Regional Environmental Change (2024) 24:87
https://doi.org/10.1007/s10113-024-02256-x

ORIGINAL ARTICLE

Elevation and local climate variation control changes in Aleppo pine growth responses to hydroclimate and drought in semi-arid Spain

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Received: 15 December 2023 / Accepted: 16 May 2024

Abstract

In the Mediterranean region, inner rural and mountain areas suffered abandonment and land marginalization. Extensive conifer afforestations were established in these areas, which are particularly vulnerable to climate change and its associated risks. To identify critical areas where climate change could negatively impact forest vitality, we need to understand how the temporal variability of tree growth and its vulnerability to climate and drought have arisen and what their possible causes are. We used dendrochronological techniques to examine the effects of stand structure, physiography, and local climate variations in determining the growth dynamics of Aleppo pine plantations and temporal shifts in their susceptibility to hydroclimate and drought in semi-arid northeastern Spain. We found that structural traits strongly modulated growth dynamics and forest productivity. Young and small trees showed more synchronized growth and greater inter-annual ring width variability, and widely spaced trees in better quality stands had higher productivity. In contrast, temporal shifts in growth susceptibility to hydroclimate and drought were dependent on local physiography and climatic variability. Trees in low-elevation eastern stands with less continental conditions and milder winters showed decreasing dependence on water availability and increasing growth resistance and resilience to severe droughts. However, in high-elevation sites with wetter climates and cold winters, increasing growth response to water availability and decreasing resistance and resilience to drought were found. Our results highlight that adaptation to local physiographic and climatic conditions is a better strategy to mitigate the impacts of climate warming on Aleppo pine plantations in the semi-arid Mediterranean region.

Keywords Drought mitigation · Forest productivity · *Pinus halepensis* · Resilience · SPEI · Weather extremes

Introduction

The Mediterranean region is an environmental, historical, and biogeographical unit that is considered one of the global hotspots of exceptional biodiversity (Myers et al. 2000; Comes 2004). Mediterranean landscapes have been used intensively by humans for millennia and have been significantly altered by deforestation and overgrazing (Médail et al. 2019; Pausas and Millán 2019). In the twentieth century, the population migrated to urban and coastal areas, while rural inland and mountain areas experienced rural exodus and marginalization (Cramer et al. 2018; Quintas-Soriano

Communicated by Victor Resco de Dios

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et al. 2023). Since the 1940s, large-scale reforestations with conifers were carried out to mitigate land degradation and revitalize the economy in depopulated areas of inland Spain (Vicente-Serrano et al. 2010b; Moreno-Gutiérrez et al. 2012). Massive afforestation created extensive, dense, and uniform artificial forests that are particularly vulnerable to climate change and its associated risks (Velázquez et al. 2022).

Projected annual and summer warming in the Mediterranean region is expected to be 25% and 40% above the average global increase, respectively (Giorgi and Lionello 2008; Mariotti et al. 2008). Increasing aridification will lead to a decline in agricultural and forestry productivity, with an increased risk of crop failures, forest dieback, forest pests, and forest fires (Anav and Mariotti 2011; Moriondo et al. 2016). Drought intensification is likely to be particularly pronounced in the Spanish Mediterranean region, where the implementation of adaptation measures for water management and agroforestry systems will be crucial (Andrade et al. 2021). To understand the impact of increasing temperatures and decreasing water availability on forests and plantations, it is important to examine how trees respond and adapt to water stress (Keenan 2015; Nunes et al. 2022). A comprehensive understanding of the driving factors that determine how trees and forests respond to climate variability and environmental stresses is commonly investigated by assessing the relationships between tree-ring growth and environmental information at different geographical scales (Babst et al. 2019; Anderegg et al. 2020; Gazol et al. 2020; Bohner and Diez 2021).

Aleppo pine (*Pinus halepensis* Mill.) is a thermophilic tree species that is often planted in productive afforestation and environmental restoration programs in semi-arid Mediterranean areas due to its low water requirements and high adaptability (Chambel et al. 2013; Choury et al. 2017). Precipitation and soil water content in the previous winter and during the active growing season are the main factors affecting cambial activity and secondary growth rates of this species (Pasho et al. 2011a, b; de Luis et al. 2013; Novak et al. 2013; Camarero et al. 2020). Aleppo pine exhibits facultative bimodal xylogenesis associated with the two wetter and warmer seasons in the Mediterranean climate in spring and autumn (Camarero et al. 2010; Pacheco et al. 2018), which is more marked in coastal than inland sites. Under semi-arid Mediterranean conditions, warming is expected to lengthen Aleppo pine growing season, but a more intense and longer summer break would actually reduce future growth rates (de Luis et al. 2011). A decline in forest productivity, a dieback of the driest populations, and a shift in the potential range of Aleppo pine are expected (Sánchez-Salguero et al. 2012; Marqués et al. 2016; Morcillo et al. 2022).

There is increasing evidence that forest stand characteristics, physiography, and local climate variability can influence the response of trees to limiting climatic conditions. Trees growing at lower densities were found to be less vulnerable to drought (Bottero et al. 2017; Andrews et al. 2020). In addition, physiographic traits such as latitude, longitude, and elevation have been found to be important in modulating climate responses of trees (Babst et al. 2013; Tei et al. 2021). Understanding how stand structure and environmental gradients influence tree growth and its sensitivity to climate and drought can help managers adapt forestry practices to mitigate the effects of climate warming and drying in Mediterranean areas (Gazol et al. 2020; Nunes et al. 2022; Gazol et al. 2023). Previous studies have shown that tree-ring growth responses to hydroclimate and drought in the Mediterranean region can be modulated by structural traits, particularly stand density, which strongly determine the intensity of competition between trees (Tsamir et al. 2019; Helluy et al. 2020). Thinning improves carbon assimilation, water use efficiency, and forest productivity by reducing the intensity of competition between trees in Aleppo pine stands (Olivar et al. 2014; Tsamir et al. 2019). Furthermore, small trees of this species growing in denser stands have been found to be more susceptible to water stress and aridification than large trees in open stands (de Luis et al. 2009; Moreno-Gutiérrez et al. 2012).

Although the influence of structural traits and management practices on the climate response of Aleppo pine is relatively well known, there is a lack of knowledge about the role of local physiography and climate conditions in modulating its vulnerability to climate and drought (e.g., del Río et al. 2014; Camarero et al. 2020). With climate change, temporal shifts in growth responses are expected, and site-specific conditions would potentially modulate the sensitivity of tree growth to climate and the drought-related vulnerability of forests to biotic and abiotic disturbances and risks (Babst et al. 2019; Thrippleton et al. 2023). Recent studies suggest that the temporal variability in tree growth responses to climate depends on multiple factors, among which local climate and stand structure play an important role depending on the studied species (Peltier and Ogle 2020; Tumajer et al. 2023). Therefore, understanding the temporal variability of growth sensitivity, considering the role of local climate conditions, forest stand characteristics, and physiography as potential drivers of tree climate vulnerability, is crucial to identify critical areas where climate change could negatively impact forest productivity and vitality.

Our aim was to evaluate the role of stand traits, physiography, and local climate variability on tree-ring growth, as well as on the temporal changes in hydroclimate and drought responses of growth in Aleppo pine plantations in semi-arid northeastern Spain. Complementary to other studies that have analyzed static responses of tree-ring growth to climate (e.g., Pasho et al. 2011a; de Luis et al. 2013; Novak et al. 2013), we seek to determine the key structural and environmental drivers of tree growth and its time-varying responses of a drought-tolerant thermophilic tree species to climate in recent decades. Specifically, we ask the following research questions: (i) What are the main climatic factors controlling the growth of Aleppo pine in the semi-arid Mediterranean region of Spain? (ii) How have tree growth responses to hydroclimate and drought changed over time in recent decades? (iii) What are the relative roles of stand structural traits, physiography, and local climate variability in controlling tree growth dynamics and changes in growth responses to climate and drought? We hypothesized that stand structure, physiography, and local climate variation influence tree growth dynamics and temporal shifts in growth responses to climate and drought as they determine key physiological processes that control xylogenesis, phenology, and tree growth rate.

Materials and methods

Study area

The study stands are 48 plantations on the southern edge of the Ebro Basin in the Aragón region, northeast of the Iberian Peninsula (Fig. 1a), at elevations between 431.8 and 1011.3 m (Table S1). The mean annual temperature is 12.9 °C and varies between 11.4 and 14.3 °C (Table S1). The warmest months are July and August, and the coldest months are December and January (Fig. S1), with a mean maximum temperature of 30.6 °C in the warmest month, which ranges from 29.3 to 32.2 °C, and a mean minimum temperature in the coldest month of 0.15 °C, ranging from − 1.36 to 1.83 °C (Table S1). The average annual total precipitation in the study area is 410.4 mm and ranges from 359.2 to 466.1 mm, with a humid period occurring mainly from October to May (Fig. S1). A dry period lasts from June to August, according to the standardized precipitation evapotranspiration index (SPEI), and the duration of the dry period varies between 2.1 and 3.9 months (Table S1). The climate in the study area corresponds to the semi-arid cold BSk type, according to the Köppen-Geiger climate classification (Beck et al. 2018). The mean annual temperature in the study area showed a significant increasing trend from 1985 to 2016 (Fig. 1b), while precipitation was almost stable (Fig. 1c). The annual SPEI showed a decreasing trend from 1985 to 2016, indicating increasingly drier conditions especially since 2004, and significant SPEI minima occurred in 1995, 2005 and 2012 (Fig. 1d).

Field work and quantification of forest structure

The field work was carried out in April 2017. We selected 48 homogeneous forest stands that were free of silvicultural interventions, according to Aragón's Forest Service records,

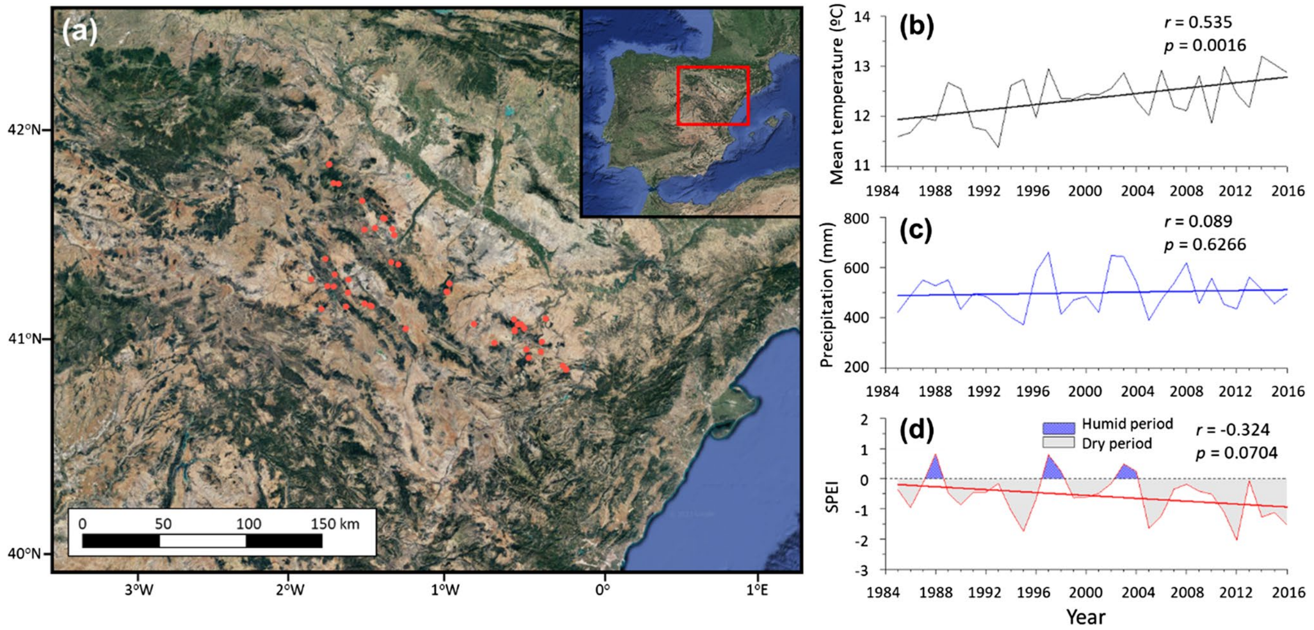

Fig. 1 Location of the study area (red square) and the study stands of Aleppo pine (red dots) in northeastern Spain (**a**). Annual variation of mean temperature (**b**), total precipitation (**c**), and annual SPEI (d) in the study area calculated as the mean for the 48 study sites. The humid (blue areas) and dry (gray areas) periods, according to the annual SPEI, are highlighted in (**d**). Linear fit, correlation coefficient (*r*), and its statistical significance (*p*) are shown. Meteorological data were downloaded from the Climate Explorer of the World Meteorological Organization (http://climexp.knmi.nl/) for the period 1985–2016

and without evidence of tree stumps in the field. The structure of the study stands was characterized based on an average number of 30 trees per stand within a circular plot with a radius of 8.46, 11.28, or 14.10 m (225, 400, or 625 m^2 area), depending on the local tree density. This approach adjusted the plot radius based on forest density to ensure that each sampling point contributed equally to the inventory and minimized sampling effort, thereby optimizing resource use and improving data representativeness (Lessard et al. 2002). Elevation, latitude, and longitude of the center of each circular plot were measured with submetric precision using a GPS Trimble GEO 7X. The number of trees with a diameter at breast height (DBH) of at least 7.5 cm within each circular plot was recorded and their DBH measured. The total height of the six trees closest to the center of each circular plot was measured with a Haglöf Sweden® Vertex instrument. We sampled eight wood cores from the six trees closest to the center of the stand for further dendrochronological processing. From four of these trees, one core per tree was taken, and from two of these trees, two cores per tree were taken at breast height using a Pressler increment borer (Haglöf, Sweden).

Different stand level variables (Table S2) were calculated and used to account for differences in forest structure between stands. The stand density (N) was quantified as the number of trees per hectare by counting the number of trees in each plot multiplied by 10,000, and divided by the area sampled per plot in hectares (Reineke 1933). The stand basal area (G) was measured as the basal area of the sampled trees in a plot and expanded to hectares (Flewelling and Iles 2004). The quadratic mean diameter (Dg) was calculated as the square root of the arithmetic mean of the squared diameter values and represents the diameter of the average tree per tree basal area (Curtis and Marshall 2000). The dominant diameter (Do) and the dominant height (Ho) were quantified as the average diameter and height of the dominant trees in a stand (Assmann 1970; Molina-Valero et al. 2019). In addition, we used a site index (SI) that was quantified as the dominant height that a stand reaches after 60 years (Rojo-Alboreca et al. 2017), a metric not influenced by forestry practices that is often used as a reliable indicator of stand productivity. The relative spacing index (RSI) is defined as the ratio of the average distance between trees to the average dominant height of the stand (Zhao et al. 2010). These structural traits were considered to quantify the potential role of stand structure in regulating tree growth and its response to climate and drought.

Dendrochronological procedures

The wood cores were air-dried, glued to wooden mounts, and polished with progressively finer sandpaper until the cellular structure of the xylem was clearly visible in cross-section. The series of tree-ring widths were then visually cross-dated using standard dendrochronological methods and measured to the nearest 0.01 mm under magnification using a measuring stage (Velmex Inc., Bloomfield NY, USA). The quality of the cross-dating was checked using COFECHA software (Holmes 1983) and possible dating errors in the tree-ring series were identified and corrected. The age of the trees was estimated based on the number of annual rings in the cores and no corrections were made for the number of missing rings due to coring height or failure in pith interception. The trees showed almost concentric growth and most cores intersected or narrowly missed the pith, significantly reducing errors in age estimation. Since tree age can significantly alter growth trajectories (Martínez del Castillo et al. 2018), we also considered possible age effects by using the mean of the estimated ages per stand.

Annual tree-ring width series of a total of 380 wood cores from 285 individual trees were accurately cross-dated and measured. To calculate the stand chronologies, we used eight raw tree-ring series per stand, which were standardized using the software *detrendeR* (Campelo et al. 2012) in R environment (R Core Team 2022) following a double standardization procedure to obtain dimensionless ring width indices (RWI). Trends in the raw radial growth time series associated with aging and growth dynamics were first removed from each series using a linear or negative exponential function and then a cubic smoothing spline with a 50% frequency response cut-off of 32 years was applied. For each of the 48 stands, a chronology of RWI was calculated as the arithmetic mean of the series of growth indices for each stand. The quality of the chronologies obtained in the optimal common period 1985–2016 was assessed using basic statistics (Table S2) to measure the common signal (Campelo et al. 2012). These were expressed population signal (EPS), mean inter-series correlation (Rbar), signal-to-noise ratio (SNR), and mean sensitivity (MS). EPS is a measure of the common signal of the tree-ring series of a chronology, which quantifies the degree to which the chronology represents the theoretically perfect chronology. Rbar is the average correlation coefficient between tree-ring series. SNR quantifies the strength of the observed common signal between trees in a chronology, and MS is the mean percent change from each growth index to the next (Speer 2010). In addition, annual basal area increments (BAI, cm^2 $year^{-1}$) were calculated from raw tree-ring widths (Biondi and Qeadan 2008) with the bai.out() function in the dplR package (Bunn 2008). Mean BAI slope (SlpBAI, i.e., the trend in basal area increment as tree ages) was calculated as the slope of the linear regression between individual BAI series and tree age. Mean BAI (MBAI) and SlpBAI were calculated for the individual and stand levels over the period 1985–2016.

Climate data

To characterize the local climate at each stand, we downloaded monthly data of precipitation, mean, minimum, and maximum temperatures at 1 × 1 km resolution from AEMET's Climate Atlas for the period 1981–2010 (https://www.aemet.es/es/serviciosclimaticos/datosclimatologicos/atlas_climatico). From these data, we calculated (Table S1) mean annual temperature (T), mean maximum temperature of the warmest month (MxTW), mean minimum temperature of the coldest month (MnTC), total annual precipitation (P), and summer precipitation (SP) for every stand. Annual evapotranspiration (ET) was calculated according to Thorntwaite and Mather (1957), and drought intensity (DI) and drought duration (DD) were calculated according to Walter and Lieth (1960).

To calculate the relationships between tree-ring growth and climate, we used monthly gridded datasets for total precipitation (Prec), soil moisture to a depth of one meter (SoilM), evapotranspiration (ET), and mean air temperature obtained from Climate Explorer of the World Meteorological Organization (http://climexp.knmi.nl/; CRU TS 4.06, 0.5° × 0.5°, period 1901–2020), Climate Research Unit, University of East Anglia (Harris et al. 2014). In addition, we used the standardized precipitation evapotranspiration index (SPEI), which represents a standardized measure of water balance and accumulation of water deficits/surpluses at different time scales, with negative and positive SPEI values indicating dry and wet conditions, respectively (Vicente-Serrano et al. 2010a). SPEI datasets at scales 1 (SPE1), 3 (SPEI3), 6 (SPEI6), and 12 months (SPEI12) were used. SPEI data were also obtained from the Climate Explorer (CSIC SPEI, 0.5° × 0.5°, period 1901–2018) for the entire study area where the study stands are located.

Data analysis

All analyses were performed at the regional scale by considering the 48 study stands together. The similarity between sites in high-frequency growth patterns was checked by principal component analysis (PCA) based on the correlation matrix between Aleppo pine RWI stand chronologies, the mean chronology of all stands, and the annual SPEI series for the October–September hydrological year. The relationships between climate and tree growth were examined in the period 1982–2016, common to all chronologies, from March of the previous year (Mar(-1)) to December of the current growth year (Dec). The spatial relationships between the mean chronology and the annual SPEI were calculated using field correlations and *p*-values calculated with the Climate Explorer application (Trouet and Van Oldenborgh 2013). The effects of monthly climatic factors on the RWI chronologies were assessed using Pearson's correlation, and the percentage of stands with significant correlations with monthly climatic variables was calculated. Moving correlations between the RWI chronologies and climate variables were calculated in 21-year periods and shifted by 1 year, yielding a total of twelve moving correlations (from 1982–2005 to 1996–2016) per climate variable, selected based on the previously obtained correlations. The temporal change in the moving correlations of the RWI chronologies per stand with the climate variables was quantified as the slope (Slp) of the linear trends of the moving correlations calculated at 21-year intervals. The slope of the running correlations was calculated considering all 21-year moving correlations between 1985 and 2016, and therefore, both the direction and magnitude of change in growth-climate relationships refer to all 21-year periods. The slopes of the linear trends in the study stands were arranged in descending order to calculate the proportion of positive and negative slopes.

Tree growth responses to drought were quantified as reductions in radial growth observed in years with unusually low SPEI values. Specifically, we selected the years 2005 and 2012 because they had the lowest values of the 12-month SPEI during the study period (Fig. 2). The effects of drought on tree-ring width were quantified using indices of drought resistance (Rt), recovery (Rc), and resilience (Rs), calculated according to Lloret et al. (2011). In this study, we used a 3-year period before the drought to calculate these indices. Rt quantifies the ability of trees to buffer drought stress and continue to grow during the drought, Rc quantifies their capacity to grow again after the drought ends, and Rs quantifies their ability to restore pre-drought growth rates (Lloret et al. 2011). We first calculated the indices of growth responses to drought using both the raw ring widths and the BAI series (Schwarz et al. 2020). However, we then decided to use only the indices derived from raw ring widths because these indices and their increments showed stronger relationships with the independent variables used in this work than the BAI-derived indices. The change in drought response (i.e., Rt, Rc, and Rs) between the successive severe droughts of 2005 and 2012 was calculated as the difference in indices between 2012 and 2005 (i.e., Rt_{2012}-Rt_{2005}, Rc_{2012}-Rc_{2005}, and Rs_{2012}-Rs_{2005}).

The collinearities between independent variables were checked by correlation analysis and principal component analysis (PCA) based on the correlation matrix among the local structural, physiographic, and climatic traits used. The influence of local structural, physiographic, and climatic traits on tree-ring growth (EPS, MS, Rbt, SNR, mean BAI, BAI slope), temporal changes in hydroclimate responses (slope of moving correlations), and changes in drought response (Rt_{2012}-Rt_{2005}, Rc_{2012}-Rc_{2005}, Rs_{2012}-Rs_{2005}) were examined using stepwise multiple linear regression. Stand growth traits, changes in tree growth responses, and changes in drought response indices were the dependent variables

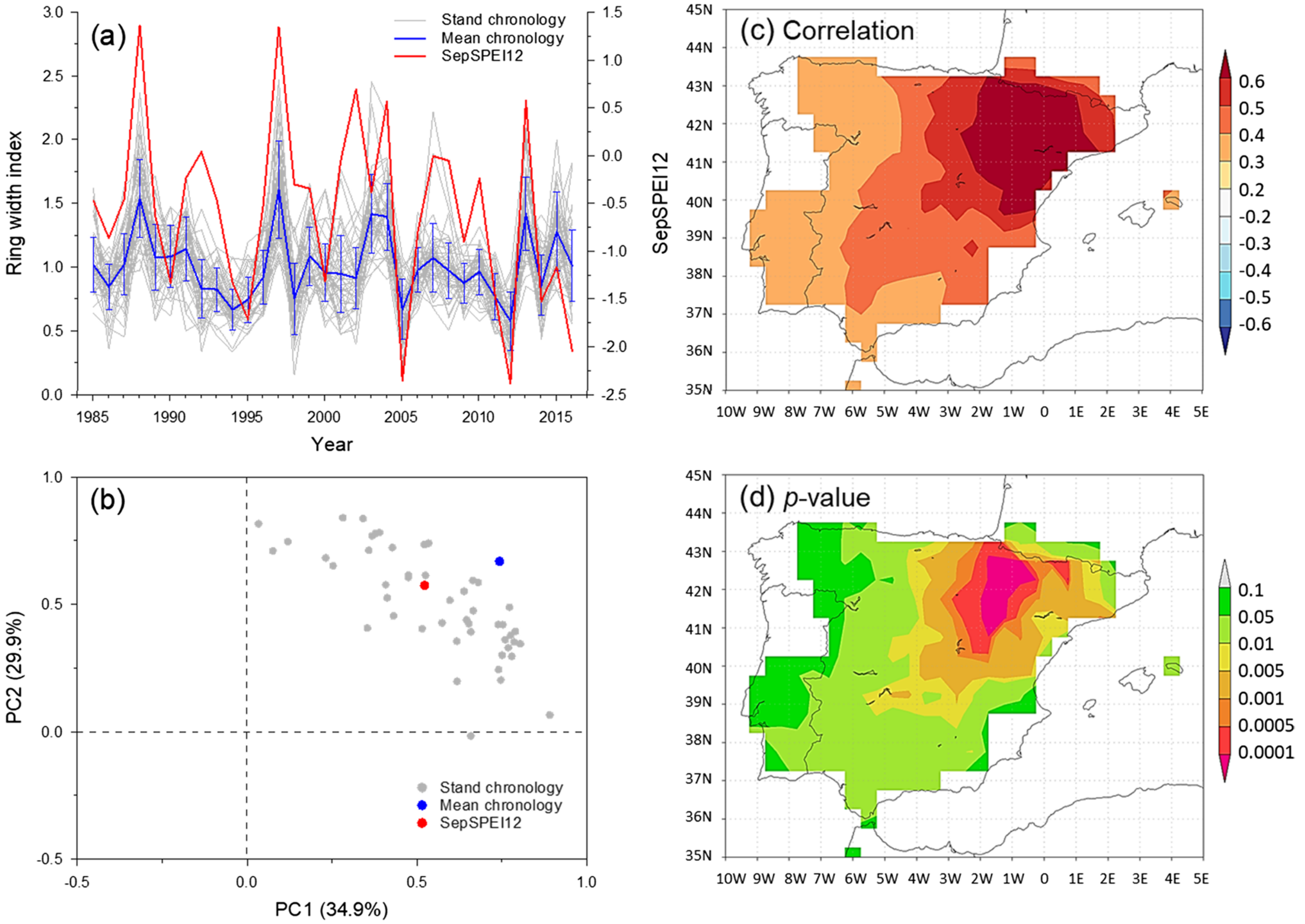

Fig. 2 Annual variation of ring width indices in Aleppo pine stands, mean chronology (±SD), and annual standardized precipitation evapotranspiration index (SPEI) during the hydrological year (from October to September, SepSPEI12) in the period 1985–2016 (**a**). Biplot of principal component loadings among stand chronologies, mean chronology, and annual SPEI, obtained from a correlation matrix among time series after a varimax axis rotation (**b**). The percentage of variance explained by each PC axis is shown. Field correlations (**c**) and *p*-values (**d**) for the spatial relationships between the mean Aleppo pine chronology and annual SPEI over the period 1985–2016

in the multiple regression analyses, and stand structural, physiographic, and climatic traits were the predictors. The stepwise approach allowed to exclude redundant and collinear predictors that could have led to an overestimation of the explained variance, and we considered including a maximum of two predictors in the model. The proportion of variation in dependent variables explained by predictors was quantified using the coefficients of determination derived from the regression models and adjusted for the loss of degrees of freedom (r_{adj}^2). We used the *olsrr* software in the R environment (R Core Team 2022) for computing multiple stepwise regression, which performs collinearity diagnosis and uses a stepwise procedure to select the best regression model based on *p*-values (Hebbali 2020).

In addition, we used redundancy analysis (RDA) which searches for linear combinations of explanatory factors that correlate with a set of response variables, as an extension of multiple linear regression applied to multiple dependent variables. Tree-ring growth traits and temporal changes in hydroclimate response and drought response were used as response variables, and stand structural, physiographic, and climatic traits found to be significant in the stepwise regression analyses were used as explanatory factors. A first RDA analysis was performed to determine the amount of variation in tree-ring growth traits and chronology statistics explained by the explanatory variables (those retained as significant in the stepwise regression analyses for tree growth traits; Table 1). A second RDA analysis was conducted to determine the amount of variation in the changes in tree growth responses and drought response indices explained by the explanatory variables (those retained as significant in the stepwise regression analyses for climate response changes; Table 1). The total variance of the response variables explained by explanatory factors was determined under reduced RDA models, including the combined effects of all significant explanatory factors. Monte Carlo tests with 999

Table 1 Summary statistics of stepwise multiple linear regression models of growth trait (EPS, SNR, MS, Rbar, MBAI, SlpBAI) and climate response changes (SlpJunJulPrec, SlpAprSepSoilM, SlpMayJulET, SlpJunSPEI6, SlpSepSPEI12, Rt_{2012}–Rt_{2005}, Rs_{2012}–Rs_{2005}) as dependent variables and stand structural traits (Age, Ho, RSI, N, SI) and local physiographic and climatic features (Ele, ET, MnTC, MxTW, SP, Long) in Aleppo pine stands as independent variables. Explanations of the abbreviations can be found in Tables S1, S2, and S3. Slp is the slope of climate response change, quantified as 21-year moving correlations over the period 1985–2016

					Regression model statistics			
Dependent variable	Independent variable	*β*	*t*	*p*	df_1 / df_2	r_{adj}^2	*F*	*p*
Growth trait								
EPS	N	– 0.505	– 3.97	<0.001	1 / 46	0.239	15.75	<0.001
Rbar	N	– 0.421	– 3.15	0.003	1 / 46	0.160	9.93	0.003
SNR	Age	– 0.388	– 2.86	0.006	1 / 46	0.132	8.17	0.006
MS	Ho	– 0.417	– 3.25	0.002	1 / 45	0.256	9.10	<0.001
	Ele	– 0.264	– 2.06	0.045				
MBAI	SI	0.749	7.68	<0.001	1 / 46	0.552	59.00	<0.001
SlpBAI	RSI	0.521	4.16	<0.001	1 / 45	0.296	10.86	<0.001
	MxTW	– 0.369	– 2.94	0.005				
Climate response change								
SlpJunJulPrec	Long	– 0.376	– 2.75	0.008	1 / 46	0.123	7.58	0.008
SlpAprSepSoilM	ET	– 0.390	– 2.87	0.006	1 / 46	0.134	8.24	0.006
SlpMayJulET	Long	– 0.584	– 4.63	<0.001	1 / 45	0.314	11.77	<0.001
	SP	0.345	2.74	0.009				
SlpJunSPEI6	Ele	0.289	2.12	0.039	1 / 45	0.154	5.29	0.009
	Long	– 0.280	– 2.05	0.046				
SlpSepSPEI12	Ele	0.364	2.65	0.011	1 / 46	0.114	7.02	0.011
Rt_{2012}–Rt_{2005}	MnTC	0.462	3.53	0.001	1 / 46	0.196	12.45	0.001
Rs_{2012}–Rs_{2005}	Ele	– 0.449	– 3.40	0.001	1 / 46	0.184	11.58	0.001

random iterations were used to assess the significance of canonical eigenvalues. A bi-variate scatterplot of the weighting coefficients for the first two RDA axes showed the relationships between the explanatory factors and the response variables. RDA analyses were performed using the *vegan* package (Oksanen et al. 2020) in the R environment (R Core Team 2022).

Results

Radial growth of Aleppo pine trees

The tree-ring chronologies showed high agreement among stands and with the SPEI records along the hydrological year. Two minimum values in 2005 and 2012 were common to all RWI stand chronologies and the September SPEI12 time series (Fig. 2a), suggesting that they were caused by severe droughts. Furthermore, the correlation between the mean chronology of all stands and September SPEI12 was 0.69 ($p < 0.0001$). A strong correspondence between September SPEI12 and Aleppo pine growth at regional scale was also provided by principal component analysis (Fig. 2b). Field correlations (Fig. 2c) and *p*-values (Fig. 2d) showed that Aleppo pine growth is strongly and significantly ($p < 0.05$) spatially related to annual SPEI in almost the entire Iberian Peninsula, except for the northwestern area, and the correlation was particularly significant ($p < 0.001$) in the northeastern area. The maximum distance between sites was 181 km and the maximum elevation difference between sites was 579 m, with an average correlation between tree-ring chronologies of 0.55 ($p < 0.0001$) and a maximum correlation between chronologies of 0.91 ($p < 0.0001$). A decreasing trend in the correlations between tree-ring chronologies was noted as both the distance between sites (Fig. S2a) and the elevation difference (Fig. S2b) increased. The high common signal among trees in each stand was suggested by the EPS values, which ranged from 0.50 to 0.98, with an average value of 0.81 (Table S2).

Tree growth responses to hydroclimate and drought

The correlations between tree-ring stand chronologies and climate records at the regional scale showed a dominant beneficial influence of water availability on tree growth, as evidenced by the positive correlations with precipitation mainly in January, April, and June–July of the growing year (Fig. 3a), soil moisture in April to September (Fig. 3b), and evapotranspiration in May to July (Fig. 3c). However, the influence of monthly temperature on tree-ring growth was almost negligible, with a very small proportion of stands showing a significant correlation (Fig. 3d). When looking at the water balance, as represented by the SPEI, positive correlations were found with a maximum proportion of stands whose tree-ring chronologies showed positive correlations with SPEI1 in January (Fig. 3e), and with SPEI3 in March

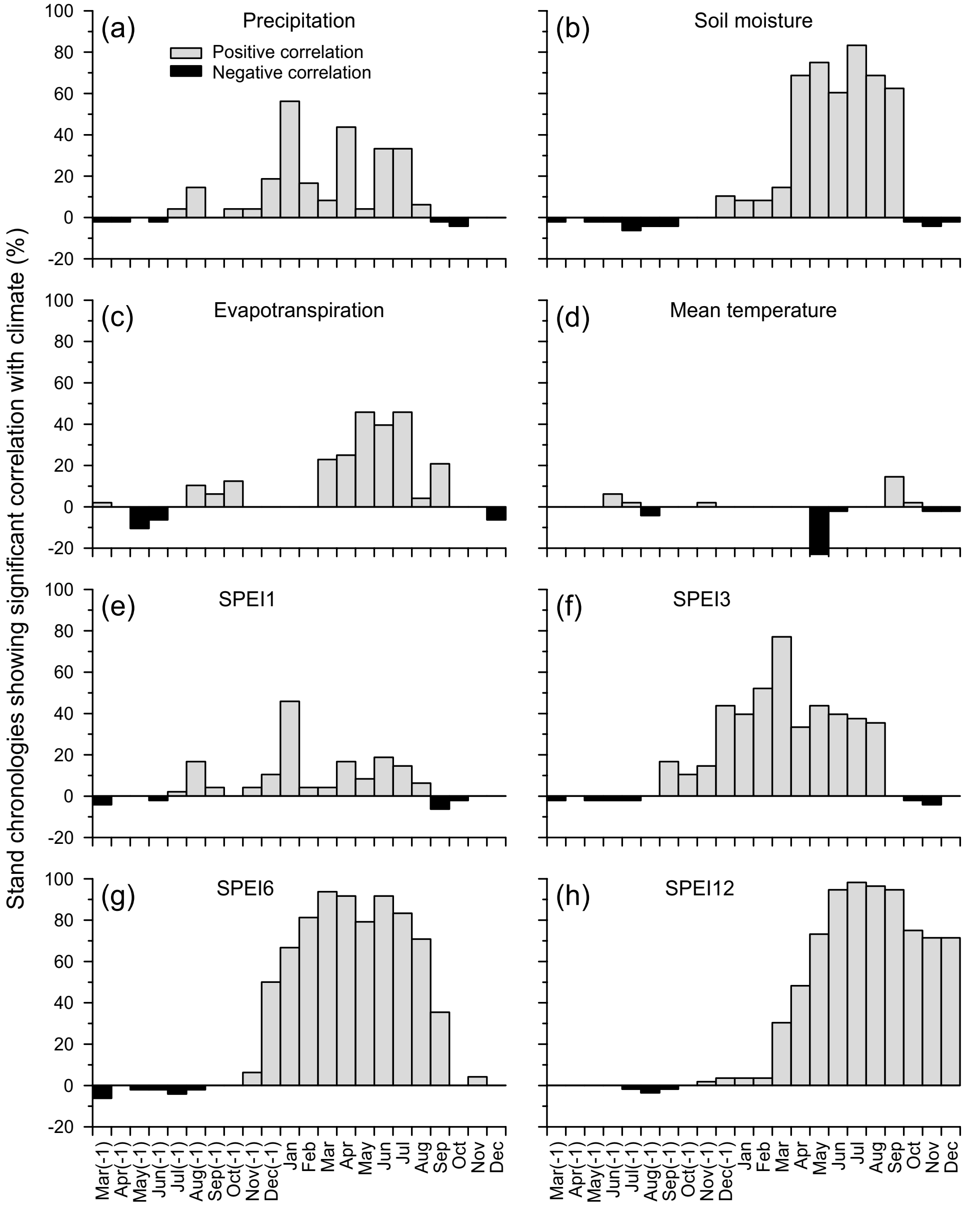

Fig. 3 Percentage of Aleppo pine tree-ring chronologies showing significant ($p < 0.05$) correlations with (**a**) precipitation, (**b**) soil moisture content, (**c**) evapotranspiration, (**d**) mean temperature, and cumulative (**e**) 1-month, (**f**) 3-month, (**g**) 6-month, and (**h**) 12-month SPEI time series. The correlations were calculated over the period 1985–2016 and the window considered for calculating the correlations extended from March of the previous year (Mar(-1)) to December of the current growth year (Dec). A positive percentage (gray bar) indicates a positive correlation, while a negative percentage (black bar) indicates a negative correlation

(Fig. 3f), SPEI6 in February to August (Fig. 3g), and SPEI12 in June to September (Fig. 3h).

When 21-year run correlations were calculated at the stand level, there was evidence that the climate responses of Aleppo pine varied over time, and that the slope of the changing responses varied among stands. Responses to precipitation mainly decreased over the period 1985–2016, particularly for January and April precipitation, while about half of stands showed a significant decreasing response and the other half showed an increasing response to June–July precipitation (Fig. 4a; Table S3). Regarding the response changes of tree-ring growth to soil moisture from April to September, evapotranspiration from May to July and SPEI in January, a decreasing response was observed in the majority of stands (Fig. 4b; Table S3). Looking at the water balance in periods of 3 and 12 months, the response increased in most stands for the particular cases of March SPEI3 and September SPEI12, while in the case of June SPEI6, the response decreased for most stands (Fig. 4c; Table S3). Since the main significant correlations between Aleppo pine tree-ring chronologies and hydroclimate were positive, increasing temporal variations in climate responses should be interpreted as an intensification of the positive correlations, while decreasing variations correspond to a reduction in the strength of the positive correlations. A comparison of tree growth resistance, recovery, and resilience to the 2005 and 2012 drought events found that growth resistance decreased in 46% of stands but increased in 54% of stands, recovery decreased in 21% and increased in 79% of stands, and

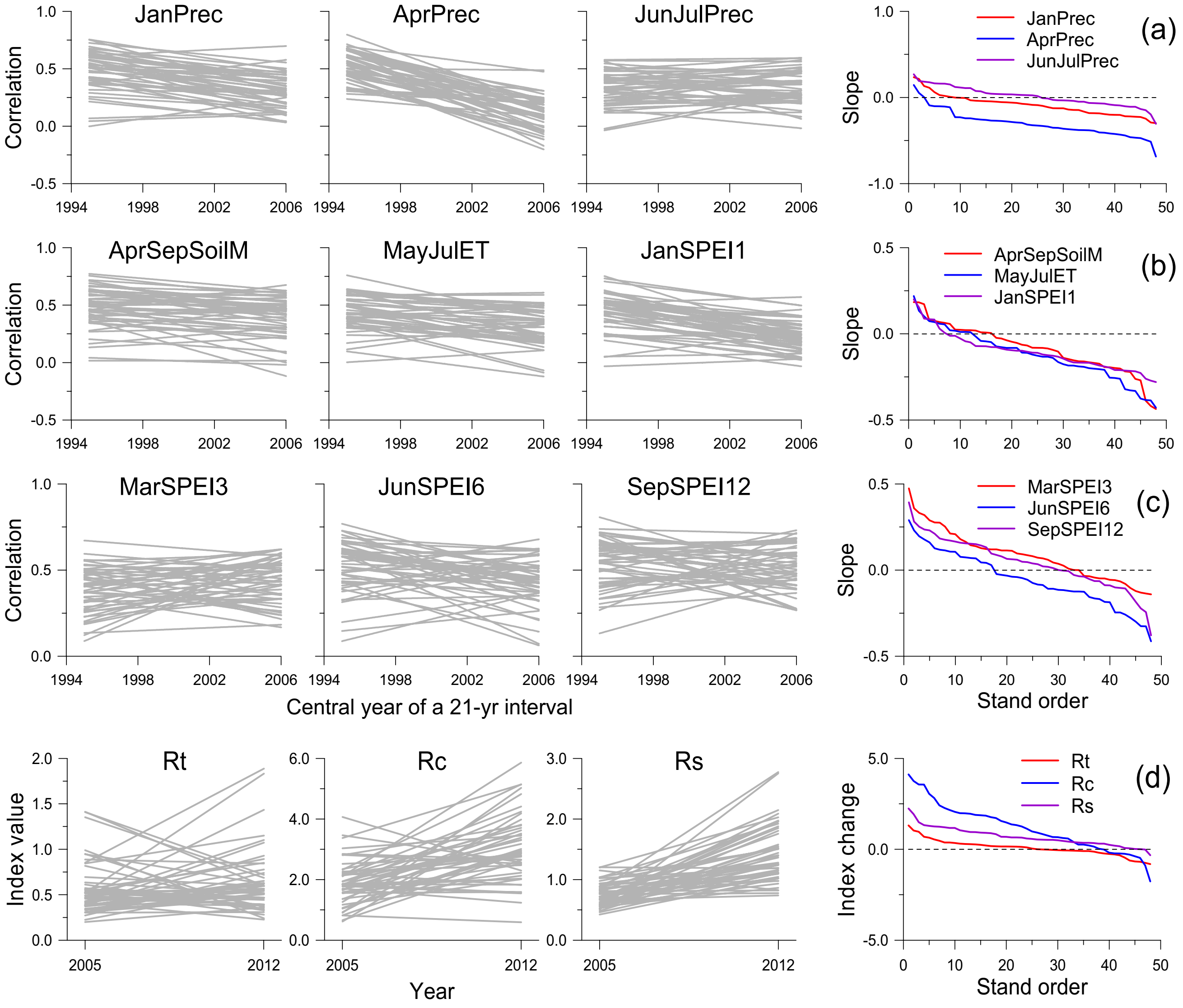

Fig. 4 Temporal change in climate response of Aleppo pine tree-ring chronologies in the study stands to precipitation in January, April, and June–July (**a**), soil moisture in April–September, evapotranspiration in May–July and January SPEI1 (**b**), as well March SPEI3, June SPEI6, and September SPEI12 (**c**). Shown are linear trends of the 21-year moving correlations calculated over the period 1985–2016 (gray lines), and the slopes of the linear trends of these correlations in descending order across the study stands (red, blue and purple lines). Resistance (Rt), recovery (Rc), and resilience (Rs) indices of growth response to drought in the dry years 2005 and 2012 (gray lines), and the changes in these indices between 2005 and 2012 in descending order in the study stands (red, blue, and purple lines), are shown (**d**)

resilience decreased in 4% and increased in 96% of stands (Fig. 4d; Table S3).

Relationships of growth traits with stand structure and local climate variations

The independent variables considered in this work showed significant correlations among them, suggesting that they were at least partially collinear (Fig. S3). The structural variables were mostly positively correlated with each other, except for RSI, which was negatively correlated with the others (Fig. S3a). The climate variables were also significantly correlated with each other, with the temperature and drought variables positively correlated, but precipitation negatively correlated with the others (Fig. S3a). Elevation was positively correlated with the temperature and drought variables, but negatively correlated with the precipitation variables. Latitude and longitude were negatively correlated (Fig. S3a), which was due to the north-west to south-east orientation of the Ebro basin, where the study stands are located. The first principal component was mainly related to physiographic and climatic variables, namely positively with temperature, drought, evapotranspiration, latitude, and longitude, while elevation and precipitation variables were in the negative extreme (Fig. S3b). The structural variables were mainly positively related to the second principal component, except for the RSI, which was in the negative extreme (Fig. S3b).

Growth traits of trees were found to be related mainly to the structural characteristics of the stand and, to a lesser extent, to local climate variations (Table 1). EPS (Fig. S4a) and Rbar (Fig. S4b) showed highly significant negative correlations with stand density (N), indicating that the densest stands have lower common signal of tree-ring series and lower correlation between series. The SNR showed a negative association with the average age of the examined trees in a stand (Fig. S4c), with the strength of the observed common signal between trees decreasing in a chronology as the trees increased in age. MS was negatively associated with both dominant tree height (Fig. S4d) and site elevation (Table 1), with smaller inter-annual variations in radial growth occurring in stands with taller trees and at higher elevations. On the other hand, growth rates depended mainly on variables related to site quality and the spacing between trees in a stand. The mean BAI in a stand was positively related to site index (Fig. S4e), with higher growth rates occurring in the stands with higher site quality. Finally, the BAI slope in a stand was positively related to the relative spacing of trees in the stand (Fig. S4f), and negatively related to the maximum temperature of the warmest month (Table 1), showing higher positive slopes of BAI in stands with widely spaced trees and in areas with colder summers.

According to the reduced RDA model, the RDA1 axis explained 83.4% and the RDA2 axis explained 14.7% of the variation in growth traits and explanatory factors (Fig. 5a). The main explanatory factors controlling growth traits were the average age of trees in a stand and the stand density, which were found to be negatively correlated with RDA1 (Table 2) and the growth traits, and the relative spacing index, which was found to be positively correlated with RDA1 and the growth traits (Fig. 5a). The other explanatory factors played a minor role in controlling growth traits, explained less than 5% of the growth variance, and were mostly negatively correlated with RDA1 and positively correlated with RDA2 (Table 2).

Relationships of climate response changes with local physiography and climatic variations

Responses to January and April precipitation and to January SPEI1 consistently decreased at the regional scale, and responses to March SPEI3 predominantly increased in the study area, independent of local variations in forest structure, physiography, and climate (Table S3). Furthermore, tree growth recovery following drought events largely increased at the regional scale (Fig. 4d), independent of local variations in forest structure, physiography, and climate. In contrast, the changes in the other growth responses to climate considered, as well as the resistance and resilience indices of the growth response to severe droughts, depended on the local variations of independent variables (Table 1).

The slope of the June–July precipitation response was positively correlated with longitudinal position, and showed the strongest increasing trends for stands west of the study area (Fig. S5a). Slopes of growth response to soil moisture from April to September were dependent on local evapotranspiration, with the most negative slopes occurring in areas with greater evapotranspiration (Fig. S5b). Changes in growth response to evapotranspiration in May to July were primarily related to longitudinal position with a negative association and to summer precipitation with a positive association, with the most decreasing trends occurring in stands with drier summers to the east of the study area (Fig. S5c).

For responses to SPEI, the slopes of growth responses to SPEI6 in June (Fig. S5d) and SPEI12 in September (Fig. S5e) were positively associated with elevation, with the response decreasing in stands at lower elevations. Furthermore, the slope of growth response to SPEI6 in June also depended on longitudinal position with a negative relationship (Table 1), showing an increasing trend for stands in the west of the study area. Changes in tree growth resistance and resilience to the severe droughts of 2005 and 2012 were also dependent on local variations in physiography and climate. The shift in resistance was related to local variations in the mean minimum temperature of the coldest month (Fig. S5f), with growth resistance to drought decreasing in stands with cold winters and increasing in stands with temperate winters. The change in growth resilience to drought was negatively related to elevation (Fig. S5g), with resilience increasing primarily in lower-elevation stands.

According to the reduced RDA model, the RDA1 axis explained 90.6% and the RDA2 axis explained 9.3% of the variation in climate response change and explanatory factors (Fig. 5b). A clear grouping of the response variables considered was found, with the slopes of climate responses grouped in the right half of the biplot and the changes in resistance and resilience indices of growth to drought in the left half of the biplot. In fact, the correlations between the slopes of climate responses were positive and significant, ranging from 0.384 ($p = 0.0035$) for the slopes of June–July precipitation with April–September soil moisture to 0.929 ($p < 0.0001$) for the slopes of JunSPEI6 with SepSPEI12. The changes in resistance and resilience indices were also positively related, with a correlation between them of 0.374 ($p = 0.0044$). The main explanatory factors controlling the change in climate responses were elevation and summer precipitation, which were positively correlated with RDA1 (Table 2) and the slopes of climate responses, and negatively correlated with the changes in resistance and resilience (Fig. 5b). The other relevant explanatory factors associated with changes in climate

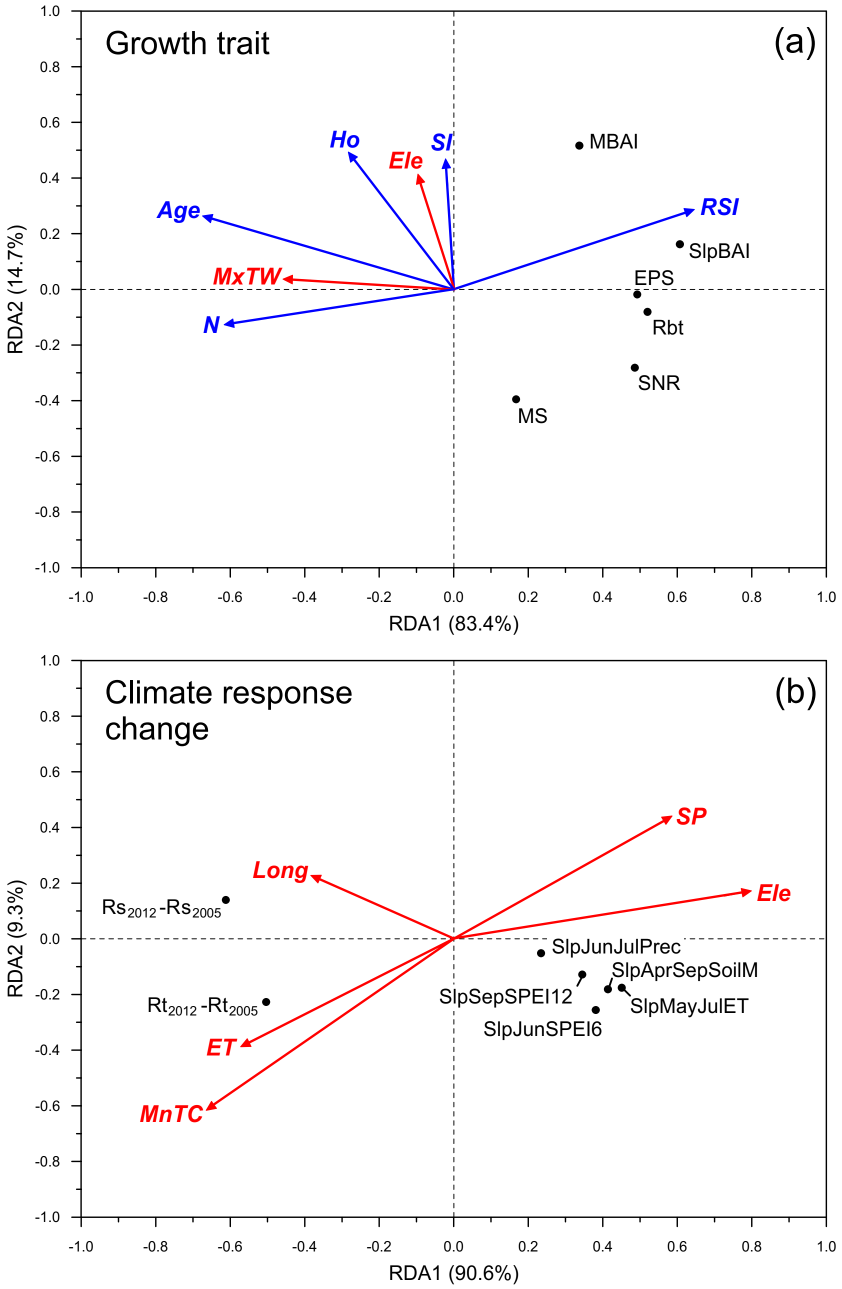

Fig. 5 RDA biplot ordinations showing the relationships of response variables (dots) related to growth traits (**a**) and growth-climate response change (**b**), with explanatory factors related to stand structure traits (blue arrows) and local physiographic and climatic traits (red arrows), obtained under the reduced RDA models of Table 2. The percentage of tree growth traits and climate response changes explained by each RDA axis is shown. Explanations of the abbreviations can be found in Tables S1, S2, and S3. Slp is the slope of climate response change, quantified as 21-year moving correlations over the period 1985–2016

responses were the minimum temperature of the coldest month and local evapotranspiration, with longitudinal position playing a minor role and explaining less than 5% of the variance (Table 2). These explanatory factors were found to be negatively correlated with RAD1 and the slopes of climate responses, and positively correlated with the changes in resistance and resilience (Fig. 5b). Indeed, the correlations between changes in climate responses in 1985–2016 and increments in growth resistance and resilience in the 2005 and 2012 droughts were significant and negative (Fig. S6).

Discussion

Aleppo pine growth is driven primarily by water availability

Our study showed that water availability during the growing season, quantified as precipitation, soil moisture, or the standardized precipitation evapotranspiration index, was the main driver of Aleppo pine growth in the semi-arid Mediterranean climate. This result is consistent with

Table 2 Summary statistics of reduced RDA models for the relationships between growth traits (EPS, SNR, MS, Rbar, MBAI, SlpBAI) and climate response changes (SlpJunJulPrec, SlpAprSepSoilM, SlpMayJulET, SlpJunSPEI6, SlpSepSPEI12, Rt_{2012}–Rt_{2005}, Rs_{2012}–Rs_{2005}), with stand structural traits (Age, Ho, RSI, N, SI) and local physiographic and climatic features (Ele, ET, MnTC, MxTW, SP, Long) in Aleppo pine stands. Explanations of the abbreviations can be found in Tables S1 and S2. The two reduced RDA models correspond to the ordination biplots shown in Fig. 5. λ indicates the variation in response components explained by each model

					Reduced RDA model		
Response component	Independent variable	r with RDA1	r with RDA2	Explained variance (%)	*λ*	*F*	*p*
Growth trait	Age	– 0.454	0.102	10.1	0.370	3.35	0.002
	RSI	0.433	0.122	9.5			
	N	– 0.412	– 0.059	8.2			
	MxTW	– 0.303	0.006	4.4			
	Ho	– 0.191	0.182	2.8			
	SI	– 0.002	0.159	1.1			
	Ele	– 0.064	0.149	0.9			
Climate response change	Ele	0.524	0.055	11.1	0.354	4.61	0.001
	MnTC	– 0.470	– 0.164	9.4			
	SP	0.385	0.141	6.3			
	ET	– 0.373	– 0.124	6.0			
	Long	– 0.245	0.072	2.5			

previous studies showing that the growth of this species is correlated with precipitation, soil water availability, and drought intensity (Rathgeber et al. 2005; Vennetier et al. 2018; Helluy et al. 2020), and the most significant positive correlations with growth were found for winter, spring, and summer precipitation (de Luis et al. 2013; Bouachir et al. 2017). The strong dependence of tree growth on hydroclimatic conditions has been demonstrated in the seasonally dry Mediterranean climate, where soil water availability during the growing season is mainly determined by precipitation and the water-holding capacity of the soil (Martín-Benito et al. 2013; Pacheco et al. 2015).

Our results also showed that temperature plays almost no direct role in determining the growth rates of this species. Our study is limited to a relatively warm and dry period characterized by recurrent droughts since the 1980s, in contrast to the previous decades, which were wetter and colder in northeastern Spain (Tejedor et al. 2017; Serrano-Notivoli et al. 2023). No significant changes in mean annual precipitation were detected in our study area, but an increasing trend in mean annual temperature was noted, as already observed in other Mediterranean areas (del Río et al. 2014; Pacheco et al. 2015; Marqués et al. 2016). This suggests that soil temperature likely increased, which increased evaporation and then soil water availability decreased (Morcillo et al. 2022), leading to the observed relevance of soil moisture and SPEI to tree growth throughout the growing season, mainly from April to September. Significant correlations of Aleppo pine growth with temperature have previously been shown, mainly positive in winter and negative in spring and summer (de Luis et al. 2013; del Río et al. 2014), but these occurred in areas where thermal stress is likely to be greater than in our study stands, which are located inland in a continental mountainous region.

Stand structure modulates tree growth dynamics and wood productivity

According to our findings, stand structure has a strong influence on Aleppo pine growth dynamics, with stand density, tree age, and size being the main factors that determine the common growth signal between trees. Since the structural variables in our Aleppo pine plantations are closely linked (see Fig. S3), we can assume that higher stand density means lower spacing index and greater tree height, which modulates tree growth traits, particularly growth rate, mean sensitivity, and common signal of the tree-ring series. We found that tree density strongly influenced the common signal of tree-ring series, with EPS and Rbar values being higher in the less dense stands. This is in line with a previous study by Camarero et al. (2021) who found that EPS and Rbar were higher in natural pine stands than in dense plantations. However, other studies have shown the opposite pattern (Moreno-Gutiérrez et al. 2012; Sánchez-Salguero et al. 2013), with tree-ring series from dense pine plantations showing a stronger common growth signal than open natural forests. Our study stands of young and small trees showed higher SNR and MS than the stands of older and taller trees. Radial growth of trees with high levels of competition has been shown to have low mean sensitivity, probably because in environments with higher competition, trees are expected to grow less plastically and have lower inter-annual growth variability (Rozas and Olano 2013; Rozas 2015). This would be a reasonable interpretation of our results because competition intensity in a forest increases as trees grow older and taller, reducing growth variability. In addition, tree height also has an effect on the mean sensitivity of tree-ring series, which is probably related to the influence of tree height on hydraulic conductance and tree growth (Zaehle 2005).

We found that widely spaced Aleppo pines with lower inter-tree competition in high-quality stands had higher average growth rates and increasing productivity trends, supporting previous results (Bottero et al. 2017; Rojo-Alboreca et al. 2017; Cattaneo et al. 2018). Aleppo pines growing at high densities have lower stomatal conductance, photosynthesis rates, and growth rates because they are more stressed by water deficiency than trees growing at lower densities (Moreno-Gutiérrez et al. 2012; Olivar et al. 2014). In fact, reducing tree density through thinning in semi-arid Aleppo pine plantations has been recommended to alleviate drought stress, promote tree growth, and reduce tree mortality (Calev et al. 2016; Manrique-Alba et al. 2020). The observed relationship between local variations in mean maximum temperatures in the warmest month and the BAI temporal trend suggests that Aleppo pines have a lower ability to increase wood production in areas with warm summers compared to areas with mild summers. In the Mediterranean region, wood formation is interrupted in summer due to high temperatures and lack of precipitation, leading to inhibition of xylem cell division and enlargement due to low water potentials (Camarero et al. 2010; Calev et al. 2016). The detrimental effects of high summer temperatures on the BAI slope of Aleppo pine suggest that prolonging the summer water stress period would significantly reduce wood production in the future. Overall, managing dry pine forests at low tree density represents a useful adaptation strategy to reduce the negative effects of water stress on tree productivity and forest vitality in the coming decades (Bottero et al. 2017; Candel-Pérez et al. 2022).

Elevation and local climate variations modulate changes in responses to climate

It is important to note that some relevant tree growth responses examined continuously decreased (January and April precipitation, January SPEI) or increased (March SPEI) in the majority of stands studied, independent of local variations in structural, physiographic, and climatic traits. These results should be interpreted as consistent temporal changes in hydroclimate vulnerability at the regional scale pointing to a strong sensitivity of Aleppo pine growth to soil water recharge during previous winter and spring (de Luis et al. 2013; del Rio et al. 2014; Camarero et al. 2020). Furthermore, xylogenesis of this species begins in March–April in semi-arid northeastern Spain (de Luis et al. 2007; Camarero et al. 2010), which may determine the importance of water availability during these months for subsequent annual growth. However, the observed dependence of both decreasing and increasing growth responses to climate and drought on local conditions suggests that Aleppo pines are capable of adapting to local climatic constraints, particularly water availability (del Castillo et al. 2015; Gazol et al. 2017).

At the regional scale, we found highly significant decreasing correlations between Aleppo pine tree-ring chronologies with increasing distance and elevation difference between stands. This is consistent with the observed relevant role of physiography and local climate variation in modulating time-varying growth responses to climate and drought. Our results suggest that the climatic factors controlling tree growth depended on local site conditions, with nearest stands and stands at similar elevation showing similar growth behavior and response to climate. Previous studies have shown that physiographic and climatic differences between sites are key factors in the response of Mediterranean pines growth to climate (Vicente-Serrano et al. 2010b; del Río et al. 2014; Gazol et al. 2017). In the particular case of the Aleppo pine, it underwent intense climate-driven selection during post-glacial expansion in the Mediterranean region (Voltas et al. 2018; Ruiz Daniels et al. 2018), which induced genetic adaptation to a particular environment and plastic adjustment of physiology, xylogenesis, and wood anatomy to local environmental conditions (García-Esteban et al. 2010; Patsiou et al. 2020).

Elevation was the most important factor in controlling variation in Aleppo pine response to cumulative semi-annual and annual SPEI. In our study area, increasing elevation without changing aspect means an increase in precipitation and a decrease in air temperature, evapotranspiration, drought intensity, and duration (see Fig. S3). The longitudinal location of the stands also determines the local climate, as the easternmost stands had higher temperature and evapotranspiration than the westernmost (Fig. S3). The combined effect of elevation and longitude means that tree growth in drier stands at lower elevations and/or eastern locations had a decreasing positive correlation with precipitation, soil moisture, evapotranspiration, and cumulative SPEI during the growing season. This finding may be related to the influence of mean annual temperatures on exacerbating heat stress and vapor pressure deficit (Zweifel et al. 2021), which is likely to increase the deleterious effects of water scarcity on Aleppo pine growth in water-limited ecosystems (Morcillo et al. 2022; Nunes et al. 2022). Rising temperatures without a corresponding increase in precipitation boost summer water stress and embolism risk, limit photosynthetic activity, increase respiratory rate, and then reduce carbohydrate reserves and the ability to respond to water stress, even intensifying mortality risk (Vicente-Serrano et al. 2010b;

Navarro-Cerrillo et al. 2020). Although latewood tracheid production in Aleppo pines can be intensified in response to high summer temperatures, a sharp decline in cell enlargement is expected in summer in response to low water availability (Pasho et al. 2011a). Mediterranean pines maintain low growth rates during the summer dry period, and heat stress can even drive a complete cessation of xylogenesis in summer, which can delay latewood development and reduce the positive effect of early autumn precipitation on growth (de Luis et al. 2011; Camarero et al. 2010; Pacheco et al. 2015).

The two droughts in 2005 and 2012 that affected our Aleppo pines and large areas of the western Mediterranean Basin resulted in reduced growth of conifers in those years (Camarero et al. 2015; Rubio-Cuadrado et al. 2018; Gazol et al. 2020; Acuña-Míguez et al. 2023). Post-drought growth recovery consistently increased across our study stands irrespective of site conditions, but we found a site-dependent pattern of changing growth responses to drought between 2005 and 2012. Trees in lower-elevation stands with mild winters showed increasing resistance and resilience to drought, while trees in higher elevation stands with cold winters showed decreasing resistance and resilience to drought. This result may be related to the previous evidence that Aleppo pine growth in dry sites was more resilient to drought than trees in wet sites (Gazol et al. 2017). In general, geographic gradients reflect gradients in local climatic conditions with decreasing temperatures and then lower water stress at higher elevations (Vennetier et al. 2018). In our study area, maximum precipitation occurs in spring and autumn, with low winter precipitation and even negative SPEI values in December and February–March (Fig. S1). During dry winters, water recharge is limited in deeper soil layers, limiting water uptake during summer droughts, an effect that is particularly pronounced in dry environments (Voltas et al. 2015). The stress caused by winter drought could lead to carbon limitation as a consequence of water deficit and low temperature, which could reduce the ability of trees to cope with summer drought, especially in continental areas at high elevation (Anderegg et al. 2020; Marqués et al. 2016).

Finally, of great importance are the previously undescribed negative relationships between the changing growth response to water availability and growth resistance and resilience to severe droughts. We hypothesize that there may be a site-dependent trade-off between growth sensitivity to water availability and resistance to severe drought, which may be mediated by the relevant role of elevation and continentality in controlling the opposing responses to water availability and drought. It is also plausible that differences in tree growth response to the two droughts are characterized by drought timing (Gao et al. 2018), giving that the 2005 and 2012 droughts differed in their onset and duration (González-Hidalgo et al. 2018; Acuña-Míguez et al. 2023). Aleppo pine is adapted to short-term water stress caused by summer drought, but its growth was found to be particularly vulnerable to medium- and long-term droughts (Pasho et al. 2011b). Furthermore, growth resilience of this species is little affected by the intensity of the drought itself, but resistance decreases and recovery increases with drought intensity (Veuillen et al. 2023).

Implications for semi-arid Mediterranean forestry

In the studied region, increasing the distance between trees would significantly increase BAI trend, which, according to our results, would intensify tree growth rate and forest productivity. The predicted warmer summer conditions will lead to a longer summer growth pause in the Mediterranean region, resulting in a decline in annual growth rates of Aleppo pine and a reduction in forest productivity (de Luis et al. 2011; Pasho et al. 2011a; Pacheco et al. 2018). This supports that to maintain forest productivity in semi-arid Mediterranean areas in a future warming and drying scenario, forestry practices aimed at reducing stand density and increasing tree spacing in Aleppo pine stands should be applied (Calev et al. 2016; Manrique-Alba et al. 2020).

Tree growth responses to climate and drought are thought to be influenced by local stand and site characteristics as these control important functional processes that can either increase or attenuate the vulnerability of trees to climatic constraints such as drought (del Rio et al. 2014; Gazol et al. 2017; Helluy et al. 2020). If the response to climate depends on forest structure, forest management can alter stand characteristics and then the sensitivity of trees to limiting climatic factors can be modulated in part by the application of specially designed silvicultural measures that mitigate these threats (Keenan 2015; Jandl et al. 2019; Andrews et al. 2020). However, we found that the stand variables considered in this analysis had no influence on the temporal variation of Aleppo pine growth responses to climate and drought, suggesting that shifts in climate response cannot be modulated by forestry actions. In contrast, site physiography and local climate variability were found to be the most important factors in modulating the temporal variation of Aleppo pine response to climate and drought at the regional scale. Our results suggest that the changing responses to hydroclimate and drought cannot be modulated by silvicultural practices in Aleppo pine plantations and forestry should take these site-dependent constraints into account, as adaptation to local physiographic and climatic conditions represents the most effective strategy to mitigate climate change impacts.

Growth resilience to drought is considered an indicator for assessing future tree mortality risk and forest decline (Camarero et al. 2015; DeSoto et al. 2020; Wu et al. 2022).

According to our results, low-elevation sites with drier climates and mild winters showed a reduced response to water availability but increased drought resistance and resilience, probably because Aleppo pine reaches its environmental optimum under these conditions. In contrast, high-elevation sites with wetter climates and cold winters showed increasing growth response to water availability, but decreasing resistance and resilience to drought. The optimal elevation range of Aleppo pine is between 0 and 600 m and this thermophilic species is limited by low winter temperatures and damaged by frost and snow in mountain areas (Chambel et al. 2013; Vennetier et al. 2018; Patsiou et al. 2020). Although this species can survive at low temperatures, Aleppo pine plantations at elevations above 600 m are currently outside their optimal thermal range and may be limited by extreme and recurrent frosts in interior mountain areas (Di Filippo et al. 2021). Indeed, we have shown that temporal shifts in the susceptibility of tree growth to hydroclimatic conditions and the occurrence of severe droughts can have implications for risk management in afforestation in the semi-arid Mediterranean region.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10113-024-02256-x.

Acknowledgements We thank Álvaro Hernández for his support in the conception and implementation of the sampling design and Angela Blázquez, Mario Goitiandia, and Alfonso Zamora for their help during the fieldwork.

Funding This work was supported by Junta de Castilla y León and UE-FEDER through SEÑALES (VA026P17) and INFRARED (IR2020-1-UVA08) projects, and by Ministerio de Economía y Competitividad, Spanish Government, through BiOLiDAR project (PTQ-15-08067). Field data collection was funded by FEADER under the provisions of the Aragón Rural Development Program 2014–2020. AG is supported by the "Ramón y Cajal" Program of the Spanish MICINN under Grant RyC2020-030647-I, by CSIC under grant PIE-20223AT003, and by the Science and Innovation Ministry and the AEI with projects PID2021-123675OB-C43 and TED2021-129770B-C21.

Data availability Data will be made available upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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