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Biogeographic, Atmospheric, and Climatic Factors Influencing Tree Growth in Mediterranean Aleppo Pine Forests

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Abstract: There is a lack of knowledge on how tree species respond to climatic constraints like water shortages and related atmospheric patterns across broad spatial and temporal scales. These assessments are needed to project which populations will better tolerate or respond to global warming across the tree species distribution range. Warmer and drier conditions have been forecasted for the Mediterranean Basin, where Aleppo pine (*Pinus halepensis* Mill.) is the most widely distributed conifer in dry sites. This species shows plastic growth responses to climate, being particularly sensitive to drought. We evaluated how 32 Aleppo pine forests responded to climate and atmospheric patterns during the second half of the 20th century by using dendrochronology. Climatic constraints of radial growth were inferred by fitting the Vaganov–Shashkin (VS-Lite) growth model. Aleppo pine growth decreased and showed the highest common coherence among trees in dry, continental sites, such as those situated in southeastern and eastern inland Spain and Algeria. Growth increased in wetter sites. Tree growth was enhanced by prior wet winter conditions and cool and wet spring conditions, whilst warm summers were associated with decreased growth. The relationships between site ring-width chronologies were spatially structured, which explains why Aleppo pine growth was distinctly linked to indices describing atmospheric circulation patterns, showing a stronger influence in western sites (Western Mediterranean Oscillation and Northern Atlantic Oscillation). The climatic constraints of growth and their biogeographical variability were captured by the VS-Lite model, with better fits in dry and continental sites, showing strong growth coherence between trees and climatic limitations of growth. Further research using similar broad-scale approaches to climate–growth relationships and in drought-prone regions deserves more attention.

Keywords: dendroecology; drought; *Pinus halepensis*; radial growth; VS-Lite model

1. Introduction

The Mediterranean Basin is a climate-warming hotspot where aridification trends have intensified since the 1980s, and are negatively impacting forest productivity and radial growth of some tree species

[1,2]. However, droughts do not impact tree populations of the same species in the same way, since there are geographical patterns in adaptation [3]. The Mediterranean Basin climate is characterized by a transition from dry and semi-arid conditions in southern and low-elevation sites towards more continental or temperate conditions in northern and high-elevation sites [4]. Regions with more continental conditions are usually drier than regions more influenced by sea convective storms (e.g., compare the Iberian and Italian peninsulas). Such geographical variability in aridity or continentality also conditions growth responses to climate warming. In addition, longitudinal patterns characterize the regional rainfall regime, with more winter–spring precipitation westwards and more autumn precipitation eastwards, and this affects tree radial growth [5]. This has led to the description of an east–west tree growth dipole across the Mediterranean Basin related to several atmospheric patterns and influencing forest productivity and tree growth [6–8]. However, local factors also influence tree growth, and may decouple regional circulation patterns from site climate conditions, as found in the eastern Mediterranean [9]. Therefore, we need better biogeographic characterizations of the forest responses to the Mediterranean climate at regional and local scales [8]. The analyses of climate–growth relationships across wide geographical and climatic gradients would help to identify tree populations or provenances more or less vulnerable to warming-related drought impacts. Tree-ring networks encompassing several sites of the same species provide a powerful tool to disentangle how tree growth responses to climate change across space [10,11].

The diversity in climate conditions and ecological settings across the Mediterranean Basin could favor growth plasticity in response to the climate of widespread tree species like Aleppo pine (*Pinus halepensis* Mill.). This is one of the main Mediterranean tree species that better tolerates summer drought [10–13]. To assess how plastic the response of Aleppo pine radial growth is to climate warming and water shortage, we need broad evaluations across its distribution range, explicitly considering climate–growth associations at different geographical scales, as well as also their connections to atmospheric circulation patterns. These geographical analyses of climate-growth responses across the region provide a spatial analogue to understand and forecast how Aleppo pine growth will respond to climate warming. In addition, considering the responses to large-scale atmospheric circulation patterns gives a more mechanistic understanding on how regional climate impacts forest productivity [5]. These atmospheric patterns explain the east–west tree growth dipole, which is modulated by different seasonal precipitation regimes in the Western and the Eastern regions of the Mediterranean Basin [6,8].

Tree growth responsiveness to climate across ample geographic and climatic gradients can be adequately characterized using process-based models of tree-ring formation [14,15], which allow quantifying climatic thresholds of radial growth [16]. These models are based on several parameters and are used as input climate variables to simulate growth variability, providing estimates of temperature and soil moisture thresholds for ring formation and tree growth [17]. Furthermore, these growth models are based on intra-annual xylem development (xylogenesis), which is very plastic in Aleppo pine [18–25]. Studies on xylogenesis have demonstrated that cambial activity and growth slow down or may stop during the warm-dry summer, and always stops during the dormant period in the cold winter.

Here we analyzed and characterized the biogeographic, atmospheric, and climatic factors influencing tree growth in Mediterranean Aleppo pine forests. The quantification of growth responses to climate and atmospheric patterns allows assessing tree adaptation to climate conditions, and inferring the vulnerability of tree populations against climate warming. We expected that Aleppo pine will show a plastic growth response to growing-season moisture, but such plasticity will be constrained by site location determining exposure to other constraints (e.g., cold winters) and the underlying atmospheric configuration. The Vaganov–Shashkin (VS-Lite) forward growth model [26] was used to infer the main climatic constraints of growth across the species distribution range.

2. Materials and Methods

2.1. Study Region and Tree Species

This study includes the Mediterranean Basin (see Table 1 and Figure 1), but it is mainly focused on eastern Spain, where the climate is mainly Mediterranean, characterized by summer drought and wet-cool conditions in spring and autumn. Nevertheless, in eastern Spain, the Mediterranean climate shows great variability, including continental (inland or in mountain areas) and mesic conditions near the coast. In Spain, seasonality shifts from wetter autumn conditions autumn eastwards to wetter winter-spring conditions westwards, depending on the influence of Mediterranean or Atlantic dynamics [27].

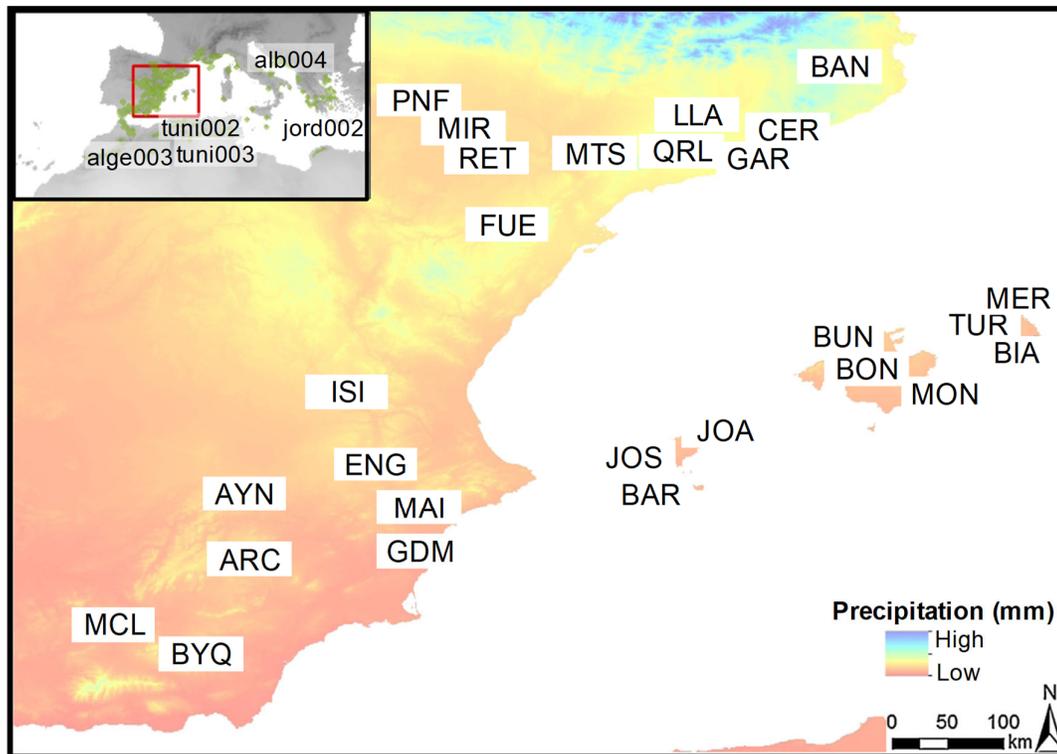


Figure 1. Map showing the location of the study sites (see sites' codes in Table 1), with a focus on eastern Spain. The box in the upper inset indicates the Spanish study area and shows the distribution of Aleppo pine in the Mediterranean Basin, as well as the approximate location of International Tree-Ring Data Bank (ITRDB) sites. The background color key of the map shows the precipitation of the driest quarter.

The Aleppo pine (*Pinus halepensis* Mill.) natural forests and plantations cover ca. 30,000 km² in the Mediterranean Basin, being more abundant in the western (mainly in eastern Spain, southeastern France, and northern Algeria) than in the eastern Mediterranean Basin [28]. This species dominates the Mediterranean's humid to arid (annual precipitation from 200 up to 1500 mm) lowlands (0 to 1000 m a.s.l., but can be found above 2000 m in the Atlas Mountains) with warm (mean annual temperature 13–20 °C) conditions [28]. It is more abundant in dry regions (350–700 mm), with a long dry period (3–7 months) encompassing summer, and often late spring and autumn. Aleppo pine is usually dominant on marly substrates with calcareous and shallow (depth <60 cm) soils [28,29]. Aleppo pine is considered a drought-avoider isohydric species with very efficient stomatal control over water loss through leaves [30]. This implies a rapid use of soil water when it is available, but a rapid closing of stomata and a reduction of carbon uptake to increase water use efficiency and avoid hydraulic failure when soil moisture is limiting [31,32].

The species shows great phenotypic plasticity and also ecotype variability [33] across its natural range of distribution, with diverse changes in anatomical [34], physiological (e.g., [30,31]), and

biochemical traits related to water use (e.g., lumen diameter, water use efficiency) and tolerance to wildfire (e.g., bark thickness, maturity age) [28]. Genetically, Aleppo pine populations are more distinct and diverse in the eastern Mediterranean Basin than in its western counterpart (Spain, NW Africa) [28].

2.2. Climate Data and Climate Indices Representing Major Atmospheric Patterns

In the case of sites located in Spain ($n = 27$ sites), we used the local climate database developed by Ribas [10] by compiling monthly climate data (mean temperature and total precipitation) from meteorological stations located near the study sites. For the rest of sites (five sites), we used the EuMedClim 1 km-resolution database, and used climate data for the period 1950–2014 considering the Mediterranean Basin [35]. In both cases, we calculated the mean annual temperature (MAT) and total annual precipitation (MAP). To determine the site dryness, we calculated the aridity index of De Martonne (AI) for each site as

$$AI = MAP / (MAT + 10) \quad (1)$$

Values of AI lower than 10 correspond to arid climates, semi-arid climates have $10 < AI < 20$, strictly Mediterranean conditions correspond to $20 < AI < 25$, and $AI > 25$ indicates humid conditions [36].

In the Mediterranean Basin, western countries (Spain, Morocco) are more exposed to the influence of the Northern Atlantic Oscillation (NAO) than their eastern counterparts [4]. The NAO is negatively correlated with winter precipitation over most of the western Mediterranean region, and affects climate and tree growth in countries like Spain [5] and Morocco [37], but also in Italy [38]. Besides the NAO, other related patterns influence the Mediterranean climate, such as the Arctic Oscillation (AO) and the Scandinavian pattern (SCA), particularly over the central Mediterranean [4]. In the eastern Mediterranean, the East Atlantic (EA) pattern also affects climate, reflecting precipitation variability not explained by the NAO, and the El Niño Southern Oscillation (ENSO) influences winter precipitation in that region [9,39]. Despite the assumed stronger influence of the NAO on Iberian climate, spring and summer precipitation are also influenced by the ENSO in this region [40]. Finally, we considered the Western Mediterranean Oscillation index (WeMO), which represents autumn-to-winter rainfall patterns over northern and eastern Iberia [41]. Positive WeMO phases correspond to high pressures over Iberia, and therefore, low precipitation. Climate indices (NAO, AO, SCA, EA, and ENSO) were downloaded from the Climate Explorer website [42], and the WeMO index was obtained from the Climatology Group website of the University of Barcelona [43].

2.3. Tree-Ring Width Data

The considered sites were those available for analyses in the ITRDB database and for our sampling sites in Spain. This may affect our analyses, but not the general conclusions, since the density of sampling sites in Spain was high. We obtained tree-ring width data for 482 trees located in 32 sites from two main sources. First, we used the full tree-ring network of Aleppo pine developed for eastern Spain, including the Balearic Islands [10] (Table 1). Second, we downloaded all of the tree-ring series for Aleppo pine from the International Tree-Ring Data Bank (ITRDB) webpage [44], which fulfilled two criteria: (i) they corresponded to populations located in the Mediterranean Basin, and (ii) the last ring of sampled trees was formed after 1998. In total, five sites were obtained from the ITRDB situated in Algeria, Tunisia, Albania, and Jordan (Table 1, Figure 1). For the 27 sites in Spain, cores were obtained from dominant trees taken at 1.3 m using Pressler increment borers. Sampled sites and ITRDB sites had not been affected by local disturbances like wildfires for the past 30 years. This is supported by the finding of old trees in sampled sites (Table 2), the unevenly-aged tree distributions, and the absence of fire scars and charcoal in the soil. In each site, we sampled 10 to 23 trees, resulting in an average of 15 trees and 30 cores sampled per site (Table 2). These wood samples were carefully sanded until rings were visible, and visual cross-dating was performed by annotating very narrow or very wide rings [45]. At least two radii per tree were dated, and ring widths were measured to the nearest 0.01 mm using either Lintab-TSAP (Rinntech™, Heidelberg, Germany) or Velmex measuring devices (Velmex TA, Bloomfield, NY, USA).

Table 1. Characteristics of the Aleppo pine study sites. Variables' abbreviations: MAT, mean annual temperature; MAP, mean annual precipitation; AI, De Martonne aridity index. * ITRDB sites [2,46–48].

Site (Country)	Code	Latitude N (°)	Longitude -W/+E (°)	Elevation (m)	MAT (°C)	MAP (mm)	AI
Sierra de Archivel (Spain)	ARC	32.092	-2.033	1086	13.6	361	15.3
Ayna Los Luisos (Spain)	AYN	38.594	-2.079	1000	14.5	466	19.0
Banyoles (Spain)	BAN	42.107	2.739	260	14.8	804	32.4
Es Cap de Barbaria (Spain)	BAR	38.657	1.077	80	18.8	364	12.6
Cala Biniancolla (Spain)	BIA	39.816	4.261	50	16.9	601	22.3
Santuari de Bonany (Spain)	BON	39.582	3.076	200	17.5	594	21.6
Comuna de Bunyola (Spain)	BUN	39.808	2.705	500	17.4	937	34.2
Pinar de Bayarque (Spain)	BYQ	37.313	-2.465	1280	12.6	347	15.4
Sta. Maria de Cervelló (Spain)	CER	41.397	1.958	300	13.1	664	28.7
Serra d'Enguera (Spain)	ENG	38.857	-0.897	800	16.1	562	21.5
Fuentespalda (Spain)	FUE	40.825	0.083	850	12.8	639	28.0
P.N. del Garraf (Spain)	GAR	41.341	1.844	300	13.2	673	29.0
Guardamar del Segura (Spain)	GDM	38.092	-0.649	10	17.7	293	10.6
Los Isidros (Spain)	ISI	39.450	-1.275	635	13.1	450	19.5
Cala Xarraca (Spain)	JOA	39.099	1.511	175	17.9	462	16.6
Sa Talaia de St. Josep (Spain)	JOS	38.909	1.256	360	17.8	412	14.8
Serra d'Ancosa (Spain)	LLA	41.450	1.533	730	12.3	607	27.2
Serra de Maigmó (Spain)	MAI	38.525	-0.636	900	14.9	351	14.1
El Mencal (Spain)	MCL	37.514	-3.173	1150	14.3	357	14.7
Es Mercadal (Spain)	MER	39.999	4.063	200	17.5	606	22.0
Miramón (Spain)	MIR	41.615	-0.331	500	14.7	376	15.2
P.N. de Mondragó (Spain)	MON	39.035	3.191	60	16.4	439	16.6
Serra de Montsant (Spain)	MTS	41.329	0.820	775	13.2	670	28.9
Vedado de Peñaflo (Spain)	PNF	41.779	-0.709	350	14.0	416	17.3
Querol (Spain)	QRL	41.387	1.433	770	13.4	493	21.1
La Retuerta de Pina (Spain)	RET	41.480	-0.242	386	15.8	428	16.6
Cala Turqueta (Spain)	TUR	39.938	3.916	63	17.5	585	21.3
Tobji * (Algeria)	alge003	34.600	3.117	1380	13.4	338	14.1
Dahllia * (Tunisia)	tuni002	36.233	8.433	950	18.0	434	15.5
Jebnoun * (Tunisia)	tuni003	35.510	9.180	800	17.3	222	8.1
Divjakë * (Albania)	alb004	41.000	19.483	3	15.9	1027	39.6
Dibeen * (Jordan)	jord002	32.140	35.490	800	16.6	350	13.2

Table 2. Tree-ring width and VS-Lite statistics for the study sites. Mean ring widths were calculated for the common period 1950–1999, except for jord002 (1971–1994). The EPS is the expressed population signal, and the best-replicated period was defined as that with EPS > 0.85. The MS is the mean sensitivity. The percent variance accounted for the first principal component (VP1), and the signal-to-noise ratio (SNR) measures the internal coherence of each series. Regarding the VS-Lite model parameters, two of them determine when growth will not occur (T_1 for temperature and M_1 for soil moisture), and the other two determine when growth is not limited anymore by climate constraints (T_2 for temperature and M_2 for soil moisture). The last column shows the correlation between observed and fitted series of ring-width indices.

Site	Tree-Ring Width Data				Statistics of the VS-Lite Model						
	No. Trees/No. Cores	Mean Width \pm SD (mm)	Best-Replicated Period	MS	VP1 (%)	SNR	T_1 ($^{\circ}$ C)	T_2 ($^{\circ}$ C)	M_1 (v/v)	M_2 (v/v)	r
ARC	15/31	0.42 \pm 0.39	1889–2001	0.41	72.7	28.5	5.60	13.83	0.09	0.17	0.62
AYN	15/30	0.53 \pm 0.27	1862–1999	0.29	53.9	14.6	5.11	13.03	0.09	0.30	0.63
BAN	15/30	2.51 \pm 0.73	1932–1999	0.34	59.1	15.0	8.47	12.16	0.01	0.39	0.45
BAR	15/30	1.43 \pm 0.72	1873–2001	0.26	61.0	16.2	3.93	10.82	0.07	0.38	0.52
BIA	12/24	1.57 \pm 0.74	1940–2001	0.27	61.8	13.9	3.91	15.77	0.06	0.46	0.67
BON	13/26	0.78 \pm 0.24	1911–2003	0.37	52.6	8.6	7.58	11.85	0.00	0.13	0.12
BUN	15/25	1.27 \pm 0.32	1864–2003	0.29	56.8	16.5	7.07	22.07	0.01	0.34	0.65
BYQ	15/29	0.99 \pm 0.42	1902–1999	0.38	73.3	37.6	7.33	11.96	0.07	0.17	0.51
CER	13/28	1.43 \pm 0.64	1916–2001	0.38	58.2	13.1	3.86	11.33	0.06	0.50	0.68
ENG	14/28	0.60 \pm 0.36	1860–2000	0.49	62.3	17.2	7.35	21.71	0.01	0.28	0.46
FUE	16/31	0.91 \pm 0.40	1907–1999	0.29	57.2	17.9	8.09	15.71	0.01	0.42	0.50
GAR	22/43	0.95 \pm 0.25	1938–2003	0.28	55.1	20.7	3.94	22.03	0.07	0.44	0.65
GDM	15/28	0.73 \pm 0.38	1915–2000	0.24	46.5	10.8	5.45	19.59	0.05	0.15	0.59
ISI	15/30	1.05 \pm 0.40	1920–1999	0.32	62.5	19.0	7.34	11.19	0.08	0.40	0.74
JOA	16/31	1.60 \pm 0.77	1915–2001	0.35	65.4	21.4	8.16	12.07	0.03	0.35	0.70
JOS	15/28	1.57 \pm 0.65	1920–2001	0.36	68.2	22.6	8.26	13.49	0.01	0.36	0.72
LLA	16/27	1.70 \pm 0.52	1949–1999	0.21	48.2	11.8	6.00	13.22	0.00	0.27	0.43
MAI	13/30	0.79 \pm 0.38	1895–1999	0.45	59.8	14.1	5.01	21.18	0.08	0.26	0.37
MCL	13/24	1.58 \pm 0.58	1893–1999	0.31	62.9	17.6	5.66	10.76	0.00	0.35	0.55
MER	11/22	2.86 \pm 1.30	1926–2001	0.29	66.8	13.8	7.01	12.34	0.04	0.47	0.52
MIR	19/38	0.68 \pm 0.44	1840–2004	0.41	54.9	18.4	6.90	11.66	0.00	0.24	0.75
MON	15/30	1.57 \pm 0.60	1909–2003	0.32	52.1	11.5	6.51	19.29	0.02	0.19	0.34
MTS	15/30	1.15 \pm 0.31	1919–1999	0.24	48.8	10.2	8.45	13.29	0.03	0.34	0.60
PNF	23/43	0.74 \pm 0.34	1860–2004	0.44	69.8	35.3	6.61	11.14	0.01	0.27	0.67
QRL	15/30	2.04 \pm 0.60	1948–1999	0.17	48.0	11.8	5.84	11.34	0.01	0.14	0.16
RET	12/43	0.85 \pm 0.36	1857–2004	0.39	70.2	26.0	8.07	12.07	0.02	0.25	0.76
TUR	10/21	1.53 \pm 0.67	1909–2001	0.25	50.1	10.0	4.58	15.99	0.06	0.41	0.44
alge003	20/39	0.99 \pm 0.70	1887–2006	0.44	71.3	44.4	7.23	12.65	0.00	0.40	0.74
tuni002	11/19	1.60 \pm 0.99	1912–2001	0.37	55.8	8.8	4.35	13.82	0.06	0.44	0.70
tuni003	14/25	1.35 \pm 0.81	1933–2001	0.38	59.6	17.0	2.77	11.82	0.07	0.44	0.67
alb004	20/40	3.99 \pm 1.81	1968–2008	0.23	32.9	7.5	4.44	16.75	0.01	0.38	0.52
jord002	14/14	1.92 \pm 1.16	1940–1994	0.35	45.7	7.0	6.40	10.93	0.05	0.13	0.73

2.4. Processing Tree-Ring Width and Climate Data

The resulting tree-ring-width data were detrended and standardized by using the software ARSTAN v.44 [49]. This procedure allows for removing growth trends due to changes in tree size, age, and stand dynamics. Detrending was done by fitting a 67% cubic smoothing spline with a 50% cutoff frequency following [47,50]. Then, the resulting detrended series were pre-whitened with low-order autoregressive models to remove growth persistence. Individual indices were combined into site mean series or chronologies using a bi-weight robust estimate of the mean [51].

Calculated over the common 1950–1999 period (excepting jord002 (Dibeen, Jordan), the 1971–1994 period), we characterized the site chronologies by obtaining the following statistics: the mean ring

width and its standard deviation (SD), and the mean sensitivity (MS) of standard ring-width indices. The MS measures the relative change in width between consecutive rings with higher values, indicating higher growth variability [51]. The percent variance accounted for the first principal component (VP1), and the signal-to-noise ratio (SNR) was also obtained to assess the internal coherence, i.e., the common variability between tree-ring series obtained for a particular site [52]. Higher VP1 and SNR values indicate a greater coherence or similarity among individual ring-width series of the same site. We used an expressed population signal (EPS) ≥ 0.85 threshold to assess the adequacy of replication in the early years of the chronology [53].

To characterize climate–growth relationships, we calculated Pearson correlations between monthly climate data (mean temperature, total precipitation) from the previous September to current October, following previous studies (e.g., [11]). In the case of atmospheric patterns, we used monthly and seasonal values of the corresponding indices (NAO, AO, SCA, EA, ENSO, and WeMO).

2.5. Statistical Analyses

To quantify to which degree growth variability depended on site location, we calculated two correlation matrices of inter-site distances between site chronologies for the common period 1950–1999. Then we plotted correlations as a function of distance, which is a kind of spatial correlogram [54].

To summarize the common variability among residual chronologies, a principal component analysis (PCA) was calculated on the variance–covariance matrix of the chronologies. We retained the first three principal components (PC1, PC2, and PC3) because they had eigenvalues higher than 1. To assess the relationship between sites and chronology features, we used the Spearman correlation coefficient (r_s), since several variables did not follow normal distributions. In the case of normal distributions, we used the Pearson correlation coefficient (r).

2.6. VS-Lite Growth Model

We used the VS-Lite forward growth model (see [26,55]) to assess differences in climatic controls of tree growth among sites. Mean site series of ring-width indices (chronologies) were simulated as a function of monthly climate variables (mean temperatures, total precipitation), based on the principle of limiting factors affecting tree growth, by using a simplified version of the process-based VS (Vaganov–Shashkin) model [17]. The VS-Lite model uses a Bayesian framework to estimate growth responses to temperature (gT, in °C) and soil moisture content (gM, in v/v) limitations by calibrating four parameters. Two parameters determine when growth will not occur (T_1 for temperature and M_1 for soil moisture), and the other two determine when growth is not limited anymore by climate constraints (T_2 for temperature and M_2 for soil moisture). The solar radiation is modeled by considering insolation (gE parameter) estimated by site latitude. We compared the observed and simulated chronologies for the common 1950–1999 period and calculated Pearson correlation coefficients among them. We evaluated the assumption of uniform priors for the growth function parameters (with independent and normally distributed errors for ring-width indices) by 10,000 iterations, using three parallel chains and a white Gaussian noise model error (cf. [55]). To estimate monthly soil moisture from temperature and total precipitation, the VS-lite model uses the empirical leaky bucket model of hydrology. The specific parameters (e.g., runoff, root depth, growing season length, etc.) were taken from a previous study using a similar but more detailed modeling framework in Aleppo pine [14]. Snow dynamics were not considered, since snowfall is rare and not abundant in most of the study sites.

3. Results

3.1. Tree Ring Statistics and Sites Features

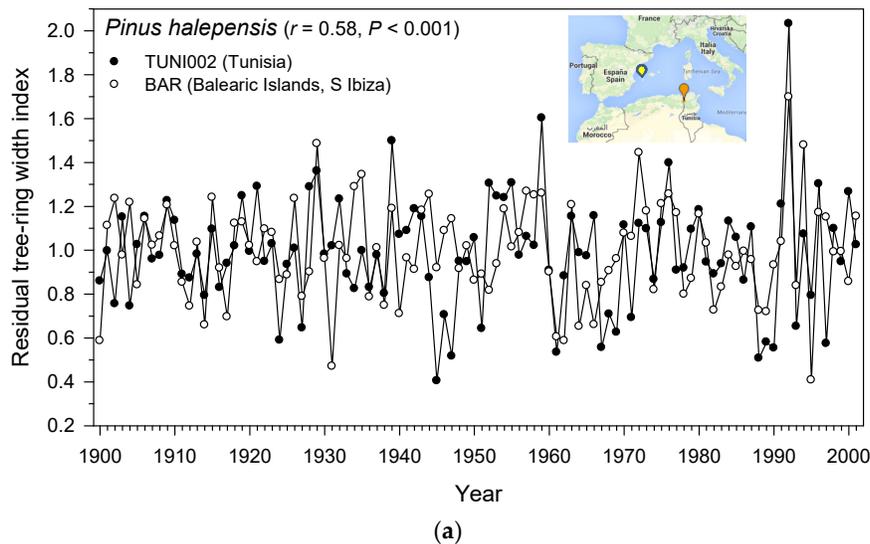
The mean ring width (\pm SD) was 1.40 ± 0.63 mm, with a minimum of 0.42 mm and a maximum of 3.99 mm, found in the dry ARC (Sierra de Archivel) and wet alb004 (Divjakë) sites, respectively (Tables 1 and 2). The longest (129–165-year) and well-replicated chronologies were developed for several Spanish stands (AYN (Ayna Los Luisos), BAR (Es Cap de Barbaria), BUN (Comuna de Bunyola), ENG (Serra d’Enguera), MIR (Miramón), PNF (Vedado de Peñafior), and RET (La Retuerta de Pina)), and

also for the Algerian alge003 (120 years) site (Table 2). The mean MS was 0.33, with a minimum of 0.17 and a maximum of 0.49 in the QRL (Querol) and ENG sites, respectively. The mean variance accounted for by the first principal component (VP1) and the SNR were 58.2% and 17.5, respectively. In several sites, the VP1 was close or above 70% of the variance (e.g., ARC, BYQ, PNF, RET, and alge003), indicating a high coherence and responsiveness to climate. The SNR reached values above 30 in the BYQ, PNF, and alge003 sites.

The growth rate increased in response to higher annual precipitation ($r_s = 0.52$, $p = 0.002$) and eastwards ($r_s = 0.63$, $p = 0.001$) location, and decreased in longer series ($r_s = -0.68$, $p < 0.001$). However, these associations did not only depend on tree age or site series, here represented by the length of the best-replicated period. After removing the dependency of the growth rate on the series length by obtaining residuals from a linear regression between both variables, we found that these residuals were still positively related to site precipitation ($r_s = 0.45$, $p = 0.01$). Sites with a higher growth rate also presented lower mean sensitivity ($r_s = -0.48$, $p = 0.006$) and a lower coherence (VP1: $r_s = -0.43$, $p = 0.014$; SNR: $r_s = -0.40$, $p = 0.023$). Consequently, the mean sensitivity (MS) was positively correlated with the chronology coherence, measured by either VP1 or SNR (VP1: $r_s = 0.61$, $p < 0.001$; SNR: $r_s = 0.52$, $p = 0.002$). This explains why both the MS and the VP1 decreased as climate conditions became more wet (annual precipitation, MS: $r_s = -0.47$, $p = 0.007$; VP1: $r_s = -0.44$, $p = 0.013$; AI (aridity index) MS: $r_s = -0.40$, $p = 0.025$; VP1: $r_s = -0.41$, $p = 0.019$). Lastly, as elevation increased MS ($r_s = 0.43$, $p = 0.015$) and SNR also increased ($r_s = 0.37$, $p = 0.040$).

3.2. Inter-Site Distance and Common Growth Variability of Aleppo Pine Sites

The coherence in growth between neighboring and even between distant sites was weak to moderate. For instance, two sites located in the southern Balearic Islands (Ibiza) and Tunisia, ca. 800 km apart, showed a significant common growth variability ($r = 0.58$, $p < 0.001$) throughout the 20th century (Figure 2a). Maximum correlations between site chronologies reached values of up to 0.90 (Figure 2b). Positive correlations were mainly found with inter-site distances of up to 1500–2000 km, albeit most of them were clustered in distances up to 800–1000 km.



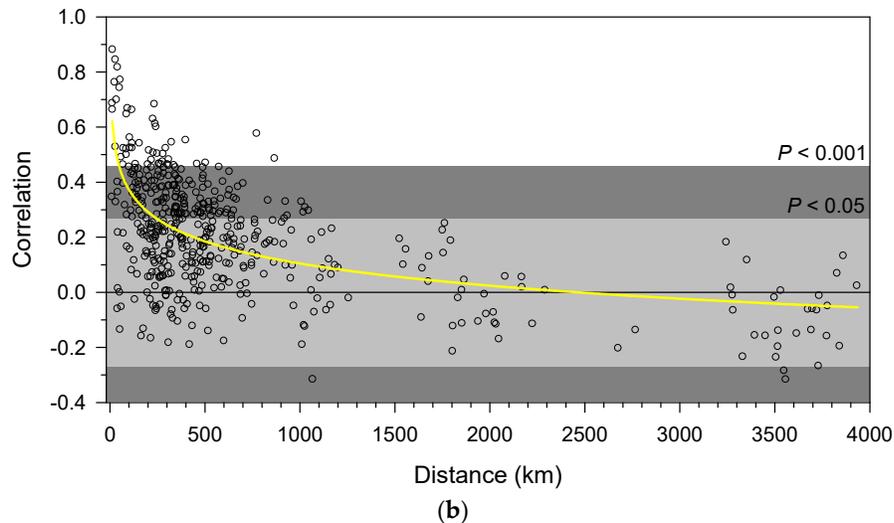


Figure 2. (a) Plot illustrating geographical synchronization in growth variability between two Aleppo pine sites situated in the southern Balearic Islands (Ibiza, site BAR) and northern Tunisia (tuni002, southernmost site). The residual chronologies were significantly correlated, despite the sites being located ca. 800 km apart. (b) Plot showing how the correlation (Pearson coefficient) between Mediterranean Aleppo pine chronologies decays as a function of distance between sites. The different grey intensities of the two boxes indicate the 0.05 and 0.001 significance levels for the analyzed 1950–1999 period. The yellow line shows a logarithmic function to describe the decay of correlations as a function of inter-site distance.

In the variance–covariance matrix for all sites, PC1, PC2, and PC3 accounted for 29.6%, 11.2%, and 10.0%, respectively, of the growth variability (Figure 3). PC1 corresponded to a longitudinal gradient separating eastern sites (e.g., jord002, alb004) from western sites, including several Iberian sites and inland populations (e.g., MIR, ISI (Figures 4 and 5). In contrast, PC2 was moderately related to site latitude with northern (e.g., MIR, RET) and southern (e.g., tuni002, alge003) sites, having low and high scores along this axis, respectively (Figures 4 and 5). Lastly, high scores of the PC3 were found for sites located in the Balearic Islands, coastal northeastern Spain, and Tunisia (e.g., MER, BAR, tuni002; see Figure 4).

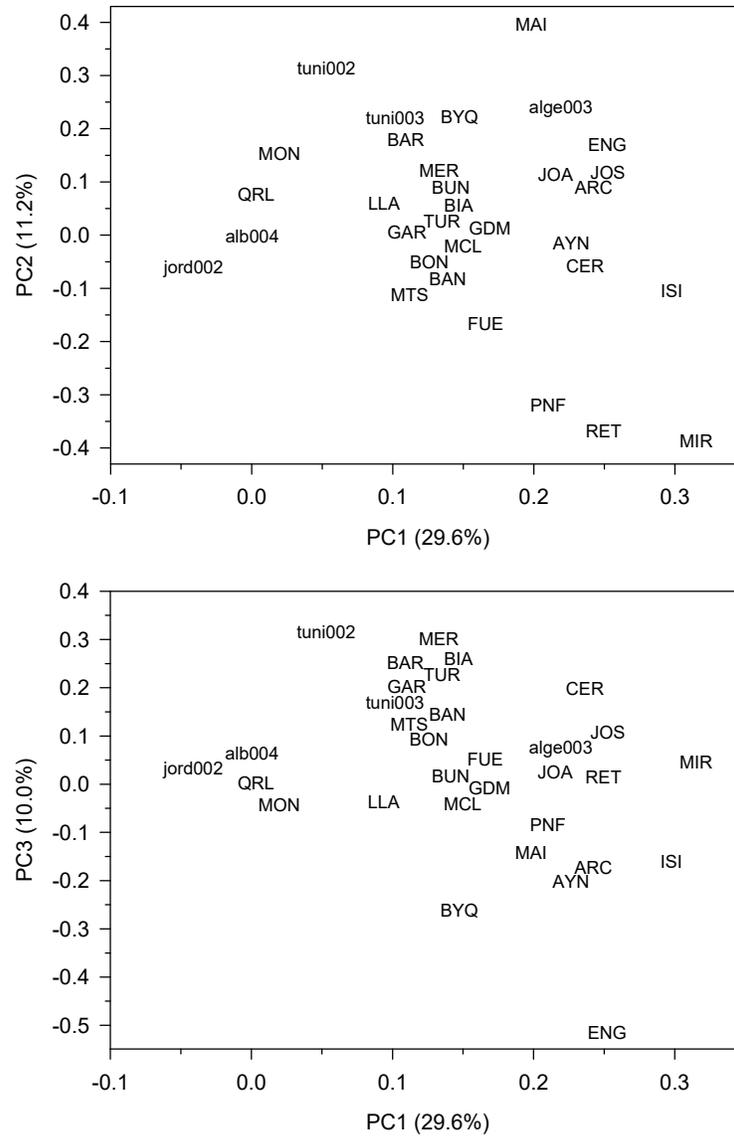


Figure 3. Scores of the Aleppo pine chronologies for the first three principal components (PC1, PC2, and PC3) of a principal component analysis calculated on the variance–covariance matrix for the period 1950–1999. Sites’ codes are as in Table 1.

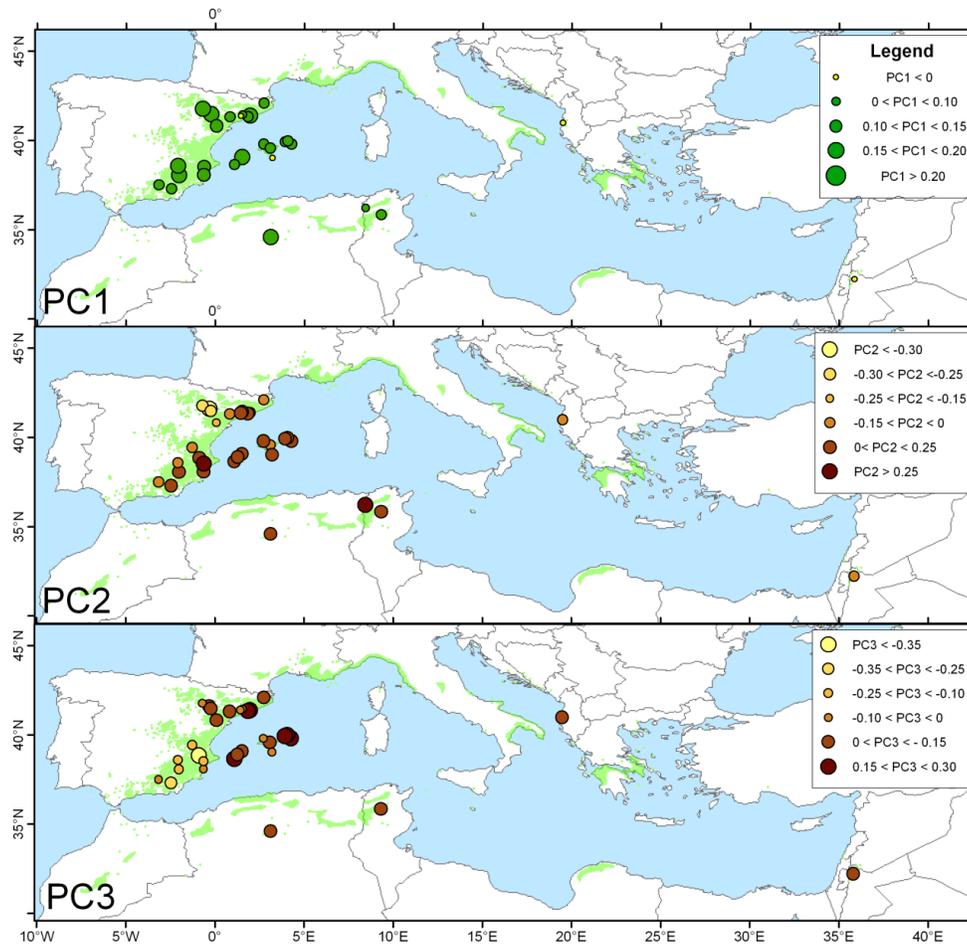


Figure 4. Map showing the scores of the first three principal components (PC1, PC2, and PC3) for the Aleppo pine chronologies distributed across the Mediterranean Basin. The green patches show the distribution of the species.

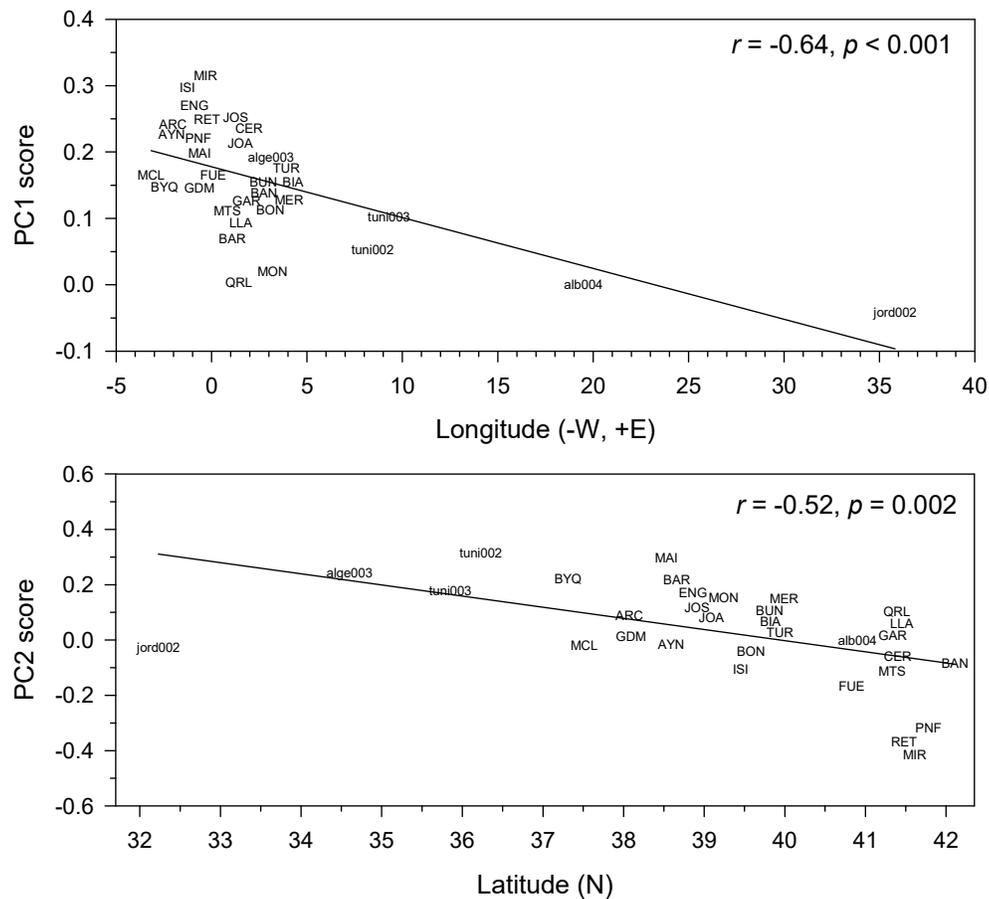


Figure 5. Relationships between location (longitude, latitude) and the scores of the first (PC1) and second (PC2) principal components scores of the analyzed network of Mediterranean Aleppo pine chronologies. The statistics show Pearson correlations (r) and associated significance levels (p). Sites' codes are as in Table 1. Note that the correlation between longitude and the PC1 scores was still significant if removing the two sites located eastwards of 15° E ($r = -0.50, p = 0.005$).

3.3. Associations between Climate Variables, Atmospheric Patterns, and Aleppo Pine Growth

Aleppo pine growth increased in response to wet May conditions and cool spring–summer (May to July) conditions (Figure 6). High precipitations in the prior winter, preceded by cool late autumn conditions, also enhanced growth.

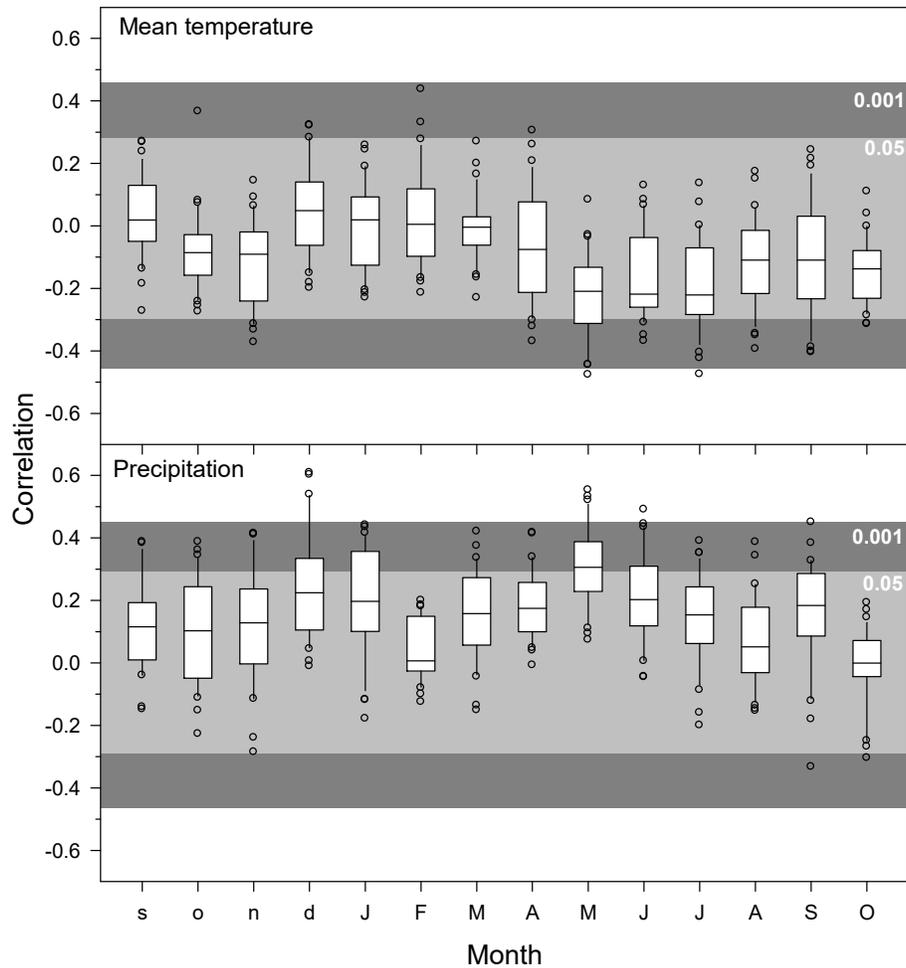


Figure 6. Climate–growth associations, characterized by two box plots showing Pearson correlation coefficients obtained by relating mean temperature and precipitation vs. residual Aleppo pine chronologies.

There were negative associations between the PC1 and WeMO and NAO indices of the previous winter (Figure 7). The PC2 showed a weak positive association ($r = 0.39$, $p = 0.004$) with the August NAO index, and a negative association with the previous fall EA. The PC3 showed a positive correlation with the March SCA ($r = 0.43$, $p = 0.002$), and a negative association with the March AO.

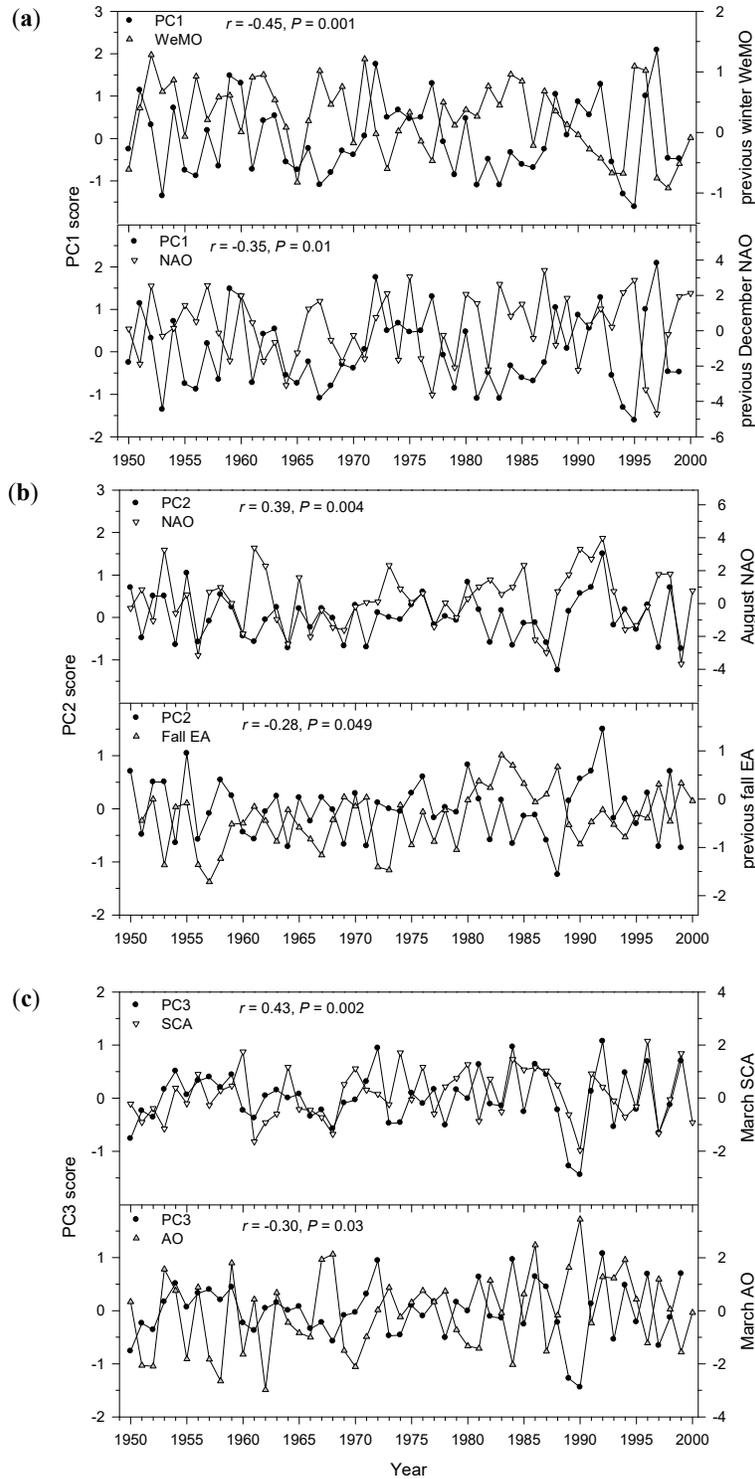


Figure 7. Major associations between the first ((a), PC1), second ((b), PC2), and third ((c), PC3) principal scores (filled black symbols) of a principal component analysis of Mediterranean Aleppo pine chronologies, and monthly or seasonal indices corresponding to different atmospheric circulation patterns (white and grey symbols). The statistics show Pearson correlations (r) and associated significance levels (p). Indices' and patterns' abbreviations: AO: Arctic Oscillation; EA: East Atlantic pattern; NAO: Northern Atlantic Oscillation; SCA; Scandinavian pattern; WeMO: Western Mediterranean Oscillation index. Correlations calculated with monthly or seasonal values of the indices or patterns of the year prior to tree-ring formation are indicated as “previous” in the y -axes.

3.4. Biogeographical Climate–Growth Associations Inferred from the VS-Lite Model

We obtained positive correlations between observed and VS-Lite simulated chronologies being significant ($p < 0.05$) in all sites excepting BON (Santuari de Bonany) and QRL. These correlations reached maximum values of between 0.74 and 0.76, i.e., 55–58% of explained variability (sites ISI, MIR, RET, and alge003; see Table 2). The mean correlation was 0.57 ± 0.16 , indicating that the model explained, on average, 32% of growth variability as a function of climate (Figure 8). The mean (\pm SD) fitted parameters were: $T_1 = 6.0 \pm 1.9$ °C, $T_2 = 14.4 \pm 3.7$ °C, $M_1 = 0.03 \pm 0.02$ v/v, and $M_2 = 0.32 \pm 0.12$ v/v. The M_1 and T_1 parameters were negatively associated ($r_s = -0.48$, $p = 0.006$). The M_1 parameter was negatively related to site latitude ($r_s = -0.36$, $p = 0.04$; Figure 8). The M_2 parameter was positively related to site annual precipitation ($r_s = 0.35$, $p = 0.05$). The correlations between the observed and fitted series of ring-width indices were positively related to SNR ($r_s = 0.41$, $p = 0.019$), indicating that in sites where the VS-Lite model fit was robust, the chronology coherence was also high.

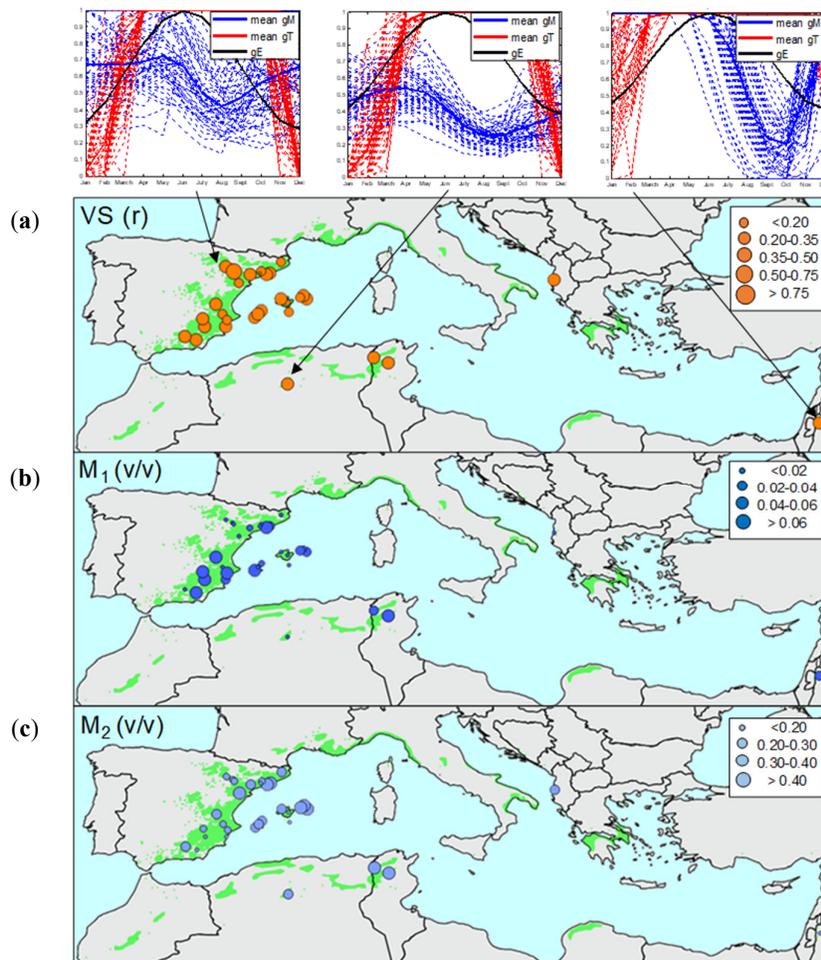


Figure 8. Parameters and statistics of the VS-Lite growth model applied to the Mediterranean Aleppo pine. The correlation map ((a), VS (r)) shows the correlation between observed and simulated ring-width chronologies. The maps show the species distribution area (green patches) and values of parameters, indicating when growth will not occur because of moisture limitations ((b), M_1) and when growth is not any more limited by moisture ((c), M_2). The three upper plots show fits in three sites (PNF, tuni003, jord002; see sites' codes in Table 1), displaying moisture (gM, blue lines) and temperature (gT, red lines) limitations for particular years and during the growing season (x -axis). The black line (gE) shows the monthly insolation.

4. Discussion

As in previous studies developed across the Mediterranean Basin, we found that Aleppo pine growth is very sensitive to soil water availability during spring and the previous winter [2,9,10–13,46–48,56–62]. It is well-known that the period with highest growth rates for this species is early spring, with dormant periods in summer and winter [18,20–23,62–65], albeit a secondary peak in autumn is also common [24,25]. Such bimodal behavior with growth peaks in spring and autumn is well-coupled to the Mediterranean climate, characterized by mild and wet conditions during those two seasons, and dry and cold constraining conditions in summer and winter, the latter constraint being more marked in continental inland sites [66]. This phenological pattern can be explained because of the photosynthesis maximums in late winter and early spring which occur when soil moisture is high and leaf vapor pressure deficit is low [67]. In summer and autumn, formed needles fix carbon and allow for storing carbohydrates for latewood production and for earlywood production in the following year, which explains why reduced growth is not related to low levels of non-structural carbohydrates [68,69]. In any case, the bimodal cambium phenology seems to be very plastic in Aleppo pine, and is controlled by site climate conditions, as indicated by empirical [10,13,24] and modeling approaches [14]. It is foreseeable to have a more pronounced bimodality in mild coastal sites, where the growing season is much longer than in continental inland sites, where growth is arrested by summer drought and winter coldness [25].

In high-elevation conifer forest areas across the Alps, tree-ring data showed strong correlations up to a mean distance of 374 km, with tree species depending more on precipitation showing the smallest distances (200–254 km), and others dependent on temperature showing broad coherence at larger scales (470–600 km) [54]. Our data on Aleppo pine suggest maximum distances of 1500–2000 km, albeit most positive correlations were clustered up to 800–1000 km, given that the sampling was unbalanced and too focused in Spanish sites, where the main distribution area of the species is found [8]. These spatial patterns and elevation-grouped growth responses to climate (cf. [70]) should be considered when using tree-ring data of Aleppo pine as moisture proxies.

Regarding the links between growth variability and atmospheric patterns, the associations of PC1 with the winter NAO and WeMO can be explained, because cool–wet conditions in the prior winter benefitted growth, particularly in northeastern inland Spain [10–12,60]. The WeMO association with Aleppo pine growth has been found before [10], and highlights the relevance of this circulation pattern over the western Mediterranean Basin. In the case of PC2, cool conditions in the previous autumn linked to the EA pattern could enhance the growth of stands located in southeastern Spain and Tunisia. The correlation of PC2 with the August NAO could be explained by cool summer conditions, although the NAO mainly influences the spring and winter Iberian climate [5,40]. The associations of PC3 with March atmospheric patterns (SCA, AO) can be due to wetter conditions in early spring favoring the growth of coastal warm Aleppo pine populations, which probably show an early cambial reactivation [23]. Nonetheless, it must be considered that PC2 and PC3 only accounted for 21% of the growth variability in our study tree-ring network.

The correlations found between climate variables and tree-ring statistics were significant, but indicated moderate-to-weak relationships. This suggests that local factors, such as microclimate, soil characteristics, or provenance type, also influence growth responses to climate and growth coherence at regional scales. Another caveat of the study is the lack of updating of most tree-ring series, which were mostly built in the late 1990s and early 2000s. Mediterranean climate has rapidly changed during the 21st century [1,2], so the presented series should be updated to achieve more robust conclusions.

Several models have suggested that the increase in atmospheric CO₂ could make trees more efficient in drought-prone areas and increase productivity in Mediterranean Aleppo pine forests [71,72]. However, field data do not support this assumption, and have demonstrated that drought stress reduces radial growth and probably forest productivity, despite rising water-use efficiency [73–75]. We demonstrated this in the studied Aleppo pine tree-ring network, through the use of the VS-Lite model that allowed definition of the climatic constraints of radial growth and how they change across the species distribution range. For instance, M₁ increased in the dry, warm sites from southeastern Spain, whilst M₂ increased in the wetter, colder (more continental) sites from northeastern

Spain and the northern Balearic Islands. These differences indicate a pronounced growth variability, which may be due to local plasticity [11,76], and is probably associated with shifts in tree-ring phenology [25] or ecotype variability mediated by genetically fixed traits [77]. Nevertheless, the VS-Lite model explained, on average, 32% of year-to-year growth variability as a function of climate variables, as also revealed by previous studies of conifers species (e.g., [14–16]).

Although every modeling approach has limitations, our approach provides robust results that are following what has been observed in field studies on Aleppo pine (e.g. [12,14,24]). Nevertheless, the low explained variance in several sites illustrates some limitations of our approach, which would be improved by including more detailed data on individual tree size and age, neighborhood competition, disturbance history (e.g., wildfires; see [78]), carbon allocation, and soil features (type, depth, texture, and stoniness). For instance, soil water dynamics determine actual drought stress, and it has been shown that Aleppo pine has a better performance in marl and chalk substrates than in limestone [29]. Recently, it was shown that higher surface rock cover and topsoil stoniness increased soil water concentration and reduced mortality in a semi-arid Aleppo pine forest [79]. In addition, experiments on Aleppo pine saplings under experimental drought triggered a shift of carbon allocation from the stem to the roots, with a 60% reduction of xylem volume in the stem [32]. Therefore, future studies could consider these factors and combine tree-ring data with variables related to tree size, carbon allocation (e.g., the concentration of non-structural carbohydrates in stem and roots), and water-use efficiency (e.g., C and O isotope discrimination; see [74]).

Aleppo pine is resistant to water shortage, but pronounced drought stress causes xylem embolism, particularly in fine roots, and reduces its growth and cone production [32,80–82]. Several dieback and pulsed-mortality episodes have been described in Mediterranean Aleppo pine forests in response to dry spells, indicating that the species is vulnerable to dry spells [83–86]. Such loss in tree vigor has been linked to xylem embolism and observed in relatively open stands, albeit a high tree-to-tree competition for water also contributes to drought vulnerability [87]. In this sense, our modeling and biogeographical framework could be used to identify the Aleppo pine populations, whose growth will be more negatively impacted by drier and warmer conditions in the prior, early, or late growing seasons. Our quantification of growth response to local climate and large-scale atmospheric patterns across a wide geographical gradient in the widespread Aleppo pine forests is crucial to reveal differences and adaptation of this species under forecasted drier and warmer climate conditions in the Mediterranean Basin (cf. [16,76]).

5. Conclusions

To conclude, correlations between climate and growth variability were moderate. Aleppo pine radial growth was constrained during the second half of the 20th century by dry–warm spring conditions, and also by dry prior winter conditions. Growth responsiveness to climate peaked in dry and continental inland sites, where the growing season is shorter, than in mild, coastal sites. Growth decreased in dry, xeric sites and increased in wet, mesic sites. The climate–growth relationships were spatially structured and linked to major atmospheric circulation patterns influencing the Mediterranean Basin climate, such as the NAO and WeMO. The VS-Lite model explained more growth variability in dry, continental sites. We advocate for similar regional approaches in drought-prone areas, using tree-ring networks of several tree species and multiple populations of each species.

Author Contributions: Conceptualization, J.J.C. and R.S.-S.; methodology, R.S.-S., M.R. and J.C.C.; software, R.S.-S.; validation, J.J.C., R.S.-S., D.M.M. and the rest of authors; formal analysis, J.J.C., M.R. and R.S.-S.; data curation, M.R. and R.S.-S.; writing—original draft preparation, J.C.C., R.S.-S., I.D.-L., E.G., L.A.-H. and all co-authors; writing—review and editing, all authors; funding acquisition, R.T., E.G., and J.J.C. All authors have read and agreed to the published version of the manuscript.

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