RESEARCH PAPER

Diverse responses of forest growth to drought time-scales in the Northern Hemisphere

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ABSTRACT

Aim To identify the main spatiotemporal patterns of tree growth responses to different time-scales of drought at a hemispheric scale using a climate drought index and tree-ring records, and to determine whether those patterns are driven by different climate and forest features.

Location Northern Hemisphere.

Methods We used a large-scale dendrochronological data set of tree-ring width series from 1657 sites and a time-dependent drought index which incorporates information on precipitation and temperature variability (standardized precipitation–evapotranspiration index, SPEI). Correlation analysis was used to quantify how tree growth responds to different drought time-scales. Variation in the correlations was summarized using principal components analysis (PCA) and the contribution of the various environmental factors was estimated using predictive discriminant analysis (PDA).

Results The period between the water shortage and the impact on tree growth differs noticeably among forest types and tree families. There is a gradient in the response of growth to drought including: (1) forests that do not respond to drought, such as those located in cold and very humid areas; (2) forests located in semi-arid areas characterized by responses to long-term droughts; (3) forests that respond to medium- to long-term droughts subjected to subhumid conditions; and (4) forests that dominate humid sites and respond to short-term droughts.

Main conclusion Forests that experience semi-arid and subhumid conditions tend to respond over longer time-scales than those located in more humid areas. The characteristic time-scale at which forest growth mainly responds to drought is a proxy for drought vulnerability, reflecting the trees' ability to cope with water deficits of different durations and severities.

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INTRODUCTION

Water availability is one of the main constraints on forest productivity, because droughts usually trigger abrupt growth decline (Orwig & Abrams, 1997) and related die-off and high-mortality events (Bigler *et al.*, 2006; Allen *et al.*, 2010; Carnicer *et al.*, 2011). Analysing the impact of drought on tree growth is therefore a priority under the current climatic conditions, in which global warming is probably increasing the severity of droughts

(Williams *et al.*, 2013). Nevertheless, determining the vulnerability of forests to drought stress is difficult due to: (1) the variety of climate conditions in which forests develop; (2) the different biomes where forests occur, presenting contrasting structures, dynamics and compositions; (3) the different vulnerabilities of different vegetation types to drought; and (4) the lack of adequate estimates of drought stress. Among the most widely used drought metrics is the Palmer drought severity index (PDSI; Palmer, 1965). This index is, however, unable to portray

how droughts change as a function of time-scale. The concept of drought time-scale (normalized cumulative precipitation or water deficit over the previous *n* months) is critical in ecology (Vicente-Serrano *et al.*, 2013). This approach is concerned with the time lag that exists between the onset of water shortage and the identification of its consequences on growth. Thus, diverse growth responses to droughts of different duration and intensity are expected from regional to local scales depending on the climatic conditions of each site and the responsiveness of each tree species (Gutiérrez *et al.*, 2011; Pasho *et al.*, 2011).

Different techniques have been used to determine the response times of vegetation to water deficit and drought (e.g. Craine *et al.*, 2012). A robust approach is to relate multiscalar drought indices with different variables, such as the widths of tree-rings or vegetation activity measured from satellite imagery (Ji & Peters, 2003; Pasho *et al.*, 2011). The most widely used drought index calculated on different time-scales is the standardized precipitation index (SPI; McKee *et al.*, 1993), which is based on precipitation data and is recommended by the World Meteorological Organization (Hayes *et al.*, 2011). The different drought time-scales (1-month, 2-months, etc.) refer to the cumulative precipitation available during a period of *n* months, which is normalized to obtain an index that is comparable in time and space and across time-scales.

An ecologically relevant drought index must not only include information on precipitation, but also on air temperature and/or vapour-pressure deficit, which also play major roles in controlling the evaporative demand of the atmosphere and affect tree functioning (Aussenac, 2002; Williams *et al.*, 2013). This is the case for the standardized precipitation–evapotranspiration index (SPEI; Vicente-Serrano *et al.*, 2010; Beguería *et al.*, 2014), which has successfully allowed the responses of vegetation productivity and growth to drought time-scales to be measured at a global scale (Vicente-Serrano *et al.*, 2013). The SPEI shows an advantage over previous indicators in that it combines the sensitivity to the evaporative demand of the atmosphere included in the PDSI with the multiscalar character of the SPI.

Here, we aim to identify the main spatiotemporal patterns of tree-ring growth responses to drought time-scales across the Northern Hemisphere using the SPEI, and to determine if these patterns are driven by the biophysical, climatic and ecological conditions that characterize each forest. We fulfil this general objective by taking into account the role of global warming on drought severity, including both precipitation and temperature records in the SPEI calculations.

MATERIALS AND METHODS

Data sets

Drought index data set

The SPEI is based on precipitation and potential evapotranspiration (PET), and it combines the sensitivity of PDSI to changes in evaporative demand with the multiscalar nature of the SPI.

Details of the method used to calculate the SPEI can be found in Vicente-Serrano *et al.* (2010) and Beguería *et al.* (2014). As an example, we present the evolution of the 2-, 6-, 12- and 24-month SPEI between 1945 and 2006 in the Pratomagno range of the Appenine Mountains (Italy) (see Fig. S1 in Supporting Information). At the shortest time-scales (e.g. 3 months), there is a continuous alternation of dry (negative SPEI) and wet (positive SPEI) periods. At longer time-scales (e.g. 12–24 months), droughts are less frequent, but last longer than at shorter time-scales. Global SPEI data were obtained from the SPEIbase (Beguería *et al.*, 2010; available at: http://sac.csic.es/spei/database.html; last accessed 1 February 2014).

Tree-ring data set

We selected tree-ring data of forests located in the Northern Hemisphere available at the International Tree-Ring Data Bank (ITRDB) (Grissino-Mayer & Fritts, 1997). This repository contains tree-ring data from over 2000 sites covering six continents and representing over 100 tree species. These are mainly series of annual tree-ring width data obtained from extratropical forests, mostly located in North America and Europe. These series are kindly provided by dendrochronologists and are available online at http://www.ncdc.noaa.gov/paleo/treering.html (last accessed 1 February 2014). We selected tree-ring width series with at least 25 years of data within the period 1945–2009; a total of 1657 site chronologies were analysed. The mean length of the samples used was 40 years. Each local chronology represents the average growth series of several trees (typically more than ten) of the same species growing at the same site. The wood samples are taken and processed following standard protocols and taking two radial cores per tree at 1.3 m (Stokes & Smiley, 1968).

Tree-ring width measurements were detrended and standardized by the scientists who contributed the chronologies to the ITRDB. Usually, individual series of tree-ring widths are fitted with negative exponential curves or linear functions and residuals are obtained by dividing the observed by the fitted values. The resulting residuals are subjected to an autoregressive modelling and then averaged for each year using a biweight robust mean to obtain a mean chronology of growth indices for each site. Low- to medium-frequency variability and the first-order autocorrelation are both removed to obtain residual or prewhitened tree-width indices. The comparison of several detrending types did not alter the main patterns of tree-ring width responses to the SPEI (Fig. S2).

Statistical analyses

The influence of droughts on tree growth was assessed using Pearson correlation coefficients computed between the residual site chronologies of tree-ring width indices and the 1- to 24-month SPEI series of the 0.5° grid that included the corresponding site (see, for example, Fig. 1). Thus, for each tree-ring width series, we obtained 288 correlations (12 months × 24 time-scales). The 1- to 24-month SPEI series were detrended for
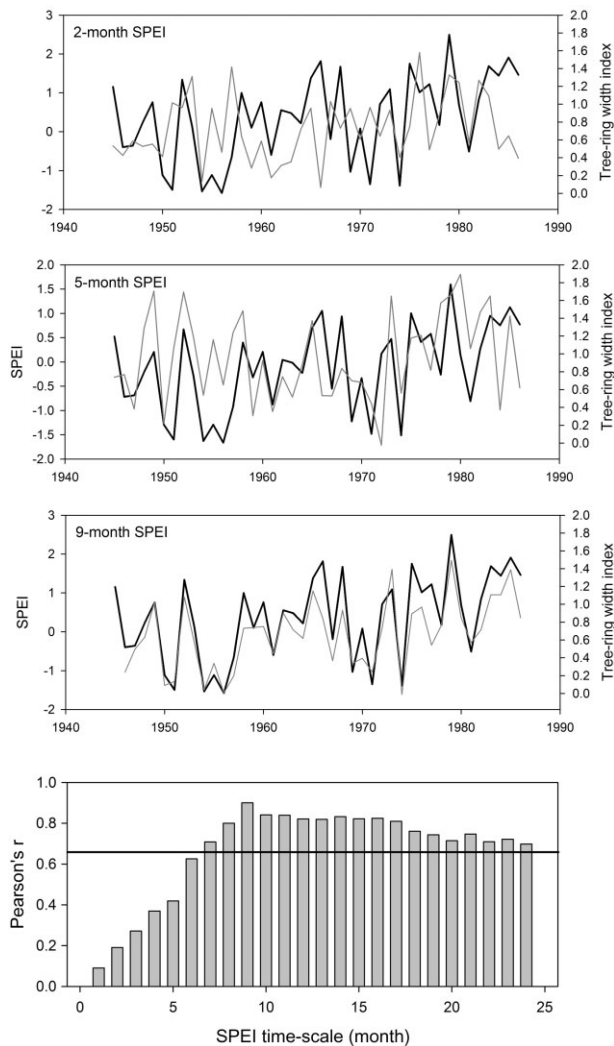
Figure 1 Example of the analyses used to relate residual tree-ring width indices (black lines) with detrended standardized precipitation–evapotranspiration index (SPEI) (Mimbres Junction Recollection forest, USA, latitude 33° N, longitude 108° W). The presented SPEI series (grey lines) correspond to 2-, 5- and 9-month long series calculated for May. The bottom panel shows the Pearson correlation coefficients (bars) calculated between the May SPEI and the tree-ring chronology for time-scales ranging from 1 to 24 months (the horizontal line indicates the 0.05 significance level of the Pearson correlation).

the period 1945–2009, before calculating correlations by using a linear regression model fitted to SPEI and time. The average SPEI of each series was added to the residual series of the model.

The high variability in the correlations between the tree-ring growth series and the SPEI series was summarized by conducting a principal components analysis (PCA; Richman, 1986). This approach allowed the 1657 chronologies to be classified on the basis of the similarities of correlations obtained between the tree-ring and the SPEI site chronologies at different time-scales. This classification involved calculating a PCA in S-mode to identify general patterns in those correlations. Given strong dif-

ferences in the spatial density of sampling sites among different regions, each tree-ring growth series was weighted by the inverse of the site density calculated within a radius of 300 km. The number of components extracted was chosen based on the percentage of the total explained variance (see Fig. S3). We used a correlation matrix to calculate the PCA (Barry & Carleton, 2001). The classification was based on the PCA loadings and following the maximum loading rule. The loadings are the correlation coefficients between the pattern of correlation between tree-ring growth and SPEI in each forest and the general pattern representative of a number of forests that correspond to a principal component (PC). Mapping the loadings allows the forests in which the tree-ring growth response to drought resembles any PC pattern to be identified.

We used several sources of information to determine the influence of different biophysical (e.g. topography) and climate conditions on the different responses of the tree-ring width chronologies to SPEI time-scales. First, we used data classification for the different forests sampled. Second, we focused on the phylogeny (angiosperm vs. gymnosperm species or families) or leaf phenology of each forest species (deciduous vs. evergreen species). Third, we focused on the role played by several climatic variables (precipitation; mean temperature; potential evapotranspiration, PET; and water balance – precipitation minus PET – used here as a surrogate for aridity). Climate data was obtained from the CRU TS 3.21 data set (Harris *et al.*, 2014). Fourth, several geographical and topographic variables (latitude; elevation; slope; terrain curvature; and potential incoming solar radiation, inferred from terrain aspect) were also used. Topographic variables were obtained from the GTOPO30 digital terrain model at a spatial resolution of 1 km (https://lta.cr.usgs.gov/GTOPO30; last accessed 1 February 2014) using the MiraMon software. Lastly, we also used remote-sensing data to estimate forest productivity by means of the average normalized difference vegetation index (NDVI; Rouse *et al.*, 1974) obtained from the Global Inventory Modeling and Mapping Studies (GIMMS) data set (Tucker *et al.*, 2005). This data set was used to provide a measure of the average forest cover at each sampled site between 1981 and 2011, because NDVI is closely related to vegetation biomass and leaf area (e.g. Carlson & Ripley, 1997).

We calculated seasonal averages of climate variables and NDVI for each forest. For descriptive purposes, the average values for these variables were obtained for the selected PCA groups that summarized the response of the tree-ring growth to the SPEI time-scales. The contribution of several variables (climate, topography and NDVI) to explaining the spatial differences in the tree-ring growth responses to SPEI at different time-scales was estimated using predictive discriminant analysis (PDA). PDA explains the value of a dependent categorical variable based on its relationship to one or more predictors (Huberty, 1994). Given a set of independent variables, PDA attempts to identify the linear combinations of those predictors that best separate the groups of cases of the predictand; these combinations are termed discriminant functions (Hair *et al.*, 1998). PDA allowed us to assess which predictors contributed to
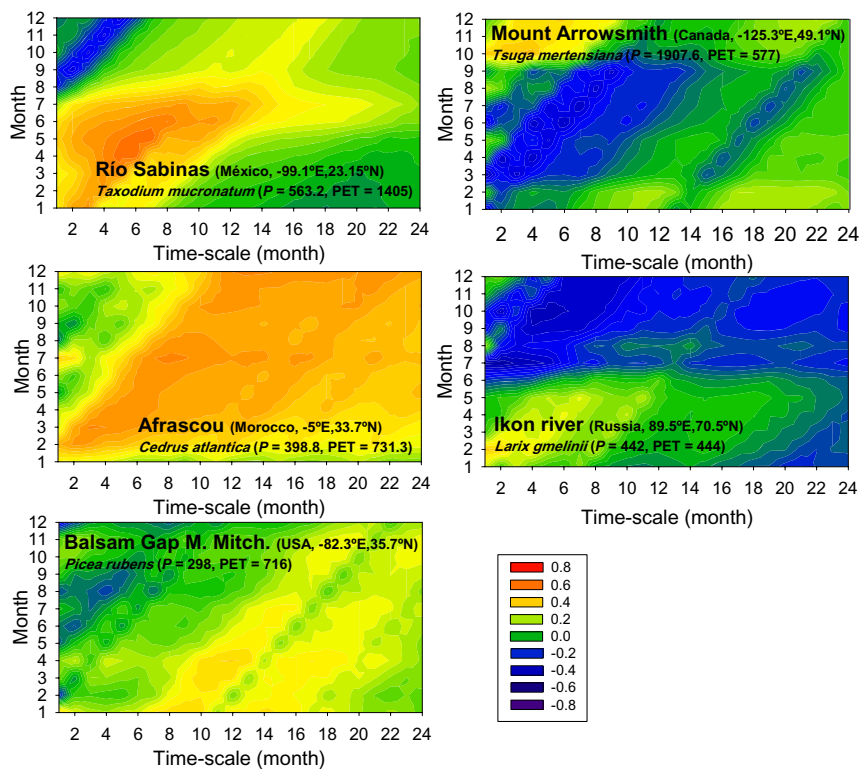
Figure 2 Correlation coefficients calculated between tree-ring width and standardized precipitation–evapotranspiration index (SPEI) series of each month (*y*-axis) at 1- to 24-month long scales (*x*-axis) in five forests with contrasting climatic conditions: three arid sites (Río Sabinas, Afrascou and Balsam Gap–Mount Mitchell) in which average annual potential evapotranspiration (PET) is higher than average annual precipitation (P); one humid forest (Mount Arrowsmith) in which average annual precipitation is much higher than annual PET; and one boreal forest (Ikon river) with low and similar annual precipitation and PET values.

most of the intercategory differences of the PC modes that summarize the growth–SPEI correlations.

RESULTS

Spatio-temporal patterns of growth responses to drought

A variety of growth–SPEI correlations were observed at 1-month to 24-month temporal scales (see Fig. 2 for examples). For instance, at a cold site in Russia (Ikon River) and a humid site in Canada (Mount Arrowsmith), correlations observed between SPEI and the tree-ring width indices are mainly negative. In contrast, at a semi-arid site in Mexico (Río Sabinas), positive and high correlations are recorded at intermediate SPEI time-scales (5–6 months). Forests having lower water deficits show maximum positive correlations at longer SPEI time scales (e.g. Afrascou, 8–10 months; and Balsam Gap–Mount Mitchell, 10–12 months).

The varied tree-growth responses to the different SPEI time-scales were summarized by conducting a PCA and by analysing the first seven principal components (PCs). The two first PCs account for 52% of the variance and they indicate clear patterns of correlation between tree-ring width indices and the SPEI time-scales (Fig. 3). PC1 presents strong growth–SPEI correlations ($r > 0.50$) at time-scales ranging from 10 to 16 months during the boreal spring and early summer (March to July). These forests are defined as showing 'long-time-scale responses'. In contrast, forests represented by PC2 show the highest correlations at SPEI time-scales of 3–11 months, during the boreal

summer and early autumn (June to September) and are characterized by presenting 'intermediate-time-scale responses'. Thus, patterns of tree-ring growth response to drought time-scales correspond to very different temporal patterns related to the seasonality and the drought time-scale, i.e. the period with the most pronounced cumulative water deficit, in which drought limits growth. PC3 represents 10.9% of variance and shows strong negative and positive correlations between the tree-ring indices and the SPEI at short time-scales (3–5 months) in winter and summer, respectively. These forests may be classified as sites showing 'short-time-scale responses'. The fourth to seventh PCs show more complex growth responses to drought, and represent less than 10% of the total variance, corresponding to more local patterns than the first three PCs (see Fig. S4 in Appendix S1). We retained the first three PCs for further analyses because of their more coherent and representative patterns.

The sites showing long-time-scale responses to drought (PC1) are mainly forests located in western and south-western North America, but also include some forests from the eastern USA and Alaska, the central Iberian Peninsula and eastern Russian forests (Fig. 4). The forests presenting intermediate-time-scale response to drought (PC2) correspond to forests located in central and south-western North America and also in Central Europe. The northernmost boreal forests from Siberia tend to show negative correlations between the annual tree-ring width indices and the summer SPEI. Overall, the geographical patterns of the forests showing long (PC1) and intermediate (PC2) time-scale responses represent different regions.

The maximum loading rule allowed the different forests to be classified according to the growth responses to different SPEI
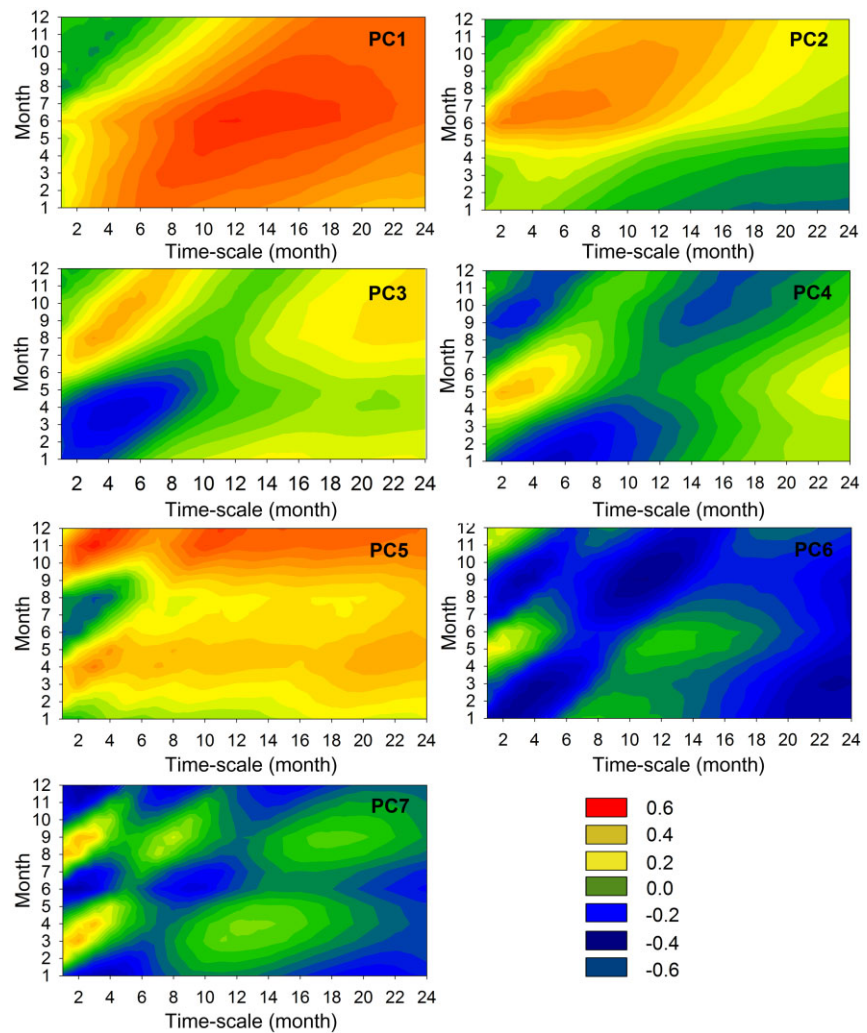
Figure 3 Major modes of tree growth responses to 1- to 24-month long standardized precipitation–evapotranspiration index (SPEI) time-scales based on the first seven principal components (PCs) of a principal components analysis. The PCs are shown in the original variables (Pearson correlation coefficients) to improve the interpretation of the results.

time-scales. Forests with long-time-scale responses to drought represent 45% of the analysed sites, but 37% correspond to a positive response of growth to drought (positive loadings) whereas the remaining 7% of those forests show a negative response to drought (i.e. negative loadings representing negative correlations between the tree-ring width indices and the spring–summer SPEI values at time-scales 10–16 months long). This means that we obtained two differentiated groups of forests based on PC1, characterized either by positive (+) or negative (−) responses to drought. Applying the same procedure to the other extracted components, we found that sites with intermediate-time-scale (PC2) and short-time-scale (PC3) responses to drought represent 30% (18% positive loadings; 11% negative loadings) and 13% (9% positive loadings; 4% negative loadings) of studied forests, respectively.

Factors driving growth responses to drought

The ITRDB data set is biased towards gymnosperms (83%) and evergreen tree species (75%), with angiosperms (17%) and broad-leaved (usually deciduous) tree species being less well

represented (25%). This distribution nonetheless differs from the classification obtained from the PCA (Table 1). For instance, forests with a positive and short-time-scale response to drought (PC3+) and the three groups with a negative response to drought show a higher representation of gymnosperms (> 90%) than in the total across forests. In contrast, forests characterized by long- and intermediate-time-scale responses to drought (PC1+) show a higher frequency of angiosperms (18%) than the remaining forests. This is even more evident for the forests with intermediate-time-scale responses to drought (PC2+), which includes many forests dominated by angiosperm (30%) and deciduous species (37%), despite most of the tree species sampled by dendrochronologists (75%) being evergreen.

The tree family that has been most intensively sampled by dendrochronologists is Pinaceae, representing 73% of the analysed forests (see Table S1). Forests with short-time-scale responses to drought (PC3+), and those with a negative response to drought (PC1− and PC2−) show a high proportion of Pinaceae species (at least 76%), whereas forests with long-time-scale responses (PC1+) show a ratio similar to that observed across all forests. In contrast, only 57% of the forests
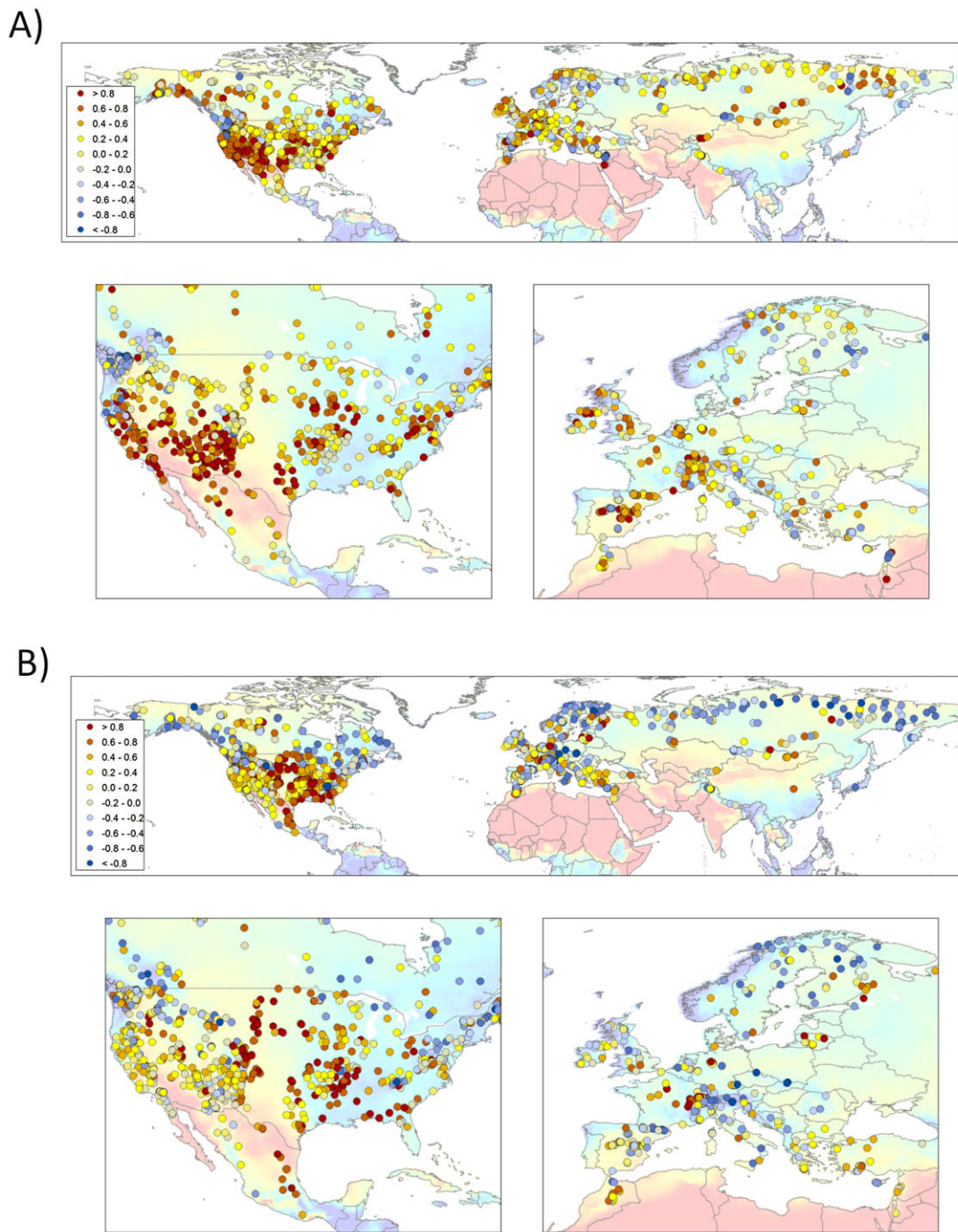
Figure 4 Spatial distribution of the loadings of the first (a) and second (b) principal components of the principal components analysis summarizing the responses of tree-ring width series to standardized precipitation–evapotranspiration index (SPEI) at global and regional (North America, Europe) scales.

with intermediate-time-scale responses to drought (PC2+) are dominated by Pinaceae, meaning that this group was dominated by deciduous angiosperm tree species in the family Fagaceae (25%), or by other gymnosperm families, such as Taxodiaceae (7%). Thus, PC2+ included tree species from humid, warm or mesic sites, such as *Quercus stellata* and *Taxodium distichum* (see Table S2). In addition, forests with negative responses to

drought (PCs with negative loadings) showed higher proportions of Cupressaceae species than the total across forests, corresponding to species that dominate in arid or cold areas.

The forests presenting negative responses to drought are located in colder and more humid conditions (i.e. areas with higher precipitation, lower temperature and PET, and more positive water balance) than the forests showing positive

Table 1 Percentages of forest types based on the tree phylogeny and leaf phenology, considering the first three principal components of a principal components analysis (PC1, PC2 and PC3) summarizing the growth responses to the standardized precipitation–evapotranspiration index (SPEI) drought index. The effects of the principal components are shown in parentheses.

Group (effect)	Phylogeny		Leaf phenology	
	Angiosperm	Gymnosperm	Deciduous	Evergreen
PC1 (+)	17.7%	82.3%	21.3%	78.7%
PC2 (+)	29.9%	70.1%	37.2%	62.8%
PC3 (+)	10.3%	89.7%	12.2%	87.8%
PC1 (−)	8.2%	91.8%	19.7%	80.3%
PC2 (−)	5.1%	94.9%	27.0%	73.0%
PC3 (−)	8.3%	91.7%	30.0%	70.0%
Total	16.6%	83.4%	24.6%	75.4%

responses to drought (Fig. 5). Thus, forests characterized by negative correlations between growth and drought – mostly boreal forests – are probably more constrained by radiation and temperature. In the case of forests corresponding to positive responses to drought, the forests of long-time-scale responses to drought (PC1+) usually correspond to drier areas (presenting the lowest water balance) than those represented by forests of intermediate-time-scale responses. Forests with long-time-scale response to drought (PC1+) also show a lower annual NDVI and are located at higher elevations than forests of intermediate- and short-time-scale responses, whereas forests with intermediate-time-scale responses show the highest values of mean temperature and PET. The forests with an intermediate-time-scale response are therefore located in areas characterized by lower climatic stress than forests with a long-time-scale response. The forests with short-time-scale responses display a growth response to drought during the boreal summer. They are located in areas with precipitation values similar to those represented by forests with intermediate-time-scale responses, but under colder conditions (lower PET), which determine a higher water balance than those forests with long- and intermediate-time-scale responses to drought. This translates into higher above-ground biomass for forests presenting short-time-scale responses, as shown by their higher annual NDVI values. There appears to be a gradient in the growth responses to drought including: (1) forests not responding at all to drought (e.g. those located in cold and very humid areas, corresponding to groups included in the first three PCs with negative loadings); (2) forests characterized by a growth response to long-term droughts (located in drier areas and showing low NDVI values); (3) forests that respond to mid-term droughts, are subjected to humid conditions and show high NDVI values; and finally, (4) forests growing under more humid conditions, which display higher NDVI values and respond to short-term droughts with lower intensity than forests from other groups (e.g. PC1+ and PC2+).

The PDA allowed the relative importance of the various climatic and environmental factors as drivers of the growth

responses to drought to be quantified (Table 2). The first PDA function (PDA1) accounts for 38% of the total variance and allows the six patterns (PC1+, PC2+, PC3+, PC1−, PC2− and PC3−) of forest growth response to different drought time-scales to be distinguished. This function represents mainly the latitude, temperature and PET conditions at each site, showing the different seasonal and annual values of those two climate variables negative and significant coefficients with PDA1. PDA2 (18% of variance) shows positive coefficients for summer season temperature and PET. PDA3 (14% of variance) displays positive coefficients with precipitation and water balance during the main period of forest activity (from spring to autumn). These three functions emphasize the importance of the average climate conditions (temperature and PET, which are largely determined by latitude, and the water availability during the period of vegetative activity) to discriminate the different patterns of forest response to drought.

PDA1 discriminates between forests with positive and negative responses to drought (Fig. 6). It means that differences between positive and negative responses are mainly controlled by latitudinal gradients, which ultimately determine temperature and PET. Thus, the three forest groups characterized by a negative response to drought and the forests showing short-time-scale responses to drought (PC3+) show positive coefficients in PDA1, whereas forests presenting long (PC1+) and intermediate (PC2+) time-scale responses to drought show negative coefficients. Nevertheless, forests characterized by intermediate-time-scale response (PC2+) show higher values in the PDA1 than forests having long-time-scale response (PC1+). This means that spatial gradients in temperature and PET not only determine the positive and negative response to drought, but also determine whether the response is recorded at intermediate or long drought time-scales in forests that respond positively to drought. PDA2 also discriminates between forests with positive and negative response to drought, and also differentiates between the forests with responses at long (PC1+) and short (PC3+) time-scales and the forests with responses at intermediate time-scales (PC2+). Summer temperature affects evaporative demand in the period of higher water stress by trees. Because water availability during the summer in forests with responses at long, intermediate and short time-scales differ, the water-demand conditions, determined by PET, may affect the response of growth to drought time-scale. This is suggested by PDA3, which represents summer water availability and clearly separates between forests which respond to drought at intermediate (PC2+, more humid) and long (PC1+, drier) time-scales.

DISCUSSION AND CONCLUSIONS

The diversity of environmental conditions evaluated here allowed us to detect a gradient in forest growth responses to drought. We found that some forests from cold and humid areas respond to shorter drought time-scales than forests from dry areas, which usually respond to longer time-scales. We also found forests that do not respond to drought variability, such as
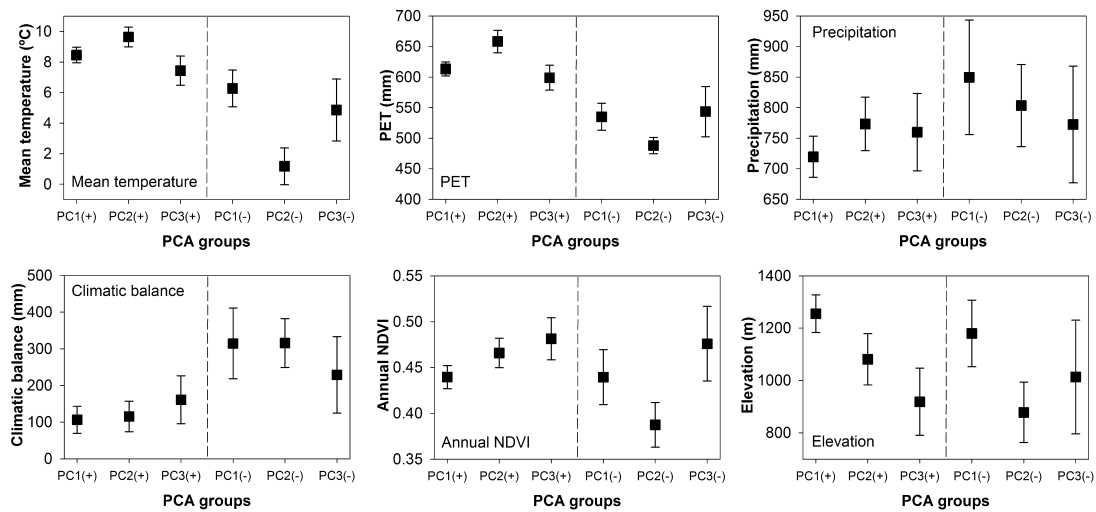
Figure 5 Mean values of the main variables (annual mean temperature, potential evapotranspiration – PET, precipitation, climatic water balance, annual NDVI and elevation) characterized by the first three principal components (PC1, PC2 and PC3; their effects are shown in parentheses) of the tree-ring width responses to standardized precipitation–evapotranspiration index (SPEI) time-scales obtained in a principal components analysis. Error bars indicate two standard errors of the average.

those located in cold and humid regions, here represented by negative responses to drought (negative loadings in the first three PCs). At the other extreme, forests characterized by growth responses to long drought time-scales (12–14 months) are located in semi-arid sites and show lower cover and biomass (NDVI) than other forests. Other forests present growth responses to mid-term droughts (6–8 months) and dominate humid locations, where they accumulate high biomass values. Finally, forests in cold and humid sites tend to respond to very short drought time-scales (3–5 months). The patterns of forest response to drought are therefore highly complex even at local scales and among coexisting species or even specific individuals. In this sense, growth and responses to drought are modulated by site conditions such as soil type, specific functional traits and the intensity of competition among neighbouring trees (Orwig & Abrams, 1997; McDowell *et al.*, 2008; Linares *et al.*, 2010; Pasho *et al.*, 2011).

We were able to separate contrasting families, such as the Pinaceae, Cupressaceae and Fagaceaeae, based on their responses to drought. This classification agrees well with the vulnerability to drought of the compared species, in that increased resistance to cavitation is a key mechanism of drought tolerance in conifers and evergreen angiosperms, whereas in deciduous angiosperms, hydraulic conductivity increases with decreasing rainfall (Maherali *et al.*, 2004). Most tree species operate close to their safety margins for hydraulic failure, making them vulnerable to warming-induced droughts across biomes (Choat *et al.*, 2012). To simplify, the wide vessels of angiosperms allow them to reach much higher hydraulic pressure than gymnosperms, whereas gymnosperms maintain much greater safety margins to prevent xylem embolism (Johnson *et al.*, 2012). Our findings provide evidence that the patterns of growth response to drought do not follow a general geographical structure and that these patterns are driven by the biogeo-graphical, topographic and climatic conditions of each site, showing that forests located in different continents have the same pattern of response to drought time-scales. In fact, several of the analysed drivers are related (e.g. topography affects temperature and precipitation, water balance determines NDVI, etc.), but we found coherent relationships between the analysed variables and the growth response to SPEI time-scales in agreement with the different climate factors that limit primary production at a global scale (Nemani *et al.*, 2003).

Forests located in cold and wet regions show low PET rates and, in general, high precipitation values and positive water balances. These forests are not frequently affected by water deficit, because growing-season temperature is the main constraint of growth (Briffa *et al.*, 1998). Temperature and growth trends may nevertheless have been diverging over recent decades in some boreal forests (Briffa *et al.*, 1998). In fact, some authors have suggested that warming-related drought could cause this recent divergence between temperature and growth at high northern latitudes (Barber *et al.*, 2000; Wu *et al.*, 2012). This would explain why these forests (represented by negative loadings in the first three PCs) show negative correlations with the SPEI, because higher precipitation corresponds to cloudiness, lower solar radiation and, in general, lower temperature, which is the major constraint of tree growth in these areas. On the other hand, a warming-induced rise in PET could constrain growth by increasing soil water losses, but it could also enhance respiration and carbohydrate consumption (Barber *et al.*, 2000). These forests may nonetheless respond to water shortage if drought becomes more severe than it was during the observed record, which is suggested by pre-instrumental tree-ring records and recent high-mortality episodes (Payette & Delwaide, 2004; Peng *et al.*, 2011).

The forests that present short time-scale responses to drought are characterized by lower water availability than those forests

Table 2 Structure matrix of the first three components (the variance explained by each component is shown in parentheses) of the predictive discriminant analysis (PDA). The table shows the correlation values of each predictor variable with the three discriminant functions. DJF, winter (December, January and February); MAM, spring (March, April and May); JJA, summer (June, July and August); SON, autumn (September, October and November); NDVI, normalized difference vegetation index; PET, potential evapotranspiration. The variables represented in each of the first two functions are marked with asterisks.

| | PDA functions (proportion of variance) | | |
Variables	PDA1 (37.6%)	PDA2 (18.1%)	PDA3 (14.2%)
Annual Temperature	−0.478*	0.139	−0.026
Temperature DJF	−0.584*	−0.091	0.096
Temperature MAM	−0.478*	0.083	0.011
Temperature JJA	−0.026	0.487*	−0.251
Temperature SON	−0.464*	0.185	−0.044
Annual PET	−0.105	0.338	−0.126
PET DJF	−0.468*	−0.417	0.339
PET MAM	−0.346	0.039	0.006
PET JJA	0.351	0.495*	−0.244
PET SON	−0.465*	0.127	−0.035
Annual precipitation	−0.038	−0.089	0.365
Precipitation DJF	−0.064	−0.145	−0.098
Precipitation MAM	−0.210	0.001	0.325
Precipitation JJA	0.043	−0.061	0.685*
Precipitation SON	0.080	−0.094	0.367*
Annual water balance	−0.002	−0.194	0.386
Water balance DJF	0.201	0.100	−0.275
Water balance MAM	−0.055	−0.018	0.324
Water balance JJA	−0.164	−0.316	0.610*
Water balance SON	0.259	−0.141	0.371*
Annual NDVI	−0.235	0.052	0.217
NDVI DJF	−0.420	−0.155	0.241
NDVI MAM	−0.324	−0.002	0.153
NDVI JJA	0.237	0.300	0.127
NDVI SON	−0.283	0.049	0.215
Latitude	0.673*	0.370	−0.281
Elevation	−0.330	0.232	−0.105
Terrain curvature	0.089	0.098	0.171
Slope	−0.219	−0.174	0.111
Solar radiation	−0.088	−0.187	0.021

showing a negative response to drought, but by colder and more humid conditions than forests having responses to drought over intermediate and long time-scales, mainly as a consequence of low PET rates. Leaf biomass and NDVI values tend to be high in forests with short-time-scale responses to drought and, although the response to SPEI variability is lower than that found for forests that respond over intermediate and long time-scales, the former forests respond mainly to drought at short time-scales in the season of higher vegetation activity, i.e. summer. This behaviour probably suggests that these forests are more vulnerable to water deficit because, although water avail-

ability is commonly sufficient in these forests, it is lower than that observed in the forests from the coldest sites. Thus, forests that show a short-time-scale response to drought are probably affected by periods of summer water stress, which are increasing in frequency and severity as a consequence of global warming (Dai, 2011; Trenberth et al., 2014). Because forests located in humid regions commonly show little acclimatization to water-deficit conditions (Maherali et al., 2004), even short drought episodes, here illustrated by short SPEI time-scales, probably affect forest growth (Wu et al., 2012).

The main pattern of growth response to drought, represented by forests that respond to drought over intermediate and long time-scales, clearly presented a stronger response to drought than that observed for the other identified patterns. These forests are characterized by lower water availability and higher air temperature than the remaining sites. This is consistent with the fact that tree growth is more sensitive to drought in arid sites than in humid areas (Orwig & Abrams, 1997; Pasho et al., 2011). Drought variability therefore determines a high proportion of the temporal variability of the annual growth of forests in xeric sites under semi-arid conditions. In xeric sites, the growth response to drought is mainly recorded in summer, given that this season is characterized by higher vegetation activity, water demand and dryness. Nevertheless, the differences found between forests with responses to drought over intermediate and long time-scales allow a preliminary finding – pointed out by Vicente-Serrano et al. (2013) using different vegetation metrics – to be confirmed, namely that the forests in semi-arid and subhumid conditions tend to respond to longer time-scales than those located in more humid sites characterized by higher vegetation biomass and NDVI values.

The different responses to drought observed in semi-arid and subhumid forests is directly linked to their contrasting vulnerabilities to water shortage, being therefore necessary to discriminate between response and resistance or vulnerability. In general, tree species that are able to regulate their metabolism to make more efficient use of water resources usually show greater resistance to drought (Abrams et al., 1990). According to a global compilation of xylem resistance to drought-induced embolism, tree species from humid forests are more vulnerable to water shortage than tree species from dry forests (Maherali et al., 2004), probably as a consequence of physiological or morphological acclimatization of species from dry forests for coping with recurrent water deficits. This agrees with studies that have analysed the spatial distribution of tree species across these areas (Pockman & Sperry, 2000; Kursar et al., 2009). Here, we have shown that the time-scale at which forest growth responds to drought may be used as a proxy for drought vulnerability, possibly being more related to the resistance to cope with water deficits of different durations and severities than to the vulnerability to xylem embolism. Therefore, the forests that respond to short drought time-scales, characteristic of humid and cold environments, would have greater vulnerability to water deficits, because their growth is mainly constrained by short-term droughts. In contrast, forests located in drier environments respond to long-term droughts, which means that they may
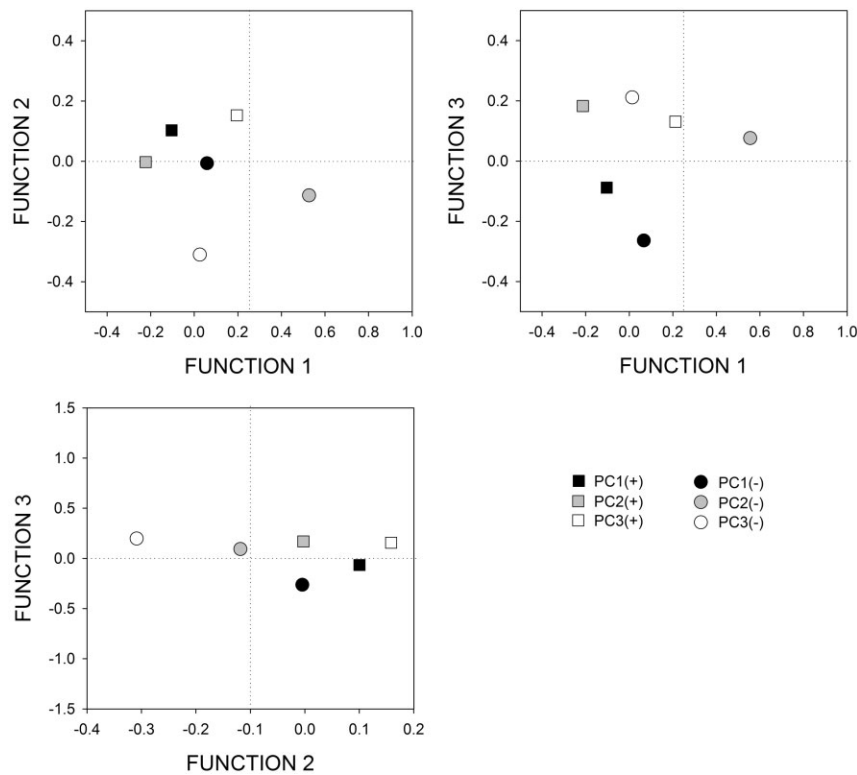
Figure 6 Centroids of the groups obtained through a principal components analysis (effects are shown in parentheses) corresponding to the first three functions of the predictive discriminant analysis (PDA).

cope with short-term water deficits, but longer and more severe water deficit episodes can affect their radial growth. This suggests that tree species require different time periods to recover (resilience) after water conditions return to average values in dry environments (Granda *et al.*, 2013) and even in humid temperate forests (Cavin *et al.*, 2013). The findings of this study therefore not only support the different growth responses to drought in forests in contrasting environmental conditions, but stress the importance of considering different drought time-scales for better understanding how forests respond to drought under different climatic and environmental conditions. If the severity, geographical extent and frequency of droughts increase as a consequence of climate warming, as suggested by different studies (Dai, 2011; Trenberth *et al.*, 2014), novel growth responses to drought could be recorded in areas not previously detected (e.g. boreal forests). We should also assess up to which point forests from semi-arid or dry areas will keep their tolerance to water deficit by keeping their characteristic long-term growth responses to drought, because novel or extreme climate conditions can profoundly alter these responses and trigger a decline in growth and related die-off, even in areas without pronounced water shortage, once these tolerance thresholds are surpassed. Thus, future warming scenarios suggest increased forest vulnerability to drought stress (Williams *et al.*, 2013).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Evolution of the 2-, 6-, 12- and 24-month-long standardized precipitation–evapotranspiration index (SPEI) drought index over the period 1945–2006 in the Pratomagno range of the Appenine Mountains (Italy).

Figure S2 The detrending procedure did not modify the correlations (colour scale) obtained between tree-ring width indices and standardized precipitation–evapotranspiration index (SPEI) at different monthly time-scales (x-axis).

Figure S3 Cumulative and relative (percentages) variances of the principal components (PC) obtained by principal components analysis (PCA).

Figure S4 Spatial distribution of the loadings of the (a) third, (b) fourth, (c) fifth and (d) sixth principal components (colour scales) of the principal components analysis applied to the correlations calculated between the tree-ring width indices and different standardized precipitation–evapotranspiration index (SPEI) monthly time-scales.

Table S1 Percentages of tree families corresponding to the most representative groups of growth responses to drought determined by a principal components analysis.

Table S2 Percentage of tree species included within the groups corresponding to the main principal components (PC1, PC2 and PC3) obtained using a principal components analysis (PCA) based on the correlations calculated between the tree-ring width indices and different standardized precipitation–evapotranspiration index (SPEI) monthly time-scales.

Appendix S1 Supplementary figures and tables.

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Sergio M. Vicente-Serrano is a climatologist focused in the development of methods and tools to improve drought quantification and monitoring, and the analysis of hydrological, agricultural and ecological impacts of drought.

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