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ORIGINAL PAPER

Resilient but declining: drought induced dieback of Aleppo pine stands in western Algeria

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Abstract Drought affects forest productivity and tree radial growth in multiple ways. Two major impacts are growth decline and loss of resilience, i.e., the capacity to recover normal growth rates after a drought, which may indicate impending death. Growth decline and dieback processes have been reported for Mediterranean conifers, but information for natural and planted stands under semi-arid conditions is still scarce, particularly across the increasingly arid Maghreb. We addressed this by assessing growth rates, variability and resilience indices in Algerian Aleppo pine (*Pinus halepensis* Mill.) stands under Mediterranean subhumid to semi-arid conditions. Several climate variables and teleconnection patterns (NAO, North Atlantic Oscillation; WeMO, Western Mediterranean Oscillation) were investigated to determine the main drivers of growth decline. Growth resilience indices were calculated at site and tree levels and related to growth trends. Mean basal area increment (BAI) during 2000–2023 was 16.6 cm^2 a^{-1}. Negative BAI trends occurred for all sites since 2013, as aridification intensified. All stands showed growth decreases during dry years regardless of site conditions or growth rates. Growth was constrained by cold January conditions, dry conditions from the previous winter to summer, and elevated temperatures from late spring to late summer. Long (12-month) droughts peaking in summer suppressed growth, which was also inversely associated with NAO June indices. Growth decline responded to recovery and resistance indices during the 2012 and 2017 droughts. The results show that long-term aridification triggers growth decline despite short-term, post-drought recovery.

Keywords Dendroecology · Drought stress · Forest dieback · Growth resilience · *Pinus halepensis*

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Introduction

The western Mediterranean Basin is a hot spot for climate change where widespread warmer conditions and local declines in winter precipitation have been observed (Xoplaki et al. 2004; Hoerling et al. 2012). The trend to aridification of this region is mainly attributed to climate warming and to changes in the North Atlantic Oscillation (NAO), the dominant structure of the North Atlantic atmospheric variability linked to decadal changes in storm tracks and sea surface temperatures (Hurrell 1995; Mariotti and Dell'Aquilla 2012). Winter drying over the western Mediterranean is linked to a weakening of the Atlantic Ocean poleward heat transport leading to persistent atmospheric anticyclone conditions (Delworth et al. 2022). In the western Mediterranean Basin, high NAO values coincide with dry winter conditions and lower forest growth (Camarero 2011; Tramblay et al. 2013). In addition, warmer conditions and decreasing rainfall are projected in response to increasing greenhouse gases negatively impacting Mediterranean forests (Hoerling et al. 2012; Lee et al. 2021).

Algeria is among the Mediterranean countries where aridification has prompted the adoption of drought mitigation strategies in forest management (Cramer et al. 2018). The productivity, growth and vigor of some Algerian forests are threatened by increasingly arid conditions. These include pine plantations established in the wetter 1970s, such as the 'Green Barrier', to stop the northward advance of the Sahara Desert (Benalia 2009). These plantations cover 123,000 ha along the semi-arid to arid steppes of the pre-Saharan region, and they have allowed the expansion of native Aleppo pine (*Pinus halepensis* Mill.) (Benalia 2009). However, the Algerian 'Green Barrier' is subjected to climate pressures such as hotter and drier conditions (Mihi et al. 2024). Planted but also naturally-occurring Aleppo pine forests are threatened by intense droughts, as shown by tree-ring studies developed in the Ouarsenis range of NW Algeria (Sarmoum et al. 2016) and the Saharan Atlas region of central Algeria (Choury et al. 2017). However, regional approaches on growth trends are lacking, and also assessments of post-drought recovery and variability of vulnerable Aleppo pine forests across wide geographic and environmental gradients. This has been done with other conifer species showing ongoing dieback across the Maghreb, such as Atlas cedar (*Cedrus atlantica* (Endl.) G. Manetti ex Carrière (Sarmoum et al. 2024). Moreover, it is unclear if these Aleppo pine stands show growth decline and, if so, whether this is related to changes in growth resilience (Mu et al. 2022; Camarero 2023).

Aleppo pine is a pioneer, isohydric species, regulating water loss through transpiration, and considered tolerant to water shortages (Alexou 2013). However, empirical (Borghetti et al. 1998) and observational studies have shown its vulnerability to severe and lasting droughts (Sarris et al. 2011; Sánchez-Salguero et al. 2012; Camarero et al. 2015; García de la Serrana et al. 2015; Sarris and Christodoulakis 2024). Heat waves and dry spells result in widespread xylem cavitation, canopy dieback, and elevated mortality (Morcillo et al. 2022). Warmer temperatures increase the atmospheric vapor pressure deficit (VPD), raising the evaporative demand and causing excessive water loss through stomata (Grossiord et al. 2020). Both atmospheric and soil drought explain radial growth reduction and impaired capacity to recover after drought, i.e., lower post-drought resilience, particularly when several drought events occur successively (Gazol et al. 2017a, 2022; Serra-Maluquer et al. 2021; Camarero 2023; Peng et al. 2023; Gong et al. 2024). However, post-drought growth resilience depends on multiple drivers acting at several scales—from site factors (climate and soil conditions, drought severity and duration, stand structure, disturbances) to tree features (size, age, growth rates, post-drought legacy effects) (Anderegg et al. 2015; Gazol et al. 2017b; Camarero et al. 2020; Veuillen et al. 2023; Li et al. 2024a, 2024b). Therefore, a more comprehensive assessment of growth trends and post-drought resilience is required for vulnerable tree populations such as Algeria's drought-prone Aleppo pine forests.

In this study, we aimed to: (1) quantify growth variability and trends in natural and planted Aleppo pine stands of similar age but subjected to different climate conditions, (2) determine the main climate drivers and atmospheric circulation patterns of their growth variability, paying particular attention to drought severity during the warm past three decades, and (3) assess growth resilience in response to recent and successive severe droughts. Given that a loss of post-drought resilience has been associated with a higher mortality risk in conifers (DeSoto et al. 2020; Cabon et al. 2023), we hypothesize that drought stress will lead to a loss of the recovery capacity triggering recent growth decline. We will focus on growth resilience, which measures the capacity to recover pre-drought growth levels (cf., Lloret et al. 2011). Finally, we suggest that determining the resilience of trees to drought is essential for managing plantations confronted with ongoing aridification (Wang et al. 2023).

Materials and methods

Study sites and field sampling

Six Aleppo pine stands located across wide geographic and climatic gradients in northern Algeria were selected (Fig. 1). Four were natural stands, whereas two (Rechaiga, Stissen Elbayadh) were plantations located in the 'Green Barrier' (Table 1, Fig. S1). The geographical and topographical

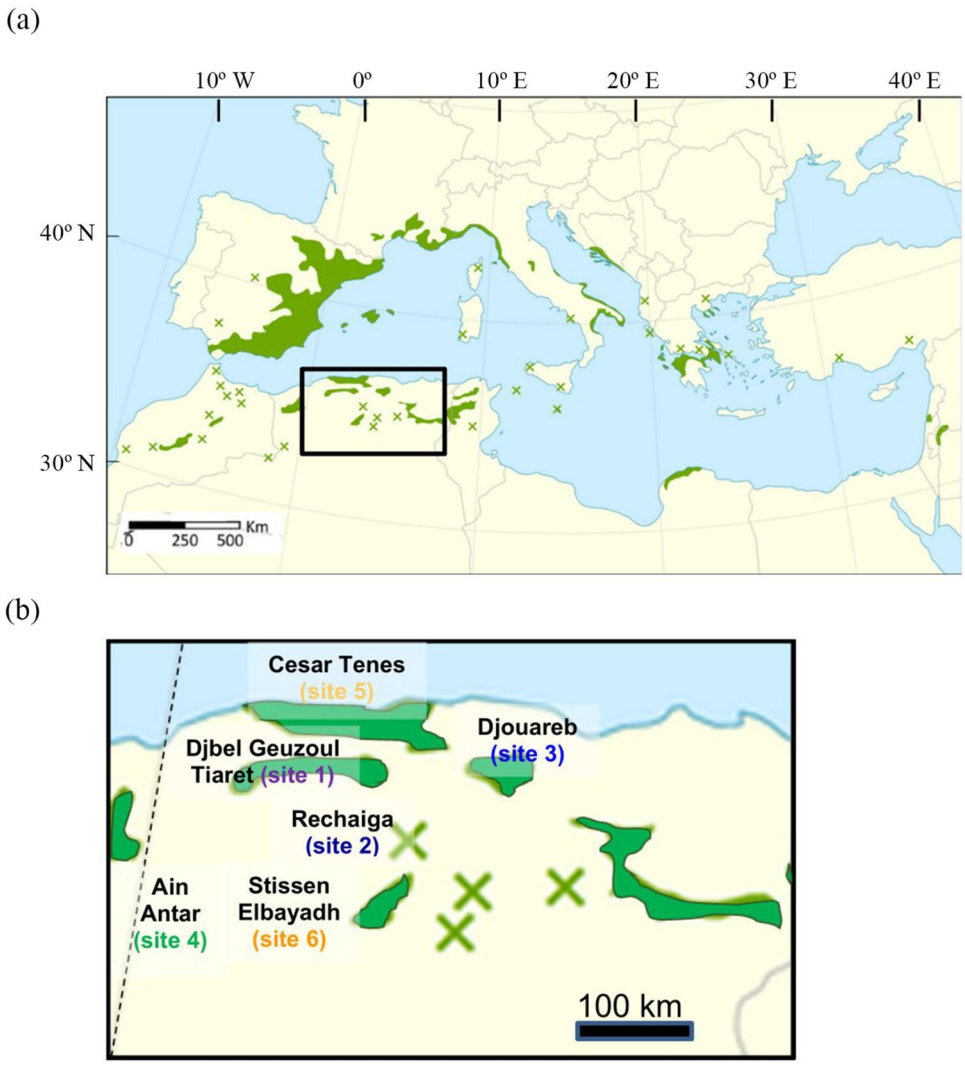


Fig. 1 **a** Distribution of Aleppo pine in the Mediterranean Basin and, **b** the sample sites in Algeria. Crosses show isolated populations. Modified from Mauri et al. (2016)

variables of each site were obtained using GPS (latitude, longitude, elevation and aspect).

We sampled 0.1-ha circular plots in representative areas of each stand and measured diameter at breast height (DBH) and height of 20 dominant trees using tapes and a laser rangefinder (Nikon Forestry Pro II). The 20 trees in each site corresponded to co-occurring declining (D) and non-declining (ND) trees. D and ND trees were classified on their canopy defoliation which was visually estimated. Defoliation was measured in late summer as relative leaf loss compared to a fully foliage "reference tree" from the same stand (Eichhorn et al. 2016). D trees were those showing defoliation > 60%, ND trees were those with defoliation ≤ 60%.

The natural vegetation is dominated by Aleppo pine, with evergreen oaks (*Quercus ilex* L.) in the wettest sites (e.g., Djouareb) and Atlas cedar in cool mountain sites (e.g., Rechaiga). The understory is dominated by Mediterranean shrubs such as *Quercus coccifera* L., *Pistacia lentiscus* L. and *Rhamnus lycioides* L. The soils are calcareous and developed on limestone or sandstone substrates. The plantations have not been thinned for the past 40 years.

Climate data and indices

Due to the lack of a long and homogeneous climate series near the study sites, we obtained monthly climate data (TMax, mean maximum temperature; TMin, mean minimum temperature; Prec, total precipitation) from the 0.5°-gridded CRU dataset v. 4.09 (period 1950–2024; Harris et al. 2020). Using this climate data, we calculated the Standardized Precipitation and Evapotranspiration Index (SPEI) to assess drought severity. The SPEI is a multiscalar drought index based on a cumulative water balance, here calculated at monthly scales (Vicente-Serrano et al. 2010). We obtained the SPEI at 1- to 24-month-long scales to determine whether growth differently responded to short- and long-term droughts. To characterize site aridity, the mean aridity index, (the ratio between precipitation and potential

Table 1 Characteristics of the study sites. MAT and TAP are mean annual temperature and total annual precipitation calculated for 1981–2023. Diameter (DBH) and height values are means ± SD. Different superscript letters indicate significant ($p < 0.05$) differences according to Mann-Whitney tests.

Site name (code)	Latitude (°N)	Longitude (°E)	Elevation (m a.s.l.)	Aspect	MAT (°C)	TAP (mm)	Aridity index	DBH (cm)	Height (m)	Stand type
Djbel Geuzoul Tiaret (1)	35.39	1.31	1100	NE	18.1	517	0.40	35.8 ± 12.5^{ab}	11.3 ± 1.4^{b}	Natural stand
Rechaiga (2)	35.34	2.08	829	S	17.1	531	0.48	26.4 ± 3.8^{a}	11.1 ± 2.1^{ab}	Planted stand
Djouareb (3)	35.88	2.05	1276	E	17.6	542	0.46	42.5 ± 13.4^{b}	10.1 ± 2.1^{ab}	Natural stand
Ain Antar (4)	33.69	1.17	1242	E	17.7	538	0.44	45.0 ± 11.7^{b}	13.5 ± 2.4^{b}	Natural stand
Cesar Tenes (5)	36.42	1.43	130	E	19.8	335	0.38	34.2 ± 12.7^{ab}	9.6 ± 2.8^{ab}	Natural stand
Stissen Elbayadh (6)	33.69	1.17	1492	E	16.3	211	0.20	20.0 ± 3.5^{a}	7.8 ± 0.6^{a}	Planted stand

evapotranspiration), gridded at a 30-arc resolution for the period 1991–2020 was used (Zomer et al. 2022).

To summarize the main atmospheric circulation patterns governing climate variability in the study area, the North Atlantic Oscillation (NAO) and the Western Mediterranean Oscillation (WeMO) indices were obtained. The NAO affects winter conditions over the western Mediterranean Basin (Hurrell 1995; Rodó et al. 1997; Xoplaki et al. 2004). The WeMO reflects the variability of rainfall in autumn and winter over the same region but potentially affects other variables such as temperature (Martin-Vide and Lopez-Bustins 2006). The NAO and WeMO indices were downloaded from https://crudata.uea.ac.uk/cru/data/nao/nao.dat and https://crudata.uea.ac.uk/cru/data/moi/Web_WeMOi-2020.txt, respectively.

Tree-ring data

Twenty dominant trees were selected per site (10 D trees and 10 ND trees) for dendrochronological analyses (Fritts 1976). Two 5-mm cores were extracted at 1.3 m height using a Pressler increment borer and at opposite sides of each tree. Cores were air-dried, glued onto wood supports, sanded until rings were clearly visible. Samples were scanned with a 2,400 dpi resolution (Epson Expression 10000XL) and visually cross-dated using dendrochronological methods (Stokes and Smiley 1968). Ring widths were measured at a 0.01 mm resolution along two radii per core using the CDendro-CooRecorder software (Maxwell and Larsson 2021). Visual cross-dating was verified by inspecting characteristic narrow rings, often linked to dry conditions (Yamaguchi 1991), and by using the COFECHA software (Holmes 1983) which calculates moving correlations between an individual series and the mean site series of ring-width indices.

To quantify recent growth trends, tree-ring widths were converted into basal area increments (BAI) which better reflect long-term changes of radial growth. The BAI series were calculated using the following equation and assuming concentric growth:

$$\mathrm{BAI} = \pi \left(R_t^2 - R_{t-1}^2\right) \quad (1)$$

where R_t^2 and R_{t-1}^2 are the radii (cumulative sums of ring widths) corresponding to the current (t) and prior ($t - 1$) years, respectively. Both BAI means and trends were calculated for the common, best-replicated period 2000–2023.

To calculate correlations between climate variables and growth indices, the tree-ring width data were normalized and detrended. Spline (30-year long) polynomials were fitted to tree-ring width data and ring-width indices then obtained by dividing observed values by fitted ones (Fritts 1976). The resulting individual series of ring-width indices were averaged site-by-site using bi-weight robust means to

obtain standard chronologies. In addition, first-order autocorrelation was removed by fitting 1st-order autoregressive models to obtain pre-whitened or residual series which were also averaged. Standard series of growth indices were used to calculate resilience indices, whereas residual series were used to calculate climate-growth relationships.

To characterize the ring-width raw and indexed series, several statistics were calculated (Briffa and Jones 1990) on raw ring-width series (mean; AR1, first-order autocorrelation) or on the indexed series (MSx, mean sensitivity; rbar, mean correlation between series; EPS, Expressed Population Signal; Wigley et al. 1984). A site chronology was considered to be well replicated for the period with EPS > 0.85. Tree age was estimated at breast height by counting the number of rings along the oldest core whenever it reached the pith or presented curved, innermost rings. All tree-ring analyses were done using the dplR program (Bunn 2008; Bunn et al. 2024) in R statistical software (R Core Team 2024).

Growth resilience indices

To calculate resilience indices, two criteria were used: (1) dry years (1993, 2002, 2005, 2012 and 2017) showing 12-month SPEI values lower than − 1.25, and (2) growth indices lower than 1 indicating growth reduction. These two conditions were used because of our interest on droughts which negatively impacted Aleppo pine growth. Three growth resilience indices were then calculated as proposed by Lloret et al. (2011), considering the five selected years. Site and individual series of standard ring-width indices were used to calculate:

(1) Resistance (*Rt*), i.e., the difference between the growth indices in the drought year (G_d) and in the preceding *n* years (G_{Pr}),

$$Rt = G_d / G_{Pr} \quad (2)$$

(2) Recovery (*Rc*), i.e., the capacity of trees to recover growth (G_{Po}) after drought

$$Rc = G_{Po} / G_d \quad (3)$$

(3) Resilience (*Rs*), a measure of the capacity to recover pre-drought growth levels.

$$Rs = G_{Po} / G_{Pr} = Rt \times Rc \quad (4)$$

We considered $n = 3$ years for calculating these indices because this interval encompasses most post-drought legacies based on previous studies (Anderegg et al. 2015). The curve of full resilience ($Rc = 1/Rt$) was fitted and compared with the observed site values to assess the relative resilience of our stands (Schwarz et al. 2020). The calculations of resilience indices were carried out by using the pointRes 2.0 R package (van der Maaten-Theunissen et al. 2015, 2021).

To assess if there was a cumulative stress memory on recent growth decline, we focused on the BAI data for 2013–2023 and the resilience indices of the dry years 2012 and 2017. We then standardized the resilience indices of these two years and calculated cumulative resilience indices by summing (e.g., $Rc_{2012} + Rc_{2017}$) or multiplying them (e.g., $Rc_{2012} \times Rc_{2017}$).

Statistical analyses

Trends in annual climate variables (temperature, precipitation, SPEI) and BAI site series were assessed using Mann–Kendall *S* tests. Mann–Whitney tests were used to compare variables (diameter, height, age, BAI means and trends) between sites or vigor classes. When linear regressions were fitted for variables measured in D and ND trees (e.g., BAI, height), one-way ANCOVAs were used to compare the slopes.

After checking the normality of ring-width indices using Shapiro–Wilk tests, the relationships among their site series were analyzed with Pearson correlations and Principal Component Analysis (PCA). The PCA was calculated on the matrix of the residual ring-width chronologies considering the best-replicated period. The resulting scores of the first (PC1) and second (PC2) principal components were plotted. The PCA was calculated using the vegan R package (Oksanen et al. 2023).

Since the resilience indices did not follow normal distributions, we calculated Spearman correlation coefficients (r_s) and growth variables for 2013–2023 (mean BAI, BAI trend). These analyses were aimed to detect signals of cumulative stress on recent growth decline. Linear regression models were also fitted to tree diameter, height, tree age and BAI trend as a function of vigor class (D and ND trees), site and their interactions using the *lm* () function of the stats R package (R Core Team 2024).

Pearson correlations were calculated between climate variables (TMax, TMin, Prec and SPEI) and site series of ring-width indices to quantify climate-growth relationships. The correlations were calculated from the previous September to the current October based on earlier studies (Camarero et al. 2020). Pearson correlations were also calculated between monthly SPEI values at 1–24 months, and the sites chronologies of ring-width series. These calculations were done using the dcc function in the Treeclim R package (Zang and Biondi 2015).

Finally, linear models were fitted to log-transformed variables (diameter, height, age, BAI means and trends for the period 2000–2023) as a function of vigor class (D and ND trees), site and their interactions. Linear models

were calculated using the JMP statistical package ver. 18.2 (JMP 2025).

Results

Climate trends

Both maximum and minimum temperatures showed significant increasing trends ($p < 0.001$), whereas precipitation showed significant negative trends in all sites except site 2 ($S = -397$, $p = 0.065$; Fig. S2). Twelve-month September SPEI values showed significant negative trends ($p < 0.001$) on all sites, indicating ongoing aridification (Fig. S3).

Differences between vigor classes

Diameter and height depended more on site, vigor and their interactions than did BAI means and trends and showed lower adjusted R^2 values (Table 2). The declining (D) trees had lower diameters, heights, ages, and mean BAI values and trends than non-declining (ND) trees (Tables S1 and S2). Age and mean BAI were negatively correlated. Remarkably, height was negatively related to the trend in BAI for both D and ND trees, and the slopes of both regressions were not different (one-way ANCOVAs, $F = 0.13$, $p = 0.72$; Fig. S4).

The last column shows the adjusted R^2 values of the fitted models.

Tree-ring variables and BAI trends

For each site, we cross-dated and measured 12–17 trees (Table 3). Tree age ranged between 31 and 60 years (mean 42 years) for sites 2 and 6, the youngest and oldest ones, respectively, and ring width varied between 1.3 and 3.2 mm (mean 2.5 mm) for sites 3 and 2, those showing the lowest and highest growth rates, respectively. For tree-ring statistics, the mean AR1 and MSx were 0.49 and 0.38, indicating high year-to-year growth variability. Site 4 showed the highest AR1 and site 2 the highest MSx. The mean rbar was 0.40, indicating high within-site coherence in growth between coexisting trees. The best-replicated period, with EPS > 0.85 in all sites, was 2000–2023. The mean BAI during this period was 16.6 $cm^2\ a^{-1}$, with the lowest and highest values found in sites 1 and 4, respectively (Table 3, Fig. 2). Over 2000–2013, no BAI site series showed significant trends, whereas all sites showed negative trends in 2013–2023.

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Year-to-year growth variability

The site indexed ring-width series showed a common pattern as reflected in the severe growth declines during dry years (Fig. 2).

The PC1 and PC2 accounted for 57.9% and 17.5% of the common variance, respectively (Fig. 3). Narrow rings corresponding to dry years had negative PC1 scores (e.g., 1993, 2002, and 2005). PC2 distinquished two groups of sites: sites 1 and 6 (positive scores) and sites 2, 3 and 4 (negative scores). The highest correlation between site series of growth indices was between sites 3 and 4 ($r = 0.841$,

Table 2 Estimates of the linear models fitted to diameter, height, age and basal area increment (BAI) means and trends (2000–2023) as a function of vigor class (D and ND trees), site and their interactions

Term	Diameter			Height			BAI mean			BAI trend		
	Estimate	*t* Ratio	Prob>|*t*|	Estimate	*t* Ratio	Prob>|*t*|	Estimate	*t* Ratio	Prob>|*t*|	Estimate	*t* Ratio	Prob>|*t*|
Intercept	34.81	42.93	<0.0001	10.82	68.92	<0.0001	2.11	28.57	<0.0001	0.11	3.42	0.0009
Vigor	− 2.99	− 3.68	0.0003	− 0.67	–4.28	<0.0001	− 0.38	− 5.22	<0.0001	–0.10	− 3.07	0.0026
Site[1]	− 0.43	− 0.21	0.8342	0.29	0.72	0.4733	− 0.09	− 0.47	0.6385	− 0.05	− 0.54	0.5921
Site[2]	− 8.76	− 5.20	<0.0001	− 0.49	− 1.50	0.1349	− 0.66	− 4.39	<0.0001	− 0.06	− 0.89	0.3737
Site[3]	7.44	4.57	<0.0001	− 0.73	− 2.30	0.0230	− 0.19	− 1.28	0.2037	0.11	1.62	0.1072
Site[4]	14.75	9.31	<0.0001	3.64	11.87	<0.0001	− 0.12	− 0.87	0.3882	− 0.06	− 1.00	0.3180
Site[5]	1.67	0.81	0.4193	− 0.66	− 1.64	0.1027	− 0.01	− 0.06	0.9519	0.01	0.01	0.9957
Vigor × Site[1]	− 2.64	− 1.28	0.2019	− 0.02	− 0.05	0.9605	0.18	0.89	0.3743	0.15	1.80	0.0747
Vigor × Site[2]	1.62	0.96	0.3380	1.36	4.17	<0.0001	0.05	0.32	0.7481	− 0.27	− 3.85	0.0002
Vigor × Site[3]	10.60	6.52	<0.0001	0.08	0.24	0.8104	− 0.14	− 0.96	0.3367	− 0.13	− 1.91	0.0583
Vigor × Site[4]	− 5.56	− 3.51	0.0006	− 0.93	− 3.04	0.0029	− 0.01	− 0.07	0.9482	0.07	1.02	0.3079
Vigor × Site[5]	− 6.31	− 3.07	0.0027	− 1.49	− 3.75	0.0003	− 0.20	− 1.08	0.2819	0.19	2.23	0.0276
Adjusted R^2	0.64			0.66			0.28			0.19		

Table 3 Tree-ring statistics for the six study sites. Trends in basal area increment (BAI) are assessed using the Mann–Kendall statistic (S) and its significance level (p). Different superscript letters indicate significant ($p < 0.05$) differences between the study sites according to Mann–Whitney tests. Values are means ± SD.

Site	Timespan	No. trees	Age (years)	Ring width (mm)	AR1	MSx	rbar	Period with EPS > 0.85	BAI 2000–2023 ($cm^2\ a^{-1}$)	BAI trend 2000–2023 *S* (*p*)	BAI trend 2013–2023 *S* (*p*)
1	1958–2023	17	37 ± 9^{ab}	2.0 ± 0.4^{a}	0.38 ± 0.28^{a}	0.44 ± 0.09^{ab}	0.30	1991–2023	9.41 ± 2.83^{a}	2 (0.98)	− 43 (0.001)
2	1977–2023	12	34 ± 4^{a}	2.83 ± 0.51^{b}	0.43 ± 0.24^{a}	0.47 ± 0.04^{b}	0.38	1989–2023	20.30 ± 4.51^{b}	− 62 (0.13)	− 29 (0.029)
3	1941–2023	13	48 ± 9^{ab}	2.18 ± 0.27^{a}	0.46 ± 0.24^{a}	0.39 ± 0.06^{ab}	0.39	1983–2023	18.68 ± 5.80^{ab}	18 (0.67)	− 29 (0.029)
4	1956–2023	15	46 ± 9^{ab}	2.71 ± 0.47^{ab}	0.67 ± 0.18^{b}	0.28 ± 0.03^{a}	0.47	1981–2023	20.04 ± 4.49^{b}	− 54 (0.19)	− 35 (0.008)
5	1955–2023	13	39 ± 8^{ab}	2.49 ± 0.42^{ab}	0.51 ± 0.29^{ab}	0.33 ± 0.05^{ab}	0.36	1986–2023	16.95 ± 3.41^{ab}	8 (0.86)	− 41 (0.002)
6	1960–2023	13	47 ± 5^{b}	2.43 ± 0.43^{ab}	0.51 ± 0.27^{ab}	0.37 ± 0.04^{ab}	0.49	1980–2023	14.49 ± 4.46^{ab}	26 (0.54)	− 27 (0.043)

$p < 0.001$), while the lowest one was between sites 3 and 4 ($r = 0.060$, $p = 0.732$; Table S3).

Resilience indices: patterns at site and tree levels

There were no significant differences between the sites with regards to the three resilience indices (Table 4). Only *Rc* (recovery) showed a near significant *F* value ($p = 0.08$) with high and low values in sites 3 and 5, respectively. Higher *Rc* values were found for *Rt* (resistance) between 0.6 and 1.1, compared with the curve of full resilience (Fig. 4).

At the site scale, *Rt* decreased in the selected drought years, particularly in 2012 (Fig. 5). As expected, *Rc* increased during the drought years, being particularly high in 2002 and also in 2012 and showing two consecutive high values in 1993 and 1994. *Rs* (resilience) showed gradual increases, lasting on average 1–3 years after the 1993, 2002 and 2012 droughts.

At the tree scale, analyzing the relationships between resilience indices of years 2012 and 2017 and BAI values or trends calculated for the period 2013–2023, there was a positive relationship between the cumulative *Rc* index and the mean BAI ($r_s = 0.285$, $p = 0.0009$), and a negative one between the standardized *Rs* index of 2012 and the trend in BAI ($r_s = -0.339$, $p = 0.0001$; Fig. S5).

There were negative associations of mean BAI for the period 2000–2023, with a relative change in 2017 with respect to 2016, i.e., BAI_{2017} / BAI_{2016}, in both D and ND trees (Fig. S6). The slopes of both regressions did not differ according to one-way ANCOVA ($F = 0.29$, $p = 0.59$), although the correlation coefficient was higher in absolute terms in the case of ND trees.

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Responses of growth indices to climate variables and teleconnection patterns

Climate-growth relationships at the site level showed that Aleppo pine growth was constrained by warm temperatures from May to August, cold conditions in January, and low precipitation from February to July (Fig. 6).

Correlations with the 12-month- long Standardized Precipitation and Evapotranspiration Index (SPEI) peaked in August. Sites 3, 4, and 5 were the most responsive to June maximum temperatures and June-to-September SPEI. At a regional level, there was a positive association between Aleppo pine PC1 scores and the 12-month long SPEI of August ($r = 0.64$, $p < 0.001$; Fig. 7). The PC1 scores were negatively correlated with the June NAO index ($r = -0.60$, $p < 0.001$), whereas the PC2 scores showed a negative correlation with the August WeMO index ($r = -0.34$, $p = 0.0466$, Fig. S7).

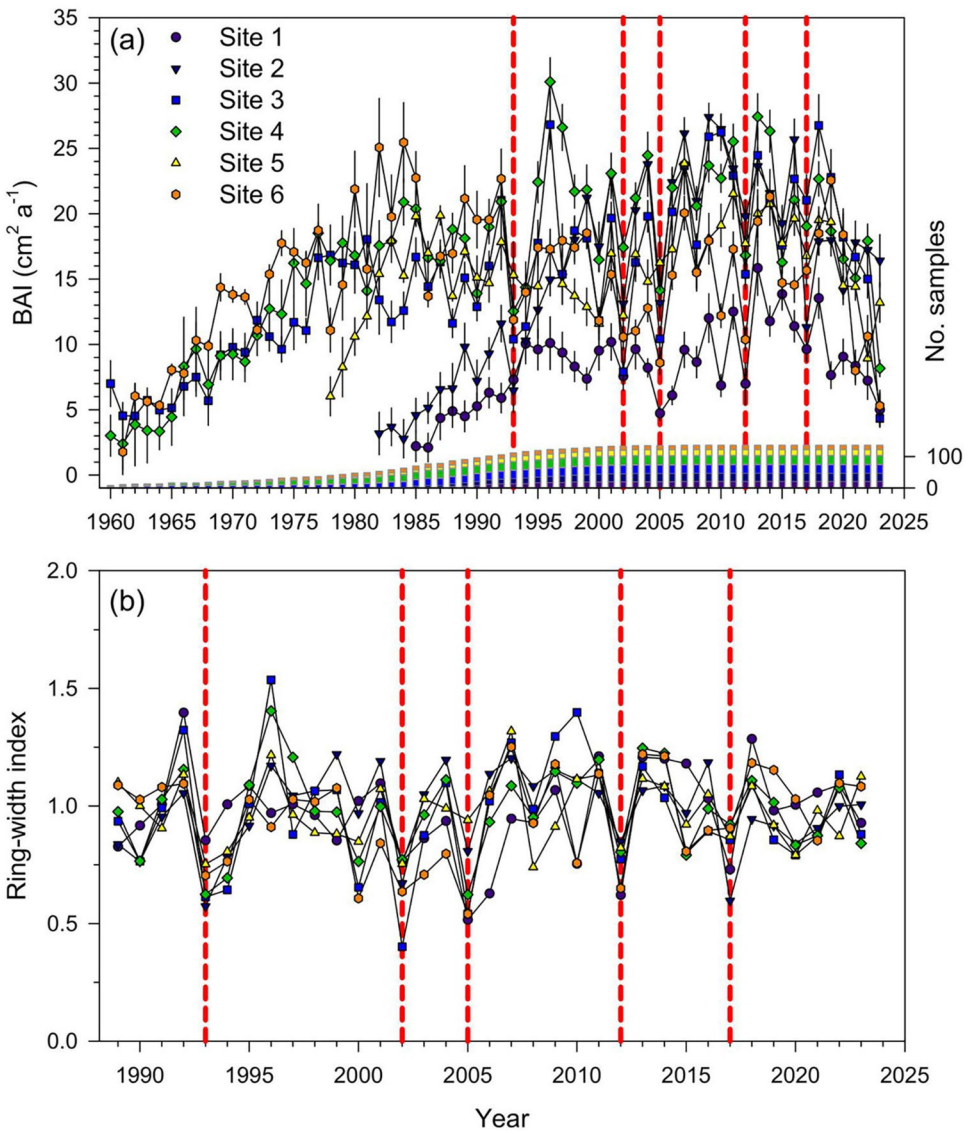


Fig. 2 **a** Trends and variability of basal area increment (BAI). Values are means ± SE. The right *y*-axis shows the annual number of measured samples. **b** Series of ring-width indices of the six study sites. The vertical dashed lines highlight the dry years with low growth (1993, 2002, 2005, 2012 and 2017). Different colors of symbols and bars correspond to the six study sites

Discussion

There was widespread decline over 2013–2023 in the Aleppo pine stands, without a loss of post-drought growth resilience, regardless if they were natural or planted stands, and considering trees of different degrees of defoliation. Given the similar ages of the stands in this study, this result does not seem to be an ontogenetic effect because the species attains a maximum lifespan of 150–200 years (Camarero et al. 2020). On one hand, slow-growing, declining trees had lower heights and greater defoliation (Fig. S4), suggesting poorer hydraulic and growth performance than less defoliated trees (Sarris et al. 2011). On the other hand, resilience indices above 1 indicate that growth fully recovered from drought.

Climate in Algeria has been warming and drying since the 1980s which has negatively impacted forest productivity (Sarmoum et al. 2024). This more arid scenario, characterized by rising VPD, exacerbates evapotranspiration rates during the growing season and leads to drier upper soil layers (Gazol et al. 2017b). The dependence of these forests on sufficient soil moisture is shown by our climate-growth analyses, which concur with previous studies in Algerian Aleppo pine forests, emphasizing the importance of winter rainfall to recharge soil reserves as has been found in Algeria (Choury et al. 2017) and Spain (Pasho et al. 2012). Under dry conditions, Aleppo pine follows isohydric stomatal regulation, but severe droughts may lead to a loss of xylem volume, inhibit needle elongation, reduce sap flux density and cause carbon starvation, crown defoliation and death (Klein et al. 2011, 2014; García de la Serrana et al. 2015).

We focused on a period of rapid aridification and detected drought stress and growth decline in sites of different aridity, indicating that warmer conditions, linked to more positive

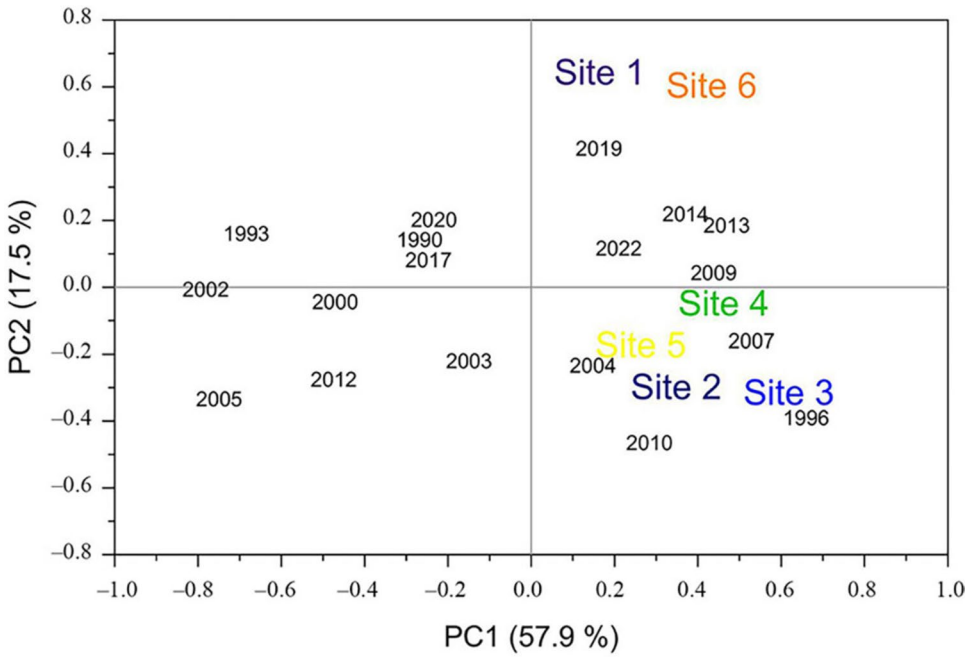


Fig. 3 Biplot of Principal Component Analysis (PCA) showing the site scores and year scores according to their growth indices

Table 4 Values of the resilience indices (*Rt*, *Rc* and *Rs*) for the six study sites considering six dry years. Values are means + SE. The bottom two lines show the *F* statistics and their associated probability levels corresponding to one-way ANOVAs.

Site	Resilience index		
	Rt	*Rc*	*Rs*
1	0.699 ± 0.045	1.406 ± 0.136	0.960 ± 0.059
2	0.702 ± 0.063	1.460 ± 0.060	1.011 ± 0.065
3	0.641 ± 0.079	1.745 ± 0.211	1.066 ± 0.092
4	0.761 ± 0.072	1.479 ± 0.092	1.106 ± 0.082
5	0.821 ± 0.033	1.268 ± 0.036	1.040 ± 0.047
6	0.813 ± 0.068	1.498 ± 0.162	1.224 ± 0.122
F	1.52	2.51	0.84
p	0.25	0.08	0.54

NAO phases, are responsible for such loss in productivity (Camarero 2011). In Aleppo pine, resilience indices depend on pre- and post-drought conditions (Veuillen et al. 2023). For instance, the severe droughts in 1994 and 2000 translated into moderate growth reductions (Fig. 2), but impacted the 1993 and 2002 resilience indices, leading to longer legacies due to dry conditions before and after the selected droughts (Fig. S3). Similar results were found for Spanish Aleppo pine forests (Gazol et al. 2017b). Selecting sites with different growth rates and aridity allowed partialling out the climate influences on growth recovery. For instance, it was noted that the recovery index from a drought occurring after a wet period (e.g., 2012) was much higher than that under a more severe drought occurring during a dry period (e.g., 2017). These differences suggest acclimation to dryness or, alternatively, a loss of resilience due to irreversible growth

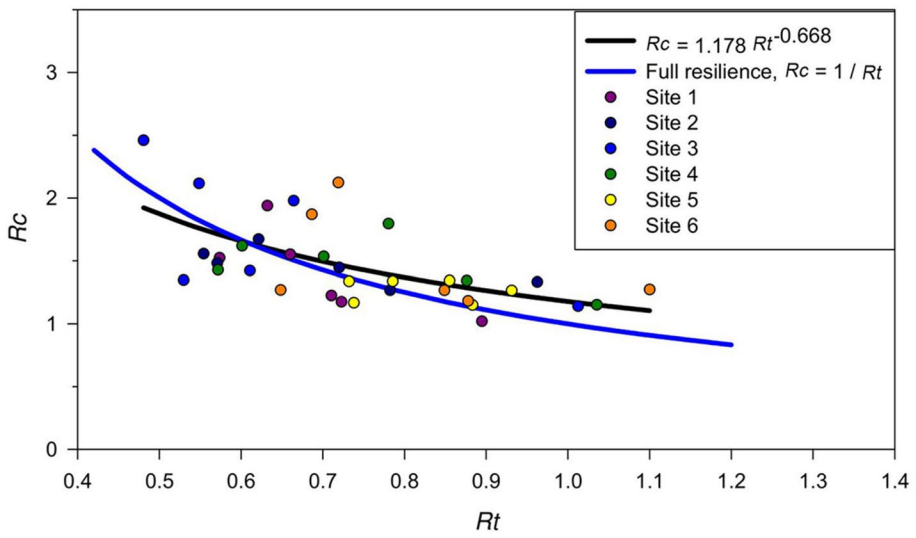


Fig. 4 Curve of full resilience (blue line) showing the relationship between resistance (*Rt*) and recovery (*Rc*) indices (*Rc* = 1 / *Rt*) as compared with the curve fitted to the study sites (black line, equation shown in the plot). Different sites have different colors

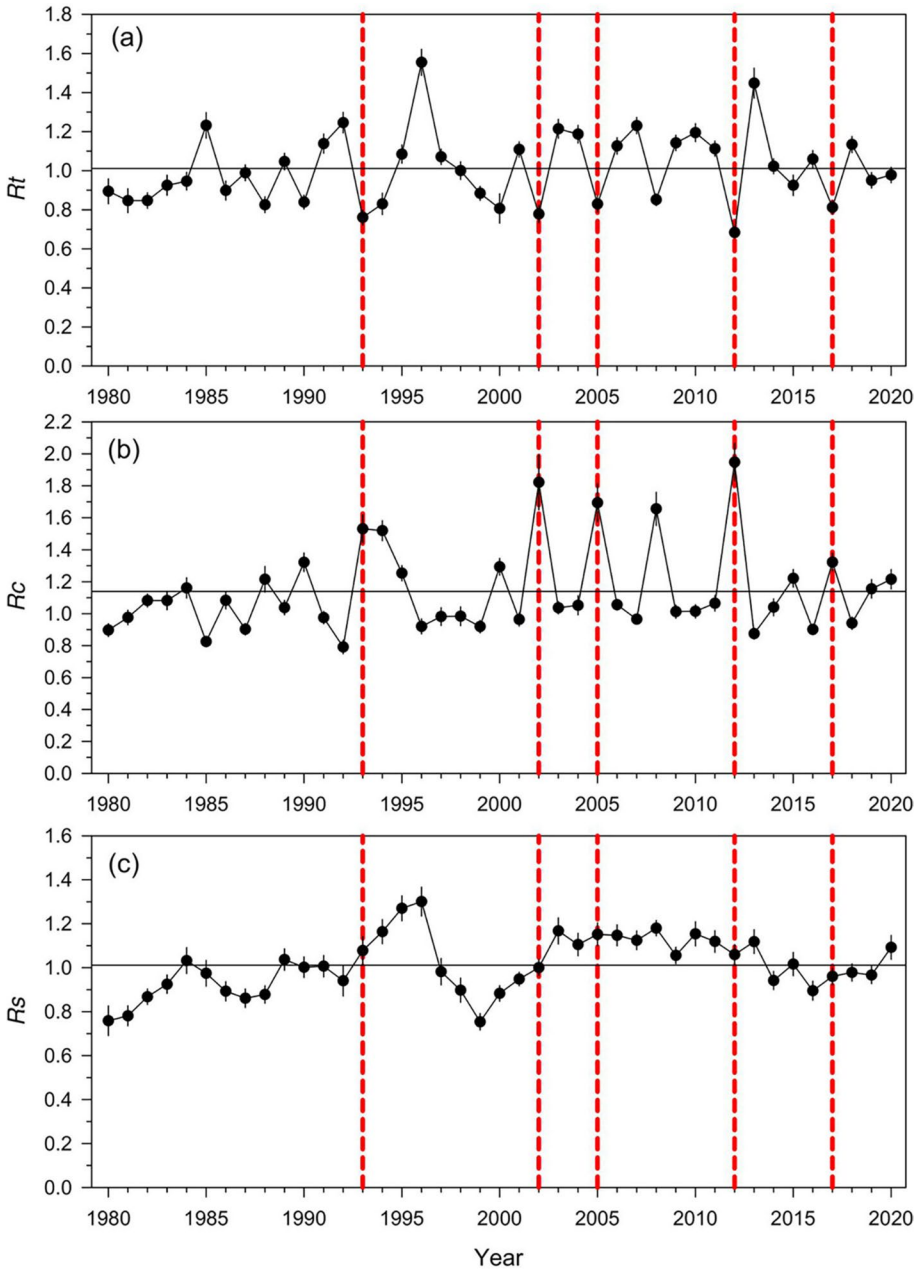


Fig. 5 Values (means ± SE) of the resilience indices: **a** *Rt*, resistance; **b** *Rc*, recovery; and **c** *Rs,* resilience. Vertical dash lines highlight the selected dry years with low growth (1993, 2002, 2005, 2012 and 2017)

decline. Given that Aleppo pine shows high growth plasticity across its distribution area (de Luis et al. 2007; Camarero et al. 2010, 2020; Gazol et al. 2017b), it could be expected that the species reduces its growth rates in response to winter-to-spring droughts or has a second growth peak as a result of wet-cool autumn to winter conditions. This second growth peak was observed under mild climate conditions in a coastal Aleppo pine forest in southeast Spain (de Luis et al. 2007). In any case, severe long droughts seem to lead to growth decline through cumulative drought stress in sites showing different tree sizes and localized aridity.

It has been suggested that the resistance to drought is enhanced in species showing a slow recovery from a first stress impact because they have invested in long-term metabolic adjustment and acclimation (Mu et al. 2022; Camarero 2023). According to this, risk strategies involving fast recovery after drought stress might lead to dieback and ultimately death (Gessler et al. 2020). However, these growth trajectories depend on drought severity and soil water deficits (Gazol et al. 2017a, 2017b; Ponton et al. 2019). In this study, drought stress corresponded to a loss of the capacity to recover growth, quantified by growth resilience indices (*Rc*, *Rs*), and declining Aleppo pines showed rapid recovery if post-drought climate conditions were favorable. This result does not fully agree with previous research focused on growth resistance. For instance, in the Qilian Mountains

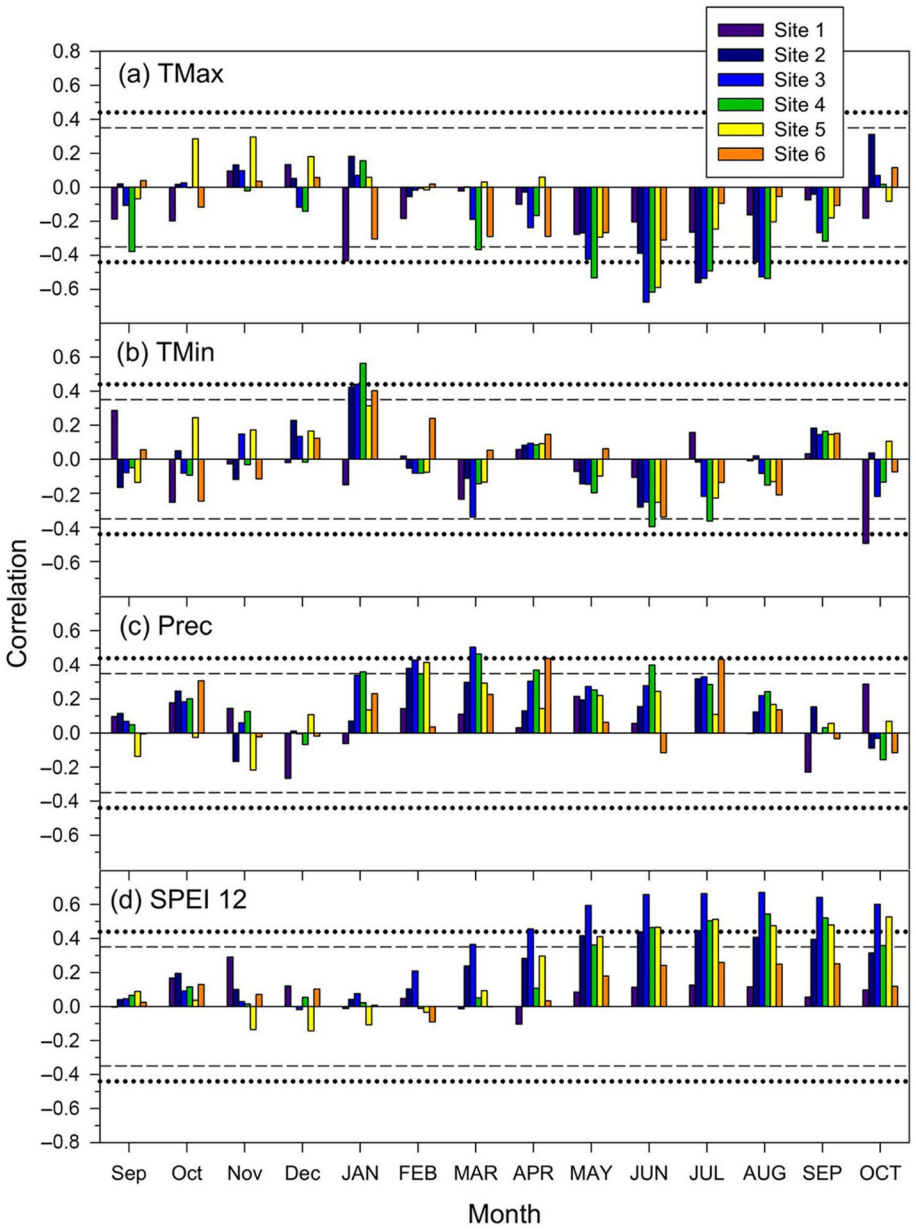


Fig. 6 Pearson correlations calculated between site series of growth indices and monthly climate variables (**a**, TMax, mean maximum temperature; **b**, TMin, mean minimum temperature; **c**. Prec, total precipitation; **d**, SPEI 12, 12-month long SPEI). The horizontal dashed and dotted lines indicate the 0.05 and 0.01 significance levels, respectively. The window of analyses goes from previous (year $t-1$) September to current (year t) October with months of year $t-1$ and t being abbreviated with lowercase and uppercase letters, respectively

(China), junipers showing a lower growth resistance also showed stronger growth decline (Dong and Fang 2024).

A caution for our results is the lack of explicit structural measures (stand density, basal area) to perform attribution analyses of growth decline considering tree-to-tree competition at the neighborhood scale. Nevertheless, natural stands were relatively open, so the impact of competition could be greater in dense plantations (Fig. S1) without periodic thinning, as has been observed in Aleppo pine and other drought-tolerant Mediterranean pine species (Sánchez-Salguero et al. 2012, 2013; Manrique-Alba et al. 2020, 2022). In addition, functional traits (e.g., wood anatomy and density, leaf area, stomatal conduntance rate) and site conditions (e.g., surface rocky cover, soil depth, stoniness across the profile; cf. Preisler et al. 2019; Gómez-Sanz et al. 2024) should be incorporated in more detailed analyses because they affect how conifer species respond to extreme climate events (Camarero 2019; Serra-Maluquer et al. 2021). Another limitation in our study is the classification of trees according to their degree of defoliation, which may have physiological causes and represents contrasting growth rates and trajectories. This requires ongoing and accurate monitoring to match it with retrospective radial growth data. In addition, further research and refinements on growth-defoliation relationships in conifer forests across the Maghreb are necessary to understand the response to compound climate extremes such as hotter droughts (Gazol and Camarero 2022).

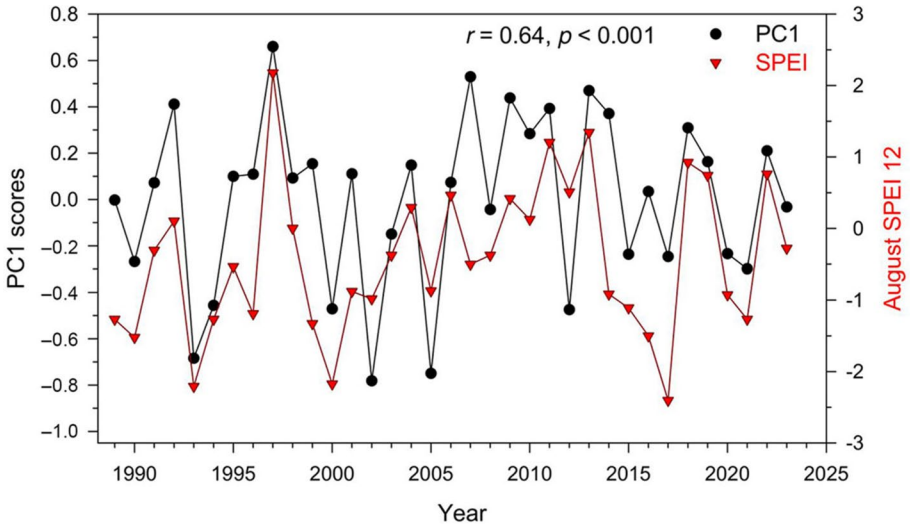


Fig. 7 Positive association of Aleppo pine PC1 scores and the 12-month long SPEI of August (right *y*-axis, red triangles) corresponding to the water balance summed from the previous September to August

Conclusion

Ongoing aridification driven by climate warming is triggering growth decline in Algerian Aleppo pine stands. The recent decline is linked to a loss of the recovery capacity after severe droughts during a period of warmer and drier conditions. The climate-growth relationships revealed that Aleppo pine is vulnerable to long, severe droughts peaking in summer and related to positive NAO phases. These droughts negatively impact growth and are characterized by low winter-to-spring precipitation and elevated maximum temperatures during the growing season. New measures of cumulative stress based on post-drought growth recovery are introduced which should be further explored to assess the sensitivity of conifers to increasing aridity (Zlobin 2022).

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Data availability Data will be made available on reasonable request.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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