas (plain localities have been mostly converted to croplands), grow under an exacerbated drought stress in undulating or moderate slopes since in these areas trees are more sensitive to the rapidly occurring water shortages (Fekedulegn et al. 2003). Topographic position has already been shown to drive the soil water availability in areas subjected to seasonal droughts affecting tree growth and the species composition of diverse ecosystems as tropical forests (Engelbrecht et al. 2007).

Xeric sites are also characterized by low precipitation and high temperatures which enhance the drought impacts on growth (Camarero et al. 2010). In these areas, high temperatures in summer most likely deplete soil water reserves causing drought-induced embolism. Slope and aspect can also influence growth locally through changes in the radiation received by trees (Tardif et al. 2003; Leonelli et al. 2009). Generally, south-facing slopes in xeric areas with low water holding capacity increase the drought impacts on tree growth (Sánchez-Salguero et al. 2010). The opposite was observed in *A. alba* forests located in north-oriented slopes with deep soils. Overall, topography acts as a local modulator of the effects of drought on growth but

further research on this subject in Circum-Mediterranean forests is desirable.

The tree features such as tree size (diameter) or the growth rate (mean tree-ring width) and vegetation activity indices (NDVI, EVI) showed positive and negative associations with the growth responsiveness to drought in xeric and mesic sites, respectively. These associations indicate that low water availability associated with prolonged and intense drought lead to a decreasing canopy growth (e.g., shoot extension, leaf production) and probably a decline in photosynthetic activity causing a reduction in cambial activity and hydraulic conductivity (Corcuera et al. 2004a, b; Linares et al. 2009; Montserrat-Martí et al. 2009; Vicente-Serrano et al. 2010). Such growth decline may further enhance the species' vulnerability against drought stress.

In conclusion, our study highlights that Mediterranean forests show high spatial and temporal variability in terms of growth responses to drought. This variability observed among species and sites was significantly driven by climatic, topographic variables, and biotic variables indicating that a combination of variables shape the species' behavior in response to drought. Since climate models predict rising temperatures and enhanced evapotranspiration for the Mediterranean Basin (Giorgi and Lionello 2008), our findings suggest that warming-related drought stress might affect growth dynamics on different time scales in mesic than in xeric forests. However, disentangling the relative effects of warmer conditions and reduced precipitation on tree growth is an unsolved challenge which probably requires a multiproxy approach based on long-term data of radial growth, isotopic discrimination in wood, and remote sensing variables.

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