

Drought overrides CO₂-driven carbon sink enhancement in Moroccan Atlas cedar forests

Juan Pablo Crespo-Antia^{a,b}, J. Julio Camarero^a, Gabriel Sangüesa-Barreda^c, Víctor Lechuga^d, Victoria Ochoa^e, Juan Carlos Linares^{b,*}

^a Instituto Pirenaico de Ecología (IPE-CSIC), Zaragoza 50059, Spain

^b Departamento de Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, Sevilla 41013, Spain

^c iuFOR-EiFAB, Universidad de Valladolid, Soria 42004, Spain

^d Centre for Advanced Studies in Earth, Energy and Environmental Sciences (CEACTEMA), University of Jaén, Jaén 23071, Spain

^e Instituto Universitario de Investigación en el Olivar y Aceite de Oliva (INUO), Universidad de Jaén, Jaén 23071, Spain

ARTICLE INFO

Keywords:

Basal area increment
Cedrus atlantica
CO₂ fertilization
Drought stress
Intrinsic water use efficiency
Dendrochronology
Carbon isotopes
Carbon sink

ABSTRACT

Increasing drought and extensive forest die-off may override the fertilization effect of rising atmospheric CO₂ (C_a), limiting the contribution of forests as carbon sinks. Tree-rings-based estimates of intrinsic water use efficiency (iWUE) have been recently improved, including the effects of diffusion through stomata and mesophyll, carboxylation and photorespiration. However, it remains unclear whether increasing iWUE is attributable to carbon gain or water shortage. We tested whether leaf gas-exchange regulation, inferred from tree-ring δ¹³C, translates into actual growth or reflects drought responses. Wood δ¹³C and basal area increment were analysed to investigate the effect of rising C_a and drought stress on growth and iWUE of Atlas cedar (*Cedrus atlantica*) forests, spanning seven centuries across a latitudinal gradient in Morocco. iWUE remained stable (~50 μmol CO₂ mol⁻¹ H₂O) across sites until the onset of the 20th century, whereas long-term growth showed greater variability. Since the 1980s, sequential increases in drought sensitivity and growth decline were observed, starting by the southernmost dry regions but extending northwards. Nonetheless, iWUE maintained rising trends, with an average C_i/C_a ratio of 0.72 and C_a sensitivity of 0.18 ppm ppm⁻¹. Growth and iWUE became increasingly decoupled in southern populations, suggesting that rising C_a no longer enhances growth under intensified drought. Local extinction risk is expected to increase at the High Atlas (trailing edge), while the highest conservation priority must be in the Rif (leading edge). We conclude that, whereas C_a and drought have synergistic effects on iWUE, increasing VPD and decreasing soil water availability prevail as drivers of the progressive decoupling between growth and iWUE.

1. Introduction

Severe and recurrent hotter droughts have been identified as major drivers of forest die-off worldwide, resulting in feedback effects on atmospheric carbon dioxide (CO₂) and climate (Anderegg et al., 2013). Experimental evidence of pervasive increases in tree die-off and mortality is raising concerns about the extent to which rising atmospheric CO₂ concentrations (C_a) will continue enhancing tree growth (Zhang et al., 2026). Forest ecosystems act as significant carbon sinks (Keenan et al., 2013; Cheng et al., 2017), yet several questions remain unsolved on how this key element of the global carbon cycle is evolving in

response to the increasing frequency and intensity of droughts (Anderegg et al., 2015).

Assumptions about generalizable patterns in leaf gas-exchange responses to varying C_a are critical for the accuracy of Earth systems models (Adams et al., 2020; Ma et al., 2021; Gong et al., 2022). For instance, it remains uncertain if rising C_a can mitigate canopy water loss and offset the negative impacts of increasing temperature and water demand through a higher vapor pressure deficit (VPD) (Williams et al., 2013; Pernicová et al., 2024). Hence, despite growing research, the physiological adaptive capacity of forests to drought-induced dieback remains poorly understood (McDowell et al., 2022), limiting predictions

* Corresponding author.

E-mail addresses: jpcrespoa@gmail.com (J.P. Crespo-Antia), jjcamarero@ipe.csic.es (J.J. Camarero), gabriel.sanguesa@uva.es (G. Sangüesa-Barreda), vlechuga@ujaen.es (V. Lechuga), vochoa@ujaen.es (V. Ochoa), jclincal@upo.es (J.C. Linares).

<https://doi.org/10.1016/j.foreco.2026.123862>

Received 15 December 2025; Received in revised form 6 April 2026; Accepted 4 May 2026

0378-1127/© 2026 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

of their responses to rising C_a and climate feedbacks (Cheng et al., 2017; Gimeno et al., 2018). Tree-ring $\delta^{13}C$ chronologies have shown increases in intrinsic water use efficiency (iWUE), defined as the ratio of photosynthesis to stomatal conductance for water vapour, across several forests, albeit with pronounced spatiotemporal variability (Frank et al., 2015; Laffitte et al., 2023; Linares and Camarero, 2012; Peñuelas et al., 2011; Saurer et al., 2004). Despite iWUE provides suitable information to assess photosynthetic performance and the trade-off between CO_2 fixation and water loss, there is no clear consensus on the estimation of iWUE from tree-ring $\delta^{13}C$ (Ma et al., 2021; Gong et al., 2022; Yu et al., 2024). Furthermore, most studies focus on the 20th century, leaving long-term assessments of growth and water-use in forests subjected to increasing and long-lasting drought conditions largely unexplored.

Climate-latitudinal gradients of drought-sensitive tree species provide useful experimental frameworks for understanding sequential responses to changing climate (Maseyk et al., 2011; De Frenne et al., 2013; Shestakova et al., 2017). Drought-prone North African Atlas cedar (*Cedrus atlantica* (Endl.) Manetti ex Carrière) forests provide a unique setting to evaluate long-term linkages between carbon and water balances through tree growth and iWUE. Recent research indicates that Atlas cedar radial growth has become more synchronized in response to warming and droughts, while grazing and soil erosion are linked to decreased soil water-holding capacity (Camarero et al., 2021; Linares et al., 2011, 2013; Sarmoun et al., 2024). Changes in radial growth and iWUE could thus be used as proxies of the physiological responses of Atlas cedar to the C_a increase and ongoing aridification across North Africa.

Here, we compare three Moroccan regions along a marked climatic gradient with humid (Rif), intermediate (Middle Atlas), and xeric (High Atlas) conditions (Benabid, 1994). By examining variables such as basal area increment (BAI), climate (temperature, precipitation, drought indexes), and different theoretical iWUE scenarios, we analyzed the impact of global C_a increase and changes in aridity on tree growth. To achieve these aims: (i) we evaluated regional climatic trends in temperature, precipitation, and drought severity; (ii) we quantified and compared long-term BAI and iWUE values, trends, and responses to climate variables and global C_a increase; and (iii) we assessed the relationships between BAI and iWUE from the early 19th century to the early 21st century encompassing the Industrial revolution and the recent phase of rapid C_a increase. We hypothesize that uncoupled trends of tree growth and iWUE will be present where increasing drought stress was more severe. As a result, increasing frequency and severity of drought in the southernmost distribution range of Atlas cedar must be associated with growth decline, despite C_a -induced enhanced iWUE might be still observed.

2. Materials and Methods

2.1. Study area and species

Atlas cedar (*Cedrus atlantica* (Endl.) Manetti ex Carrière) forests have been negatively impacted by recent droughts showing high mortality rates in some areas of Morocco and Algeria (Camarero et al., 2021; Sarmoun et al., 2024). The Moroccan atlas cedar forests occur in the Rif (RF), Middle Atlas (MA) and High Atlas (HA) between about 1400 and 2300 m asl with an area of 17,200 ha, 86,000 ha, and 26,800 ha, respectively (Cheddadi et al., 2022; Ben-Said et al., 2022), growing under semi-arid to humid conditions (Benabid, 1994). We conducted several extensive field works, sampling 14 populations across most of the Atlas cedar's distribution range in Morocco (Table 1, Fig. 1).

2.2. Climate data

Due to the lack of long and homogeneous local climate records in the study areas, temperature (Tx, mean maximum temperature; Tn, mean minimum temperature) and precipitation data were obtained from the Climate Explorer website (<https://climexp.knmi.nl>). These data corresponded to the CRU 0.5°-gridded dataset and covered the period 1902–2010 (Harris et al., 2023). Using this information, seasonal and annual means were computed, and the cumulative seasonal and annual precipitation was also estimated for the same period. To assess drought severity, the Standardized Precipitation-Evapotranspiration Index (SPEI) was calculated at 3- to 12-month long scales for the period from 1902 to 2010 using the SPEI package (Beguería and Vicente-Serrano, 2023).

2.3. Dendrochronological methods

We measured the diameter at breast height (DBH) and collected three cores at 1.3 m per tree from 114 trees. In all sites, dominant trees with DBH > 25 cm were selected. The cores were taken using Pressler increment borers. Two cores per tree were used for ring-width measurements and underwent air-drying, were fixed to wooden mounts, and sanded with progressively finer sandpapers until the tree rings became distinctly visible. Ring width measurements and cross-dating were conducted on scanned images at a resolution of 1200 dpi (EPSON XL 10000 scanner) with an accuracy of 0.001 mm, using the CooRecorder-CDendro software (Larsson, 2022). This visual cross-dating was further validated using COFECHA software (Holmes, 1983). In each region, from 11 to 24 cores were kept for C isotope analyses. They corresponded to a total of 53 trees showing the highest correlations of their individual ring-width series with the mean site series.

Table 1

Geographical, topographical and structural characteristics of the sampled sites. ACH: age at coring height (1.3 m); DBH: diameter at breast height; BAI, basal area increment. Values are means $\pm$ SE.

Region	Site code	Latitude ° N	Longitude ° W	Elevation (m.a.s.l.)	Slope (°)	Age ACH (years)	DBH (cm)	No. trees	BAI (cm ²)	No. trees for isotope analyses	Mean $\delta^{13}C$ (‰)
High Atlas (HA)	JAF	32°32'36.5"	4°54'36.9"	2111	28	214 $\pm$ 89.1	57.3 $\pm$ 14.4	6	15.1 $\pm$ 0.3	6	-23.0 $\pm$ 0.0521
	TOF	32°27'20.21"	5°19'44.77"	2238	29	535 $\pm$ 123	55.5 $\pm$ 13.0	4	5.3 $\pm$ 0.1	5	-22.4 $\pm$ 0.0345
	MTK	32°31'20.18"	4°58'19.97"	2381	20.5	189 $\pm$ 28.9	51.4 $\pm$ 3.81	8	11.4 $\pm$ 0.2	—	—
Middle Atlas (MA)	MA1	33°24'51"	5°3'19.6"	1878	10	164 $\pm$ 65.6	40.4 $\pm$ 8.1	5	9.1 $\pm$ 0.2	4	-22.8 $\pm$ 0.0753
	MA2	33°24'41.42"	5°8'33.8"	1837	45	198 $\pm$ 34.6	69 $\pm$ 7.7	7	20.3 $\pm$ 0.3	4	-22.9 $\pm$ 0.0558
	ITZ	32°56'44.5"	5°16'39.5"	1971	27	175 $\pm$ 23.1	73.9 $\pm$ 9.7	5	26.2 $\pm$ 0.5	5	-23.2 $\pm$ 0.1020
	ITE	32°59'18.3"	4°15'54.5"	2090	35	215 $\pm$ 112	74.0 $\pm$ 7.6	5	20.9 $\pm$ 0.4	5	-22.7 $\pm$ 0.0667
	ZAD	33°0'17.4"	5°4'56.7"	2250	14	207 $\pm$ 29.9	50.9 $\pm$ 3.9	14	10.6 $\pm$ 0.1	—	—
	AZR	33°25'16.7"	5°10'57.6"	1930	15.5	160 $\pm$ 20.6	54.8 $\pm$ 5.0	20	17.0 $\pm$ 0.1	—	—
Rif (RF)	KTM	34°58'2.3"	4°39'29"	1615	17.5	81.2 $\pm$ 10.3	60.8 $\pm$ 10.1	5	39.7 $\pm$ 1.2	5	-24.4 $\pm$ 0.0846
	TDG	34°51'46.76"	4°30'22.97"	1922	16.5	88.8 $\pm$ 3.15	47.7 $\pm$ 2.3	5	20.3 $\pm$ 0.5	3	-24.9 $\pm$ 0.104
	BLZ	34°58'22.9"	4°44'21.2"	1637	25	185 $\pm$ 30.9	86.9 $\pm$ 11.7	5	34.5 $\pm$ 0.4	5	-23.6 $\pm$ 0.0619
	KLT	35°21'20.43"	5°16'43.17"	1825	27	246 $\pm$ 32.9	58.7 $\pm$ 6.5	14	12.6 $\pm$ 0.1	6	-22.8 $\pm$ 0.0587
	TSM	35°8'32.2"	5°7'31"	1692	30	71.9 $\pm$ 4.66	48.3 $\pm$ 2.7	11	26.3 $\pm$ 0.5	5	-24.3 $\pm$ 0.1501

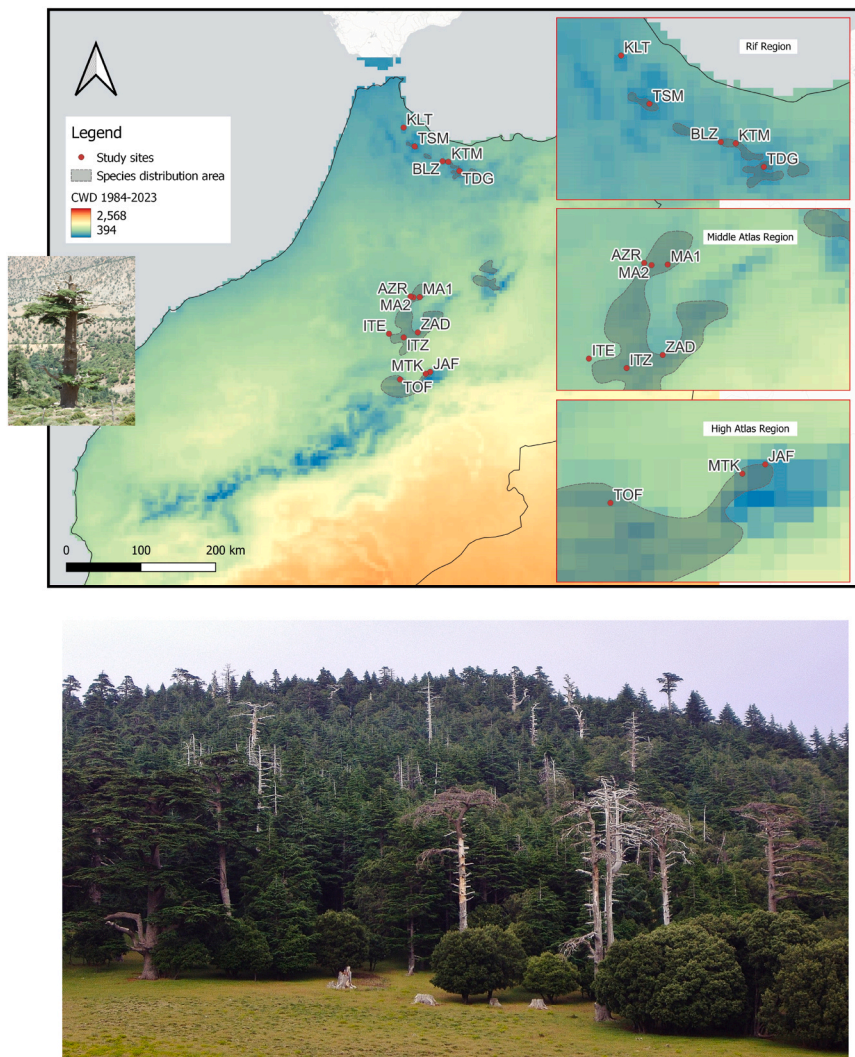


Fig. 1. Location of the study sites in Morocco. The grey polygons show the distribution of Atlas cedar (Caudullo, 2024), the dots indicate the sampled sites, The color scale indicate the average Climatic Water Deficit for the period 1984–2023 (CWD; potential minus actual evapotranspiration (mm); Abatzoglou et al., 2018), with blue indicating higher moisture availability and red indicating moisture deficit. The inset shows an old Atlas cedar tree sampled in the High Atlas. Photo J.A. Carreira. The bottom plate illustrates Atlas cedar die-off and mortality in the Middle Atlas. Photo V. Lechuga.

The tree-ring width series were used to estimate: (1) age at coring height (ACH) based on the maximum number of rings in cross-dated cores, and (2) annual BAI for all trees. The ring width was transformed into BAI due to this measure holds greater biological significance in describing tree growth, in terms of annually accumulated biomass. BAI was annually resolved from the tree ring widths as the difference between consecutive cross-sectional basal areas (Lockwood et al., 2021; Klesse and Bigler, 2025).

2.4. Temporal trends of carbon discrimination and iWUE

To compare the long-term changes in iWUE of each region, we measured the $^{13}\text{C}/^{12}\text{C}$ isotope ratios in tree rings. One core of each tree was dissected by decades under a binocular microscope using a razor blade. Decadal time resolution was chosen because most trees showed very narrow tree-ring, preventing annual dissection of enough amount of wood. Further, we were interested in long-term trends, while the use of decadal sections allowed to increase the number of individual trees analysed. 10-year pooled segments ensured sufficient sample mass for high-precision isotopic measurement and aligns with our objective of identifying long-term physiological trends and adaptive responses to environmental changes rather than inter-annual variability (McCarroll

and Loader, 2004; Saurer et al., 2004; Robertson et al., 2008). Wood samples were milled to a fine powder using a ball mill (Retsch MM301, Haan, Germany), weighed 0.5–0.7 mg of wood powder for carbon isotope analyses and encapsulated in tin capsules.

Further, since whole wood is isotopically lighter than cellulose due to the presence of lignin, we performed a regression analysis to assess the relationship between $\delta^{13}\text{C}$ values in wood and extracted cellulose. Wood cellulose was extracted from a sub-sample, including tree-rings samples from the entire latitudinal range. Cellulose extraction was performed to obtain purified α -cellulose based on a modification of the method of (Leavitt and Danzer, 1993) for the removal of extractives and lignin, as detailed in (Ferrio and Voltas, 2005). Oven-dried α -cellulose was weighed (about 1 mg) into tin foil capsules. Wood and cellulose samples were combusted using a Flash EA-1112 elemental analyser interfaced with a Finnigan MAT Delta C isotope ratio mass spectrometer at the Stable Isotope Facility (University of California, Davis, USA).

The $^{13}\text{C}/^{12}\text{C}$ isotope ratios measured in wood and extracted cellulose were expressed as the relative difference between the sample $^{13}\text{C}/^{12}\text{C}$ ratio (parts per thousand, ‰) and the standard V-PDB, resulting $\delta^{13}\text{C}$ (‰).

$$\delta^{13}\text{C} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) * 1000 \quad (1)$$

where R_{sample} and $R_{standard}$ are the $^{13}\text{C}/^{12}\text{C}$ ratios in a sample and fossil belemnite standard V-PDB.

We obtained a significant correlation between $\delta^{13}\text{C}$ in cellulose and wood ($R^2=0.87$, $p < 0.001$; see [Supplementary Material, Figure S1](#)), providing a correction factor of 1.31‰ for $\delta^{13}\text{C}_{wood}$ (2).

$$\delta^{13}\text{C}_{corr} = \delta^{13}\text{C}_{wood} + 1.31 \quad (2)$$

The isotopic discrimination (Δ) was calculated from the difference between wood isotopic ratio and atmospheric isotopic ratio (3) ([Farquhar et al., 1982](#)).

$$\Delta = \frac{\delta^{13}\text{C}_{air} - \delta^{13}\text{C}_{corr}}{1 + \frac{\delta^{13}\text{C}_{corr}}{1000}} \quad (3)$$

where $\delta^{13}\text{C}_{air}$ represents the isotopic composition of atmospheric CO_2 and $\delta^{13}\text{C}_{corr}$ is the corrected tree-ring wood value obtained from eq. 2. C_a and $\delta^{13}\text{C}_{air}$ data were obtained from published data ([Francey et al., 1999](#); [McCarroll and Loader, 2004](#); [Belmecheri and Lavergne, 2020](#); NOAA GML, 2024).

To reconcile tree-ring data with leaf-level gas exchange processes, we calculated the iWUE following the model that includes the effects of diffusion through stomata and mesophyll, carboxylation, photorespiration, and non-photosynthetic fractionation ([Yu et al., 2024](#)):

$$\text{iWUE} = \frac{C_a}{k} \cdot \frac{b - (\Delta - d) - f \cdot \frac{\Gamma^*}{C_a}}{b - a + \frac{g_{sc}}{g_m} \cdot (b - a_m)} \quad (4)$$

where k (1.6) is the diffusivity ratio of H_2O to CO_2 in air, Δ represents the photosynthetic $^{13}\text{C}/^{12}\text{C}$ fractionation obtained from Eq. 3. The non-photosynthetic fractionation (d) was set at zero, as established by [Yu et al. \(2024\)](#) for tree rings cellulose-based proxies; a (4.4‰) is the fractionation for CO_2 diffusion across stomata, a_m (1.8‰) is the combined fractionation for dissolution and diffusion of CO_2 in mesophyll, b (29‰) and f (11‰) denote the fractionations due to carboxylation and photorespiration, respectively.

The CO_2 compensation point (Γ^*) was estimated considering the effect of leaf temperature and elevation to account for Γ^* rise as temperature increases and Γ^* decline as partial pressure of O_2 decreases, respectively ([Brooks and Farquhar, 1985](#)):

$$\Gamma^* = (42.7 + 1.68(T - 25) + 0.012(T - 25)^2) \cdot e^{(-0.00012 \cdot z)} \quad (5)$$

where T is the mean temperature during the growing season (C) and z is the elevation (m a.s.l.) for each sampling site. The mean air temperature during the growing season was used as a proxy for leaf temperature to calculate the CO_2 compensation point ([Lloyd and Farquhar, 1994](#); [Saurer et al., 2004](#)). While leaf temperature can deviate from air temperature due to transpirational cooling or radiative heating, several studies have shown that for conifers in temperate and Mediterranean environments, mean air temperature effectively captures the seasonal thermal constraints on Rubisco kinetics and photosynthetic discrimination ([Farquhar et al., 1982](#); [Lloyd and Farquhar, 1994](#)). The ratio of stomatal to mesophyll conductance to CO_2 (g_{sc}/g_m), was fixed at 0.79 based on a global meta-analysis for conifers ([Ma et al., 2021](#)). Using Eq. (4), the derivative of iWUE with respect to C_a gives the sensitivity of iWUE to atmospheric CO_2 expressed in mole fraction ([Gong et al., 2022](#)):

$$C_a \text{ sensitivity} = \frac{d(\text{iWUE})}{d(C_a)} = \frac{b - \Delta}{1.6 \left[\frac{g_{sc}}{g_m} (b - a_m) + b - a_s \right]} \quad (6)$$

2.5. Theoretical scenarios of iWUE

The physiological response of trees to the increasing C_a was investigated using three theoretical gas-exchange scenarios for trends of Δ and iWUE ([Saurer et al., 2004](#)): (i) $C_i = \text{constant}$, this scenario shows a strong stomatal closure and indicates a reduction in C_i/C_a ; (ii) C_i/C_a

= constant, this scenario shows a regulation of C_i by photosynthesis and stomatal conductance; and (iii) $C_a - C_i = \text{constant}$, which reflects a weak response of stomata to the increment of C_a and iWUE is not improved. The theoretical gas-exchange scenarios were tested for the 20th century, where iWUE showed the stronger response to C_a . These three theoretical scenarios were compared to the mean iWUE values obtained from Eq. 4 in each region following [Gong et al., \(2022\)](#). To quantify the accuracy of each model, we computed the root mean square predictive difference (RMS) as the square root of the sum of squared differences between observed and predicted iWUE, divided by the number of observations. Hence, lower RMS values indicate increasing similarity among observed iWUE and theoretical estimates, supporting more accurate theoretical predictions for a given model.

2.6. Statistical analyses

The climate analyses employed a combination of parametric and non-parametric methods, according to the nature of the data. Temporal trends of annual and seasonal temperatures in each region, were examined using Pearson correlation. The trends of annual and seasonal precipitation in each population were examined through Mann-Kendall trend tests using trend package ([Pohlert, 2023](#)); an additional analysis was conducted using quantile regression for the 0.10, 0.25, 0.50, 0.75, and 0.90 quantiles to determine trends in extreme precipitation events using trend quantreg package ([Koenker, 2024](#)).

To analyze changes in drought severity, the entire regional SPEI time series data was arranged in ascending order. All annual or seasonal SPEI values lower than -1 , indicative of a dry season, were then chosen. Following this selection, the decades in which these events occurred were identified to assess whether drought events are evenly distributed over time or if their frequency has increased in recent years. SPEI was calculated using SPEI package ([Beguería and Vicente-Serrano, 2023](#)).

To evaluate regional climate responses, we conducted annual and seasonal Pearson correlation analyses between temperature (T_x , T_n), precipitation, and SPEI, with regional values of annual BAI. We analysed the inter-annual climate response on the period 1980–2010 ($n = 30$) to focus on the climate response under the most recent period with a higher frequency of drought events.

BAI and iWUE relationships were analyzed at individual tree-level in the subsample of trees where growth and carbon isotopes were measured in the same tree-rings ([Table 1](#)). BAI was averaged by ten-years periods to merge with the time period contained in the $\delta^{13}\text{C}$ wood segments of ten-years pooled, previously dated and measured. To test if the relationships between BAI and iWUE changed through time, we employed running Pearson correlation analysis across 100-year sliding time windows with 30-year long lags (1820–1920, 1850–1950, 1880–1980, and 1910–2010). Then, we evaluated whether there were significant ($p < 0.05$) differences in the magnitude of these correlations between populations. To compare differences in the mean values among regions, one-way analyses of variance (ANOVA) were conducted; the Tukey Honestly Significant Difference (HSD) test was employed for post-hoc analyses. Data are expressed by mean values $\pm$ standard error (SE). All statistical analyses were performed using R ([R Core Team, 2024](#)).

3. Results

3.1. Climate data, trends and drought severity

The study regions face more arid conditions from north to south ([Table 2](#)). Extreme low precipitations tend to decrease each year for MA and RF while high precipitation events have declined over time in HA. The annual mean temperature was significantly higher in RF, followed by HA, with the lowest value found in MA. Annual precipitation was significantly higher in RF, followed by MA, with the lowest total precipitation in HA.

All regions exhibited a gradual increase in mean temperature over

Table 2

Seasonal and annual mean temperature and total precipitation in Rif (RF), Middle Atlas (MA) and High Atlas (HA) study regions. Data are mean values $\pm$ SE.

Site (Code)	Temperature ($^{\circ}$ C)				
	Annual	Winter	Spring	Summer	Fall
Rif (RF)	13.3 $\pm$ 0.046	7.40 $\pm$ 0.061	11.4 $\pm$ 0.067	20.0 $\pm$ 0.070	14.5 $\pm$ 0.066
Middle Atlas (MA)	11.4 $\pm$ 0.050	4.29 $\pm$ 0.077	9.05 $\pm$ 0.074	19.7 $\pm$ 0.070	12.6 $\pm$ 0.071
High Atlas (HA)	12.8 $\pm$ 0.051	5.17 $\pm$ 0.075	10.8 $\pm$ 0.08	21.7 $\pm$ 0.072	13.7 $\pm$ 0.072
Precipitation (mm)					
Rif (RF)	1127 $\pm$ 32.1	484 $\pm$ 23.6	319 $\pm$ 13.3	16.3 $\pm$ 2.11	308 $\pm$ 11.7
Middle Atlas (MA)	1024 $\pm$ 23.1	423 $\pm$ 16.7	303 $\pm$ 10.8	54.5 $\pm$ 3.28	244 $\pm$ 10.2
High Atlas (HA)	415 $\pm$ 17.2	158 $\pm$ 12.9	139 $\pm$ 9.40	16.3 $\pm$ 1.30	102 $\pm$ 7.09

the period 1902–2010 (Supplementary Material, Figure S2), and the summer season contributed predominantly to this temperature rise. The Mann-Kendall trend test indicated a decrease in annual precipitation in HA, spring and annual precipitation in MA and spring precipitation in

RF. The analysis of extreme precipitation events revealed a decreasing trend in high rainfall events in HA and a reduction in the amount of precipitation during drought events in MA (Supplementary Material, Figure S3). Similarly, the RF region exhibited a significant increase in the severity of the drought events, but not statistically significant temporal trend in the SPEI (Fig. 2).

All regions exhibit an increase in the frequency of droughts from the 1950s onwards with a pronounced aridification trend after 1980 (Fig. 2). There was also a high frequency of drought events for all regions in the 1940s. The highest frequency of summer drought events occurred in the 2000s for all regions. The HA region showed high frequency of drought events during the 1990–2010 period (Supplementary Material, Figure S4).

3.2. Tree age and size, growth values and trends

The southernmost HA study sites have the oldest trees, compared to MA and RF, while there were no differences in age between the middle and the northernmost regions (HA, 278 ± 52 years; MA, 183 ± 16 years; RF, 148 ± 17 years). However, the sampled trees showed no significant differences in DBH among the three study regions, supporting lower mean growth rates southward. The mean BAI was highest in the

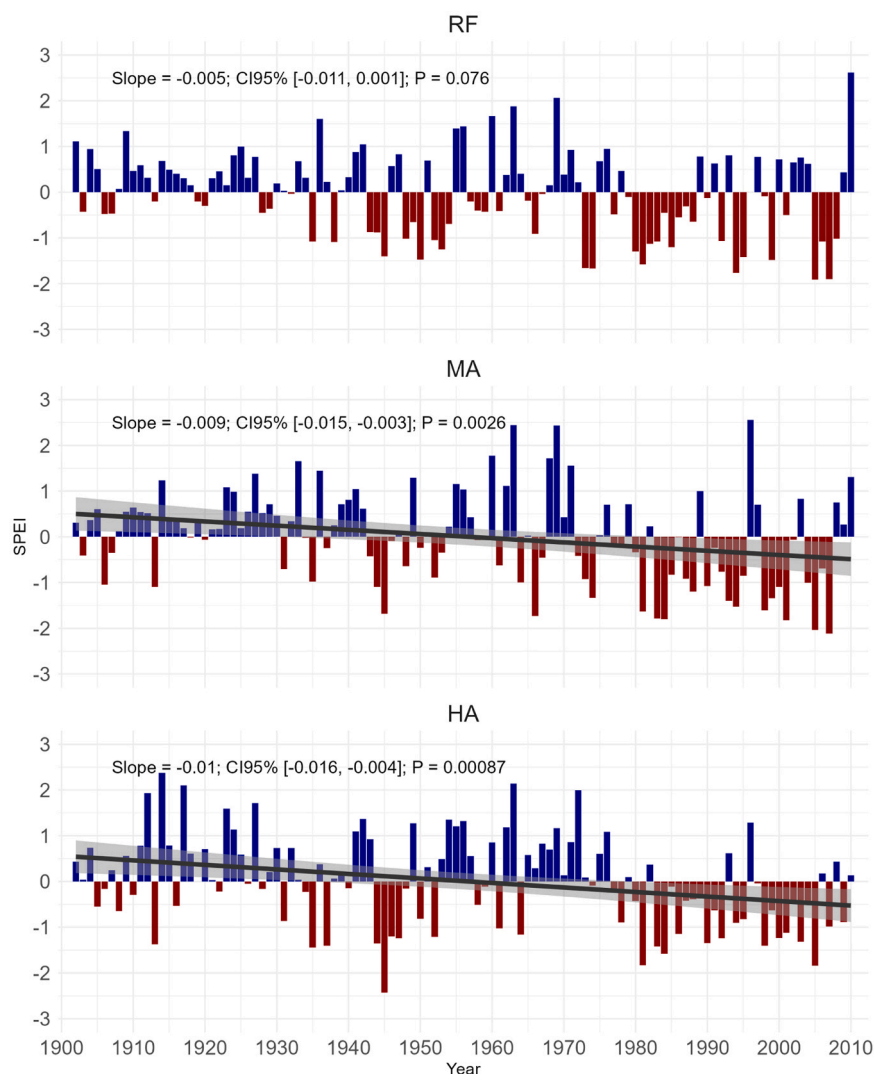


Fig. 2. Annual drought severity (12-month SPEI values from January to December) in RF, MA, and HA regions. The blue bars represent wetter-than average years, whereas red bars represent drier-than-average years. The inset indicates the slope, 95% confidence interval of the slope (CI95%), and P-values of linear regression. Significant linear regression lines with 95% confidence intervals are included.

northernmost RF region, characterized by strong growth releases between the second half of the 18th century and the first half of the 19th century (Fig. 3a). During the first half of the 20th century, the three regions showed similar and positive growth trends, although there were sudden growth declines over the 1960s decade in the HA, and thereafter over the 1970s decade in the MA, respectively (Fig. 4). The mean BAI was significantly higher in the RF, compared to the southernmost HA, except for the period 1920–1950, with mean BAI of the MA region in an intermediate position (Fig. 4, Table 3). Nonetheless, also the northernmost RF region showed a declining BAI trend at the onset of the 21st century, following a latitudinal pattern of Atlas cedar sequential growth decline.

3.3. Trends in carbon isotopes and theoretical iWUE scenarios

Tree-ring wood $\delta^{13}\text{C}$, Δ and iWUE were relatively steady and similar among regions until the 19th century (Fig. 3b, c and d). Over the 19th century and mainly in the 20th century, the tree-rings $\delta^{13}\text{C}$ decreased (became more negative) and Δ and iWUE increased. The northern RF region showed more negative tree-rings $\delta^{13}\text{C}$ values (about -2.0‰), leading to significantly lower iWUE. HA and MA showed similar $\delta^{13}\text{C}$ values (about -23.3‰) corresponding to a higher iWUE (Table 3). In the three studied regions, the theoretical more accurate theoretical scenario was those assuming a constant C_i/C_a ratio (Fig. 5), showing RMS values

of 4.1 (RF), 3.7 (MA) and 3.8 (HA), respectively. Nonetheless, the three regions showed observed mean iWUE values slightly below the theoretical constant C_i/C_a ratio. The sensitivity of iWUE to C_a (Eq. 7) was almost steady over the study period, about $0.187 \text{ ppm ppm}^{-1}$. C_a sensitivity increased slightly over the 20th century in the three regions, while mean values were significantly lower in the RF (Table 3).

3.4. Growth responses to climate

Correlation analyses performed on annual BAI and local climate data showed that winter to spring precipitations (positive correlations) are key climatic drivers for Atlas cedar growth in the drier HA and MA regions, whilst summer temperatures during the prior and the current growing season (negative correlations) limited growth in RF (Fig. 6).

3.5. Relationships between BAI and iWUE

Tree-level correlation analyses between decadal values of BAI and iWUE yielded on average a positive relationship in the three studied regions from middle 18th century to Middle 19th century (decades from 1770 to 1860), 19th century (decades from 1820 to 1910), and middle 19th century to Middle 20th century (decades from 1870 to 1960) (Fig. 7). However, during the 20th century (decades from 1920 to 2010) the correlation became almost null in MA and was even negative on HA (Fig. 7; Supplementary Material, Figure S5).

4. Discussion

Increases in forest water-use efficiency have been reported worldwide, however, the magnitude of this physiological forcing on global carbon and water balances is still under debate (Adams et al., 2020; Gong et al., 2022). We tested the fertilization effect of rising C_a , often suggested as enhancing tree growth by increasing photosynthesis (Keenan et al., 2013; Cheng et al., 2017), along a latitudinal gradient of aridity in Atlas cedar forests from north Morocco. Our findings underscore that C_a rise effect was not long-lasting, particularly in Atlas cedar forests, where recurrent drought acts as the main limiting factor for tree growth. This result is not new, as several studies worldwide have concluded that tree growth has not increased as expected, despite rising C_a concentrations and pervasive iWUE enhancement (see Laffitte et al. (2023) for a literature revision, and Zhang et al., (2026) for a theoretical basis). Nonetheless, the available information includes mostly data spanning from late 20th to early 21st centuries, including different tree species, which limit the identification of factors suggested as overriding the potential growth benefits of C_a in many sites (namely, climate change, nutrient limitations and/or physiological long-term acclimation to elevated C_a). Hence, by investigating about seven hundred years of tree growth and iWUE, we demonstrate that Atlas cedar's leaf gas-exchange responses to further increases in C_a will mainly depend on the species-specific physiological trade-off between maximizing C gain or avoiding drought stress. The results revealed within-species regional variations in growth patterns, with the driest region (HA) showing more pronounced responses to aridification compared to wetter regions (MA and RF). We also illustrate that the potential benefits of long-term iWUE enhancement appear to be offset by the severity of hotter droughts, leading to increasingly stressful conditions across all study regions, besides aggravated by logging and overgrazing (Camarero et al., 2021). These findings highlight the limitations of CO_2 fertilization effect in drought-prone environments and point out important implications to forecast the resilience of seasonally dry forests under ongoing aridification (Forzieri et al., 2022; Pernicová et al., 2024).

4.1. Regional climatic trends

The RF region presented warmer temperatures than expected, which can be attributed to the lower elevation of the study sites and the

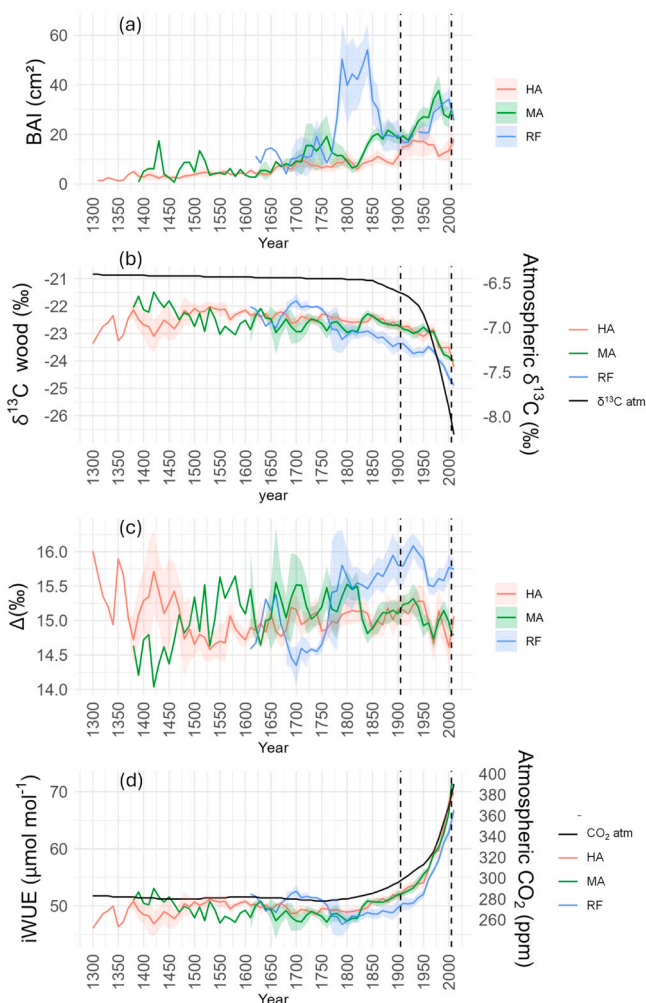


Fig. 3. Mean values of ten-years averaged BAI (a), ten-years pooled tree-ring wood $\delta^{13}\text{C}$ (b), $\Delta^{13}\text{C}$ (c) and iWUE (d) in RF, MA, and HA regions. Historical data of atmospheric $\delta^{13}\text{C}$ and CO_2 are also shown. Shadows show the SE. Dashed vertical lines indicate the period 1910–2010.

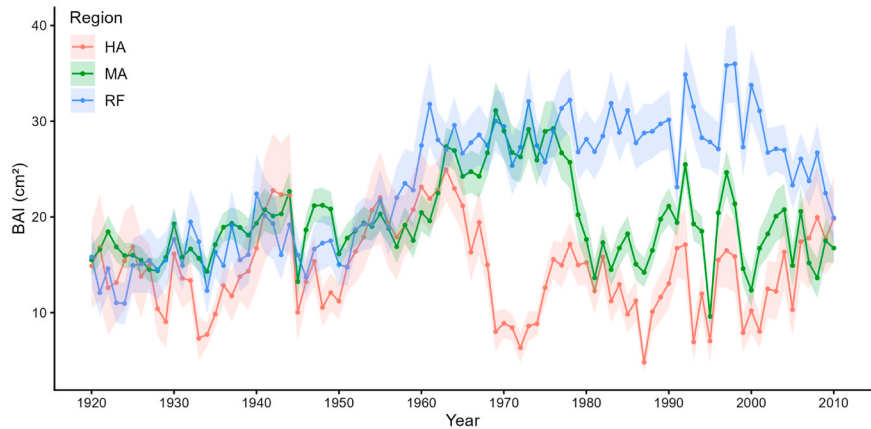


Fig. 4. Mean annual BAI of the period 1910 –2010 in the RF, MA, and HA regions. Shadows show the SE.

Table 3
Mean values of BAI, $\delta^{13}\text{C}$, iWUE and C_a sensitivity obtained in the three study regions analysed for different time periods. Data are mean values $\pm$ SE and Tukey test grouping letters among regions.

Period	BAI (cm ²)		
	HA	MA	RF
1920 – 2010	14.7 $\pm$ 0.36 ^a	19.5 $\pm$ 0.46 ^{ab}	24.3 $\pm$ 0.34 ^b
1920 – 1950	14.1 $\pm$ 0.67 ^a	17.7 $\pm$ 0.30 ^a	16.1 $\pm$ 0.51 ^a
1950 – 1980	16.4 $\pm$ 0.94 ^a	23.1 $\pm$ 0.80 ^{ab}	25.6 $\pm$ 0.87 ^b
1980 – 2010	13.1 $\pm$ 0.55 ^a	17.6 $\pm$ 0.36 ^{ab}	28.5 $\pm$ 0.55 ^b
$\delta^{13}\text{C}$ wood (‰)			
1920 – 2010	-23.3 $\pm$ 0.08 ^a	-23.3 $\pm$ 0.06 ^a	-24.0 $\pm$ 0.06 ^b
1920 – 1950	-23.0 $\pm$ 0.11 ^a	-22.9 $\pm$ 0.11 ^a	-23.7 $\pm$ 0.09 ^b
1950 – 1980	-23.1 $\pm$ 0.15 ^a	-23.1 $\pm$ 0.07 ^a	-23.7 $\pm$ 0.07 ^b
1980 – 2010	-23.7 $\pm$ 0.13 ^a	-23.9 $\pm$ 0.08 ^a	-24.5 $\pm$ 0.10 ^b
iWUE ($\mu\text{mol mol}^{-1}$)			
1920 – 2010	59.48 $\pm$ 0.69 ^a	59.37 $\pm$ 0.47 ^a	56.9 $\pm$ 0.44 ^b
1920 – 1950	53.55 $\pm$ 0.45 ^a	53.36 $\pm$ 0.47 ^a	50.6 $\pm$ 0.54 ^b
1950 – 1980	56.74 $\pm$ 0.66 ^a	57.05 $\pm$ 0.4 ^a	54.35 $\pm$ 0.41 ^b
1980 – 2010	65.71 $\pm$ 0.85 ^a	64.86 $\pm$ 0.57 ^a	62.16 $\pm$ 0.52 ^b
C_a sensitivity (ppm·ppm ⁻¹)			
1920 – 2010	0.1894 $\pm$ 0.0027 ^a	0.1892 $\pm$ 0.0020 ^a	0.1795 $\pm$ 0.0022 ^b
1920 – 1950	0.1869 $\pm$ 0.0024 ^a	0.1873 $\pm$ 0.0026 ^a	0.1744 $\pm$ 0.0027 ^b
1950 – 1980	0.1894 $\pm$ 0.0032 ^a	0.1913 $\pm$ 0.0017 ^a	0.1810 $\pm$ 0.0017 ^b
1980 – 2010	0.1913 $\pm$ 0.0033 ^a	0.1894 $\pm$ 0.0017 ^a	0.1811 $\pm$ 0.0021 ^b

moderating thermal influence of the nearby Mediterranean coast. Nevertheless, HA showed higher temperatures than the MA, reflecting the expected latitudinal influences. Besides these temperature differences, the precipitation pattern reflects a southward aridity gradient and increasingly drought conditions over the 20th century (Lazoglou et al., 2024). The three studied regions experienced a consistent rise in mean temperature, particularly during the summer, and a decline in precipitation, notably in spring, in the wettest RF and MA regions. We also detected a significant decrease in the amount of rainfall of extreme precipitation events in the HA (the 0.75 and 0.90 percentiles of total annual precipitation). These climatic trends, along with a marked increase in drought severity and frequency since the 1980s, indicate that rising temperatures and reduced precipitation are driving aridification trends across the study regions, particularly in the southernmost driest HA sites (Linares et al., 2011; Camarero et al., 2021; Lazoglou et al., 2024).

4.2. Growth and iWUE values, trends, and responses to climate

Although no significant differences in tree diameter were found among regions, tree ages and BAI differed, showing a latitudinal range with RF showing the highest growth rates, followed by MA and HA. From the 1920s to the 1960s, all regions exhibited similar BAI, although with noticeable variance. Thereafter, from the 1980s onwards, RF consistently showed higher BAI values until declining in the mid-2000s, converging with MA and HA. HA experienced a sudden growth decline in the mid-1960s and early 1970s, without a definite climate relationship. Indeed, relatively moist and cool conditions seem to prevail in this period. Nonetheless, climate analyses stated a climatic turning point since the 1970's, which does not lead to homogenous trends over north west Africa (Amraoui et al., 2011; Anchukaitis et al., 2024), while depict dry conditions since the 1980s as an extreme period within the last millennium-long context (Esper et al., 2007). Enhanced synchronization of growth patterns across regions also reflects increasingly stressful and drier conditions (Camarero et al., 2021; Maseyk et al., 2011). Under this drier scenario, Atlas cedar forests from HA might be the most vulnerable due to its older trees and genetic risk of non-adaptedness (Méndez-Cea et al., 2025; Linares et al., 2013). Besides, overgrazing exacerbates soil erosion and reduces stand regeneration in HA, further limiting tree growth (Camarero et al., 2021).

The Atlas cedar inhabits challenging landscapes where aridity and freezing temperatures co-occur as abiotic stressors, sometimes leading to the disruption of hydraulic function (Williams et al., 2013; Choat et al., 2018). Recurrent droughts and rising temperatures since the 1970s have negatively impacted Atlas cedar growth and increased drought sensitivity (Linares et al., 2011, 2013). This increase in aridity may explain the sensitivity to precipitation on HA and MA trees, whilst RF trees were negatively impacted by summer heat stress. This confirms more favorable conditions to Atlas cedar growth in RF compared with HA and MA that are translated into BAI differences and lower sensitivity to drought in the northernmost RF sites.

The trends in iWUE across the three regions revealed variations likely influenced by both C_a and changing drought conditions. The wet RF region exhibited the lowest iWUE and slightly lower sensitivity to C_a (0.18 ppm ppm⁻¹ in RF versus 0.19 ppm ppm⁻¹ MA and HA, respectively). The iWUE trends were stable from 1350 to 1800 but increased significantly after the 19th century according to rising C_a . Trees may increase carbon uptake, that is, the numerator of the A/gw quotient, at the same water cost under rising C_a , increasing iWUE (Cheng et al., 2017). Nonetheless, the theoretical iWUE scenarios showed as the best-supported model those assuming a proportional regulation of A and gw to maintain a constant C_i/C_a ratio. Further, the sensitivity of iWUE to C_a remained almost steady about 0.187 ppm ppm⁻¹ (as well as C_i/C_a about 0.72) for a dataset spanning seven centuries, contrasting to

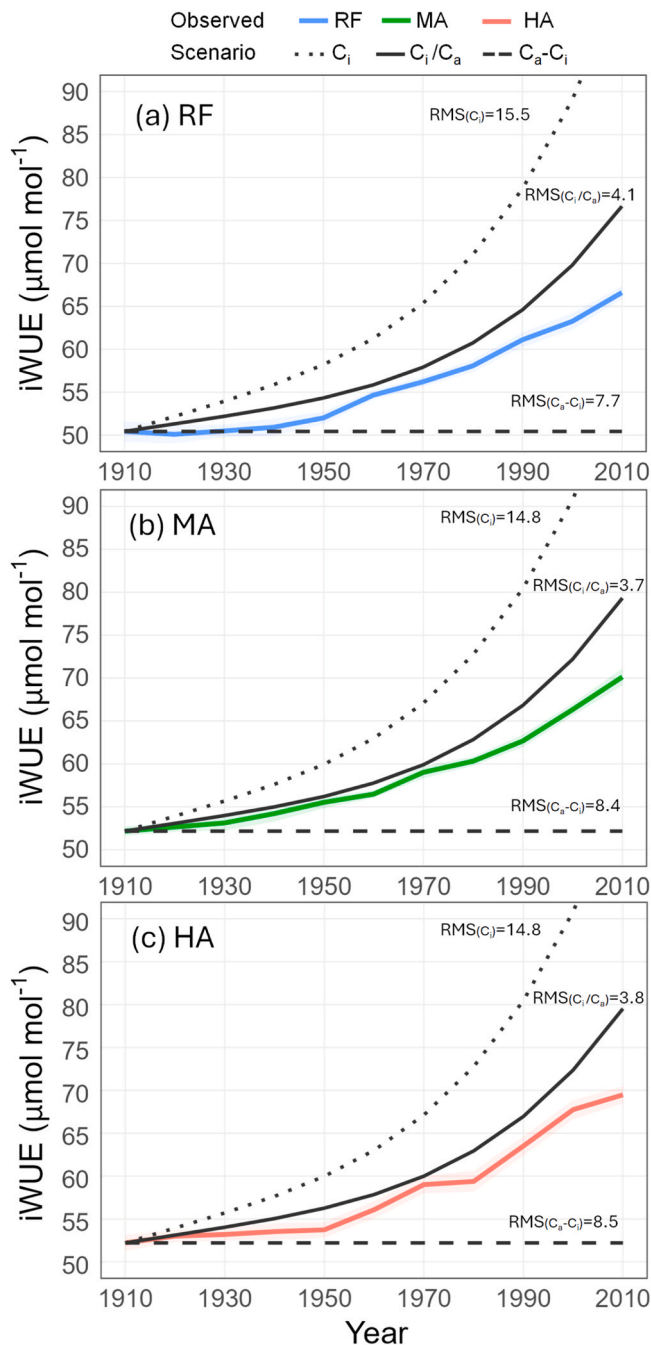


Fig. 5. Theoretical scenarios of intrinsic water-use efficiency (iWUE) obtained under the assumption of constant intercellular CO_2 concentration (C_i scenario, dotted line), constant ratio between intercellular and atmospheric CO_2 concentrations (C_i/C_a scenario, solid line), and constant difference between atmospheric and intercellular CO_2 concentrations ($C_a - C_i$ scenario, dashed line). RMS(scenario) indicates the root mean square of the predicted difference (observed minus predicted values) for each model. The starting value of C_i was the region-level C_i average of the period 1901–1910 in all scenarios.

global-scale studies that found slowing rates of change in iWUE for the 20th century (Adams et al., 2020; Gong et al., 2022). This relatively narrow and long-lasting control on the C_i/C_a ratio and $d(\text{iWUE})/d(C_a)$ suggest, consistently for the three studied regions, that Atlas cedar trees may acclimate in response to rising C_a (Saurer et al., 2004). That is, although Atlas cedar trees have responded to higher levels of atmospheric CO_2 by increasing iWUE, the response has not risen in line with increasing C_a (a constant C_i scenario). The physiological regulation of

water loss to carbon gain is a key characteristic of Atlas cedar forest function that may be central to the regional cycles of water, energy and carbon. This iWUE response must not be overestimated in our case, as we applied the model that includes the effects of diffusion through stomata and mesophyll, carboxylation, photorespiration, and non-photosynthetic fractionation. Despite we obtained lower iWUE values and C_a sensitivity, compared to previous studies, the results still support that trees are able to adjust their physiological response over time to gradually increasing C_a , which was also found in other forests from America (Puchi et al., 2021; Rodriguez-Caton et al., 2021; Szejner et al., 2021; Fajardo et al., 2019; Urrutia-Jalabert et al., 2015) Europe (Andreu-Hayles et al., 2011; Frank et al., 2015; Granda et al., 2014; Linares and Camarero, 2012; Peñuelas et al., 2008; Puchi et al., 2024; Saurer et al., 2004; Waterhouse et al., 2004), and Asia (Li et al., 2023; Weiwei et al., 2018; Lu et al., 2019; Van Der Sleen et al., 2015).

4.3. Relationships between growth and iWUE

Our results support that increased efficiency of water use does not stimulate tree growth along the aridity gradient. Increases in C_a have been accompanied by increases in drought frequency and severity, more accentuated in HA and MA (Fig. 2), and steady temperature rise, which implies that VPD increases exponentially. Both C_a and VPD rises have been experimentally related to increasing iWUE (Zhang et al., 2026). However, only the fraction of the iWUE rise driven by C_a was linked to an increase in carbon uptake, by boosting net photosynthesis, while the VPD-driven increase in iWUE showed a negative impact on tree carbon gain (Grossiord et al., 2020; Zhang et al., 2026).

Here, we demonstrate that whether an increase in iWUE leads to a concomitant increase in tree growth is highly variable among individuals (see deviation in Fig. 7), including trees showing a weak relation between iWUE and BAI, whereas others trees showed both negative and positive correlations, suggesting that tree age and size (Linares et al., 2013), soil microsite and/or stand structure might be modulating the extent to that rising iWUE translate to an equivalent stimulation of growth (Zhang et al., 2026). Water stress causes BAI inhibition by reduction of the turgor required in radially enlarging cambial cells, as well as prioritizing carbon allocation to reserve accumulation over growth (McDowell et al., 2022). Hence, soil–xylem hydraulic feedbacks may enhance drought-induced growth decline, as well as long-lasting warmer temperatures might be limiting the fraction of the carbon gain effectively allocated to growth, as autotrophic respiration becomes a more significant carbon sink (Zhang et al., 2026).

Our results support rising iWUE in all study sites, according to an almost constant C_i/C_a ratio of 0.72 and C_a sensitivity of 0.18 ppm^{-1} , supporting a significant coordination of gas-exchange processes, such biochemical acclimation and reduction of the stomatal conductance (Gong et al., 2022). However, improved iWUE was translated into a concomitant improved growth only in the moister locations (RF), while growth decline and stand-level forest dieback were observed southward (Linares et al., 2011; Camarero et al., 2021), despite a significantly higher iWUE and C_a sensitivity.

On summary, whereas C_a and drought (VPD, soil water shortage) have synergistic effects on iWUE, increasing VPD and decreasing soil water availability have a negative effect on tree growth (Pernicová et al., 2024). Furthermore, climate and iWUE might have direct and lagged effects on tree growth, as legacy effects of water availability and iWUE were more important than growing season conditions for the secondary growth of rear-edge (dry) populations of *Fagus sylvatica* (Olano et al., 2023). We conclude that mainly global C_a rise and, to a lesser extent, drought (including VPD and soil–plant hydraulics) are driving the overall iWUE increase observed, while, regarding tree growth, water shortage prevails in drought-prone sites.

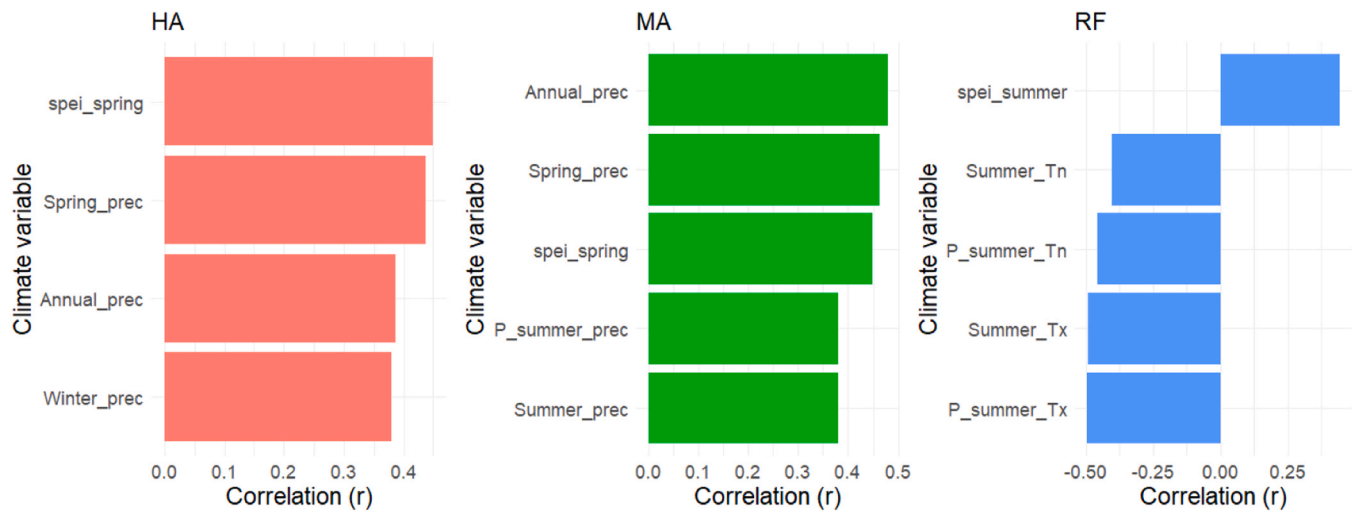


Fig. 6. Significant ($p < 0.05$) Pearson correlation coefficients (r) calculated between seasonal climate variables and annual BAI for the period 1980–2010 ($n = 30$) for Atlas cedar across three regions: HA (red bars), MA (green bars), and RF (blue bars). Previous-year climate variables are indicated with “P_”. “Tx” for maximum temperature, “Tn” for minimum temperature, “prec” for precipitation.

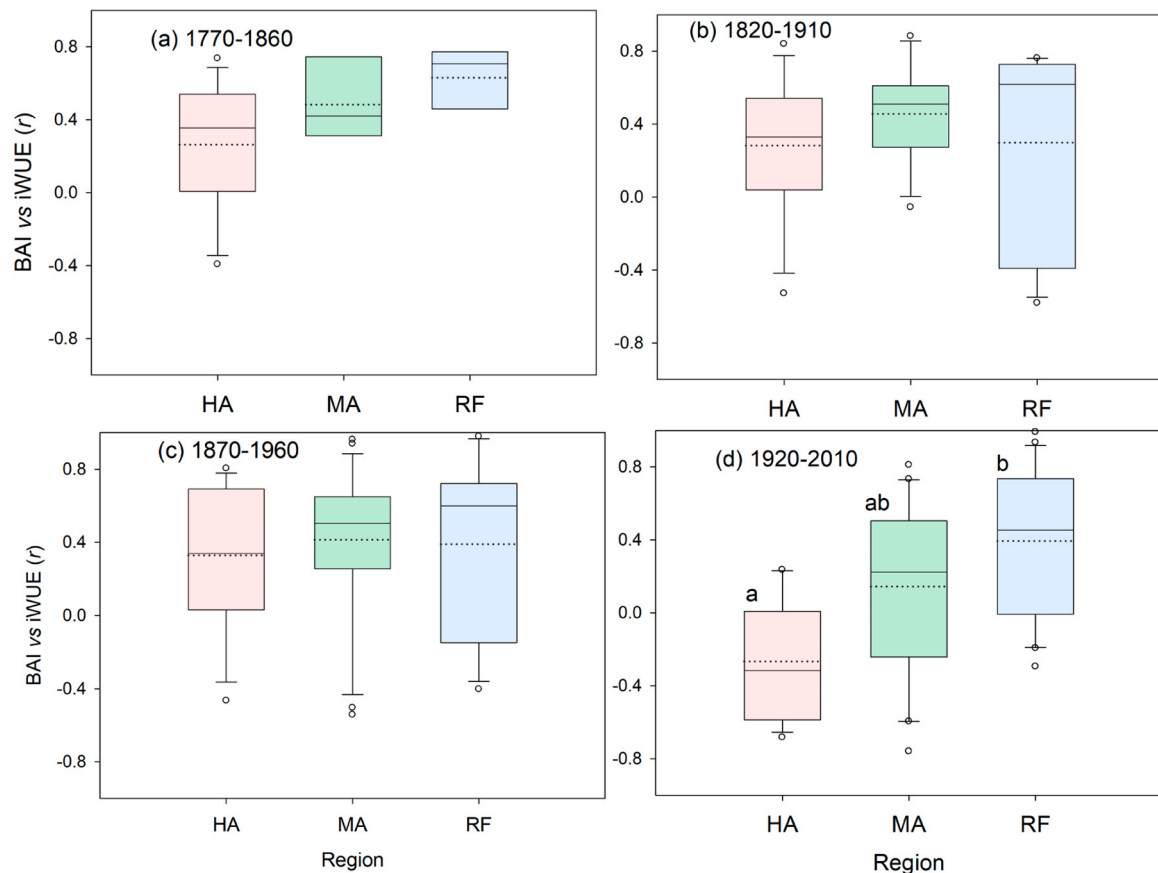


Fig. 7. Tree-level correlations between decadal values of BAI (10-years BAI averaged) and iWUE (10-years tree-rings pooled) in four 100-year periods according to key milestones of the industrial revolution (coal in 1765, gas in 1870, nuclear energy in 1969) and over the XIX and XX centuries. Rif (RF), Middle Atlas (MA) and High Atlas (HA) regions. In the box-plot figure, error bars represent the 5th/95th percentiles; boxes stand for the standard error; solid lines represent the median; dashed lines are the mean values, and points are outliers. Different letters indicate significant differences for ANOVA, $p < 0.05$ based on Tukey HSD tests.

4.4. Conservation and Management insights

Although the western Mediterranean basin has shown increasing aridity and precipitation instability over the last four millennia (Esper et al., 2007; Amraoui et al., 2011; Anchukaitis et al., 2024), the Rif

mountains have provided long-term biodiversity refugia (Cheddadi et al., 2017). The available fossil and genetic data suggest that Atlas cedar was able to cope with past climate oscillations over geological time by (1) shifting its elevation range, tracking climatic requirements, and (2) staying in microclimatic refugia, buffering regional-scale

unfavorable climate variability (Cheddadi et al., 2009, 2017; Alba-Sánchez et al., 2025). Currently, altitudinal range shifts must be unable to track the present rate of warming (Alexander et al., 2018; Ben-Said, 2022). So, priority must focus on microrefugia (Barrows et al., 2020). Local extinction risk is expected to increase in the coming decades especially at the southernmost Atlas cedar remnants (Méndez-Cea et al., 2025). Here, livestock overgrazing, logging and pollarding are the main drivers enhancing the decline of Atlas cedar forests (Camarero et al., 2021). Conservation management must limit herds and logging in the most vulnerable areas, such as the steeped slopes and the stands without cedar regeneration.

Based on genetic adaptive capacity, topographical complexity, and local climate offset, the Atlas cedar populations with the highest conservation priority are in the Rif (Cheddadi et al., 2022). Further, the Rif mountains are characterized by high species richness and endemism, supporting that it has functioned as a refugium during past episodes of environmental change (Médail and Quézel, 1999). These criteria (i.e. Atlas cedar genetic adaptive capacity, topographic suitability for microclimate, current climate offset, hotspot of biodiversity) are according to our latitudinal variation in the growth patterns, with the wettest RF region showing more favorable growth conditions, compared with the HA and MA regions, which highlights the critical role of worsen warming-related VPD and drought events southward (Lazoglou et al., 2024).

5. Conclusions

We conclude that C_a -induced iWUE rise did not translate into a significant increase in tree growth in drought-prone forests ecosystems. All the studied Atlas cedar sites increased significantly their iWUE since 1850s according to the increasing atmospheric CO_2 . Stomatal closure likely contributed to maintaining increasing iWUE during drought, while growth decline has been observed mainly since the 1980s, starting in the southernmost range limit, where forest die-off is widespread. This study provides critical insights into the complex interactions between changes in C_a , VPD and drought on the physiological regulation of water loss to carbon gain, growth and climate sensitivity of Moroccan Atlas cedar forests.

The decline in growth observed in the drier HA and MA ranges suggests that rising temperatures and the increasing frequency of extreme droughts outweigh the benefits of C_a , stated by iWUE enhancement. These findings contribute to filling gaps regarding potential fertilization effects in drought-stressed environments, providing a foundation for future studies aimed at understanding the broader impacts of climate change on Mediterranean-mountain forests ecosystems.

CRedit authorship contribution statement

Víctor Lechuga: Writing – review & editing, Software, Methodology, Investigation, Formal analysis, Data curation. **Victoria Ochoa:** Writing – review & editing, Software, Methodology, Investigation, Formal analysis, Data curation. **Juan Carlos Linares:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Juan Pablo Crespo-Antia:** Writing – review & editing, Writing – original draft, Validation, Software, Investigation, Formal analysis, Data curation. **J. Julio Camarero:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Gabriel Sangüesa-Barreda:** Writing – review & editing, Validation, Software, Methodology, Investigation, Formal analysis, Data curation.

Declaration of Competing 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.

Acknowledgments

Funding for open access publishing: Universidad Pablo de Olavide/CBUA. This study was financially supported by the Agencia Española de Cooperación Internacional para el Desarrollo, grant number: A/024752/09, A/030763/10; European Regional Development Fund (ERDF), “Programa Operativo de Cooperación Transfronteriza España-Fronteras Exteriores”, grant number: 0087_TRANSHABITAT_2.E. We thank Lahcen Taïqui for his help in the field and formal procedures. We thank the Department of Water and Forests of the Morocco Govt. for granting sampling permissions.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123862.

Data availability

Data will be made available on request.

References

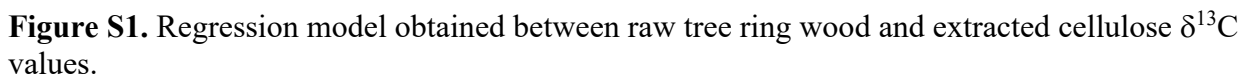
- Abatzoglou, J., Dobrowski, S., Parks, S., et al., 2018. TerraClimate, a high-resolution global dataset of monthly climate and climatic water balance from 1958 to 2015. *Sci. Data* 5, 170191. <https://doi.org/10.1038/sdata.2017.191>.
- Adams, M.A., Buckley, T.N., Turnbull, T.L., 2020. Diminishing CO_2 -driven gains in water-use efficiency of global forests. *Nat. Clim. Change* 10 (5), 466–471. <https://doi.org/10.1038/s41558-020-0747-7>.
- Alba-Sánchez, F., Abel-Schaad, D., Iriarte, E., López-Sáez, J., Cheddadi, A., Pérez-Díaz, R., González-Hernández, A. S., 2025. Postglacial dynamics of *Cedrus atlantica* in North African montane forests: A paleoecological perspective on a Mediterranean conifer. *Quat. Sci. Rev.* 370, 109633. <https://doi.org/10.1016/j.quascirev.2025.109633>.
- Alexander, J.M., Chalmers, L., Lenoir, J., Burgess, T.I., Essl, F., Haider, S., Kueffer, C., McDougall, K., Milbau, A., Nuñez, M.A., Pauchard, A., Rabitsch, W., Rew, L.J., Sanders, N.J., Pellissier, L., 2018. Lags in the response of mountain plant communities to climate change. *Glob. Change Biol.* 24, 563–579. <https://doi.org/10.1111/gcb.13976>.
- Amraoui, L., Sarr, M.A., Soto, D., 2011. Analyse rétrospective de l'évolution climatique récente en Afrique du Nord-Ouest. *Physio-Géo* 5, 125–142. <https://doi.org/10.4000/physio-geo.1959>.
- Anchukaitis, K.J., Touchan, R., Meko, D.M., Kherchouche, D., Slimani, S., Sivrikaya, F., Ilmen, R., Mitsopoulos, I., Stephan, J., Attieh, J., Hasnaoui, F., Camarero, J.J., Sánchez-Salguero, R., Guibal, F., Piermattei, A., Christou, A., Krcmaric, J., Cook, B.I., 2024. Enhancing spatiotemporal paleoclimate reconstructions of hydroclimate across the Mediterranean over the last millennium. *Clim. Dyn.* 62 (6), 5351–5371. <https://doi.org/10.1007/s00382-024-07166-6>.
- Anderegg, W.R.L., Kane, J.M., Anderegg, L.D.L., 2013. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Change* 3 (1), 30–36. <https://doi.org/10.1038/nclimate1635>.
- Anderegg, W.R.L., Schwalm, C., Biondi, F., Camarero, J.J., Koch, G., Litvak, M., Ogle, K., Shaw, J.D., Shevliakova, E., Williams, A.P., Wolf, A., Ziaco, E., Pacala, S., 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349 (6247), 528–532. <https://doi.org/10.1126/science.aab1833>.
- Andreu-Hayles, L., Planells, O., Gutiérrez, E., Muntan, E., Helle, G., Anchukaitis, K.J., Schleser, G.H., 2011. Long tree-ring chronologies reveal 20th century increases in water-use efficiency but no enhancement of tree growth at five Iberian pine forests. *Glob. Change Biol.* 17 (6), 2095–2112. <https://doi.org/10.1111/j.1365-2486.2010.02373.x>.
- Barrows, C.W., Ramirez, A.R., Sweet, L.C., Morelli, T.L., Millar, C.I., Frakes, N., Rodgers, J., Mahalovich, M.F., 2020. Validating climate-change refugia: Empirical bottom-up approaches to support management actions. *Front. Ecol. Environ.* 18 (5), 298–306.
- Beguier, S., & Vicente-Serrano, S.M. (2023). *SPEI: Calculation of the Standardized Precipitation-Evapotranspiration Index* (Version R package version 1.8.1) [Computer software]. (<https://CRAN.R-project.org/package=SPEI>).
- Belmecheri, S., Laverne, A., 2020. Compiled records of atmospheric CO_2 concentrations and stable carbon isotopes to reconstruct climate and derive plant ecophysiological indices from tree rings. *Dendrochronologia* 63, 125748.
- Benabid, A., 1994. Biogéographie phytosociologie et phytodynamique des cédraies de l'Atlas (*Cedrus atlantica*, Manetti). In *Le cèdre de l'Atlas*. Actes du séminaire international sur le cèdre de l'Atlas. Annales Recherche Forestière au Maroc, pp. 62–76.

- Ben-Said, M., 2022. Upward Shifts of Species Range in mediterranean High-Mountain forests Under Current Climate change: A Review. *Biol. Environ. Proc. R. Ir. Acad.* 122 (1), 39–52. <https://doi.org/10.1353/bae.2022.0002>.
- Ben-Said, M., Linares, J.C., Carreira, J.A., Taïqui, L., 2022. Spatial patterns and species coexistence in mixed *Abies marocana*-*Cedrus atlantica* forest in Talasemtanne National Park. *Ecol. Manag.* 506, 119967. <https://doi.org/10.1016/j.foreco.2021.119967>.
- Brooks, A., Farquhar, G.D., 1985. Effect of temperature on the CO₂/O₂ specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. *Planta* 165, 397–406.
- Camarero, J.J., Sánchez-Salguero, R., Sangüesa-Barreda, G., Lechuga, V., Viñeña, B., Seco, J.I., Taïqui, L., Carreira, J.A., Linares, J.C., 2021. Drought, axe and goats. More variable and synchronized growth forecasts worsening dieback in Moroccan Atlas cedar forests. *Sci. Total Environ.* 765, 142752. <https://doi.org/10.1016/j.scitotenv.2020.142752>.
- Caudullo, G., 2024. *Chorological data for the main European woody species* [Dataset]. Mendeley Data. <https://doi.org/10.17632/HR5H2HCGG4.18>.
- Cheddadi, R., Fady, B., François, L., Hajar, L., Suc, J.P., Huang, K., Demarteau, M., Vendramin, G.G., Ortu, E., 2009. Putative glacial refugia of *Cedrus atlantica* deduced from Quaternary pollen records and modern genetic diversity. *J. Biogeogr.* 36, 1361–1371. <https://doi.org/10.1111/j.1365-2699.2008.02063.x>.
- Cheddadi, R., Henrot, A.J., François, L., Boyer, F., Bush, M., Carré, M., Coissac, E., De Oliveira, P.E., Ficot, F., Hambuckers, A., Huang, K., Lézine, A.M., Nourelbait, M., Rhoujjati, A., Taberlet, P., Sarmiento, F., Abel-Schaad, D., Alba-Sanchez, F., Zheng, Z., Huang, K., 2017. Microrefugia, climate change, and conservation of *Cedrus atlantica* in the Rif Mountains, Morocco. *Front. Ecol. Evol.* 5, 114. <https://doi.org/10.3389/fevo.2017.00114>.
- Cheddadi, R., Taberlet, P., Boyer, F., Coissac, E., Rhoujjati, A., Urbach, D., Remy, C., Khater, C., Antry, S., Aoudjad, J., et al., 2022. Priority conservation areas for *Cedrus atlantica* in the Atlas Mountains, Morocco. *Conserv. Sci. Pr.* 4, 12680. <https://doi.org/10.1111/csp2.12680>.
- Cheng, L., Zhang, L., Wang, Y.-P., Canadell, J.G., Chiew, F.H.S., Beringer, J., Li, L., Miralles, D.G., Piao, S., Zhang, Y., 2017. Recent increases in terrestrial carbon uptake at little cost to the water cycle. *Nat. Commun.* 8 (1), 110. <https://doi.org/10.1038/s41467-017-00114-5>.
- Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., Lopez, R., Medlyn, B.E., 2018. Triggers of tree mortality under drought. *Nature* 558, 531–539.
- De Frenne, P., Graae, B.J., Rodríguez-Sánchez, F., Kolb, A., Chabrierie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., Eriksson, O., Gruwez, R., Hermy, M., Lenoir, J., Plue, J., Coomes, D.A., Verheyen, K., 2013. Latitudinal gradients as natural laboratories to infer species' responses to temperature. *J. Ecol.* 101 (3), 784–795. <https://doi.org/10.1111/1365-2745.12074>.
- Esper, J., Frank, D., Büntgen, U., Verstege, A., Luterbacher, J., Xoplaki, E., 2007. Long-term drought severity variations in Morocco. *Geophys. Res. Lett.* 34 (17), 2007GL030844. <https://doi.org/10.1029/2007GL030844>.
- Fajardo, A., Gazol, A., Mayr, C., Camarero, J.J., 2019. Recent decadal drought reverts warming-triggered growth enhancement in contrasting climates in the southern Andes tree line. *J. Biogeogr.* 46 (7), 1367–1379. <https://doi.org/10.1111/jbi.13580>.
- Farquhar, G., O'Leary, M., Berry, J., 1982. On the Relationship Between Carbon Isotope Discrimination and the Inter-cellular Carbon Dioxide Concentration in Leaves. *Funct. Plant Biol.* 9 (2), 121. <https://doi.org/10.1071/PP9820121>.
- Ferrio, J.P., Voltas, J., 2005. Carbon and oxygen isotope ratios in wood constituents of *Pinus halepensis* as indicators of precipitation, temperature and vapour pressure deficit. *Tellus B Chem. Phys. Meteorol.* 57 (2), 164. <https://doi.org/10.3402/tellusb.v57i2.16780>.
- Forzieri, G., Dakos, V., McDowell, N.G., Ramdane, A., Cescatti, A., 2022. Emerging signals of declining forest resilience under climate change. *Nature* 608 (7923), 534–539. <https://doi.org/10.1038/s41586-022-04959-9>.
- Francey, R.J., Allison, C.E., Etheridge, D.M., Trudinger, C.M., Enting, I.G., Leuenberger, M., Langenfelds, R.L., Michel, E., Steele, L.P., 1999. A 1000-year high precision record of delta13C in atmospheric CO₂. *Tellus B* 51 (2), 170–193. <https://doi.org/10.1034/j.1600-0889.1999.t01-1-00005.x>.
- Frank, D.C., Poulter, B., Saurer, M., Esper, J., Huntingford, C., Helle, G., Treydte, K., Zimmermann, N.E., Schleser, G.H., Ahlström, A., Ciais, P., Friedlingstein, P., Levis, S., Lomas, M., Sitch, S., Viovy, N., Andreu-Hayles, L., Bednarz, Z., Berninger, F., Weigl, M., 2015. Water-use efficiency and transpiration across European forests during the Anthropocene. *Nat. Clim. Change* 5 (6), 579–583. <https://doi.org/10.1038/nclimate2614>.
- Gimeno, T.E., McVicar, T.R., O'Grady, A.P., Tissue, D.T., Ellsworth, D.S., 2018. Elevated CO₂ did not affect the hydrological balance of a mature native *Eucalyptus* woodland. *Glob. Change Biol.* 24 (7), 3010–3024. <https://doi.org/10.1111/gcb.14139>.
- NOAA Global Monitoring Laboratory (GML), 2024. Atmospheric CO₂ and δ13C data. <https://gml.noaa.gov/> (accessed March 2026).
- Gong, X.Y., Ma, W.T., Yu, Y.Z., Fang, K., Yang, Y., Tcherkez, G., Adams, M.A., 2022. Overestimated gains in water-use efficiency by global forests. *Glob. Change Biol.* 28, 4923–4934.
- Granda, E., Rossatto, D.R., Camarero, J.J., Voltas, J., Valladares, F., 2014. Growth and carbon isotopes of Mediterranean trees reveal contrasting responses to increased carbon dioxide and drought. *Oecologia* 174 (1), 307–317. <https://doi.org/10.1007/s00442-013-2742-4>.
- Grossiord, C., et al., 2020. Plant responses to rising vapor pressure deficit. *New Phytol.* 226, 1550–1566. Grossiord, C. et al. (2020). Plant responses to rising vapor pressure deficit. *N. Phytol.* 226, 1550–1566.
- Harris, I.C., Jones, P.D., Osborn, T., 2023. CRU TS4. 07 Clim. Res. Unit. (CRU) Time-Ser. (TS) Version 4. 07 High. -Resolut. gridded data Mon. -Mon. Var. Clim. (Jan. 1901-Dec. 2022). <https://catalogue.ceda.ac.uk/uuid/5fda109ab71947b6b7724077bf7eb753>.
- Holmes, R.L., 1983. *Comput. -Assist. Qual. Control tree-ring Dating Meas.* 43, 69–78.
- Keenan, T., Hollinger, D., Bohrer, G., et al., 2013. Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature* 499, 324–327. <https://doi.org/10.1038/nature12291>.
- Klesse, S., Bigler, C., 2025. Growth trends in basal area increments: The underlying problem, consequences for research and best practices. *Dendrochronologia* 90, 126296. <https://doi.org/10.1016/j.dendro.2025.126296>.
- Koenker, R., 2024. quantreg: Quantile Regression (Version 5.98) [R package]. CRAN. <https://CRAN.R-project.org/package=quantreg>.
- Laffitte, B., Seyler, B.C., Li, P., Ha, Z., Tang, Y., 2023. Using tree rings to detect a CO₂ fertilization effect: A global review. *Trees* 37 (5), 1299–1314. <https://doi.org/10.1007/s00468-023-02438-w>.
- Larsson, L., 2022. *CDendro & CooRecorder program package* (Version 9.8.1) [Computer software]. Cybis. <https://www.cybis.se/forfun/dendro/>.
- Lazoglou, G., Papadopoulos-Zachos, A., Georgiades, P., et al., 2024. Identification of climate change hotspots in the Mediterranean. *Sci. Rep.* 14, 29817. <https://doi.org/10.1038/s41598-024-80139-1>.
- Leavitt, S.W., Danzer, S.R., 1993. Method for batch processing small wood samples to holocellulose for stable-carbon isotope analysis. *Anal. Chem.* 65 (1), 87–89. <https://doi.org/10.1021/ac00049a017>.
- Li, Y., Xu, C., Huang, Y., Huo, X., Shi, F., Pan, Y., Ren, L., Wu, X., 2023. Tree growth and intrinsic water use efficiency of Chinese pine plantations along a precipitation gradient in northern China. *For. Ecol. Manag.* 528, 120609. <https://doi.org/10.1016/j.foreco.2022.120609>.
- Linares, J.C., Camarero, J.J., 2012. From pattern to process: Linking intrinsic water-use efficiency to drought-induced forest decline. *Glob. Change Biol.* 18 (3), 1000–1015. <https://doi.org/10.1111/j.1365-2486.2011.02566.x>.
- Linares, J.C., Taïqui, L., Camarero, J.J., 2011. Increasing Drought Sensitivity and Decline of Atlas Cedar (*Cedrus atlantica*) in the Moroccan Middle Atlas Forests. *Forests* 2 (3), 777–796. <https://doi.org/10.3390/f2030777>.
- Linares, J.C., Taïqui, L., Sangüesa-Barreda, G., Seco, J.I., Camarero, J.J., 2013. Age-related drought sensitivity of Atlas cedar (*Cedrus atlantica*) in the Moroccan Middle Atlas forests. *Dendrochronologia* 31 (2), 88–96. <https://doi.org/10.1016/j.dendro.2012.08.003>.
- Lloyd, J., Farquhar, G.D., 1994. ¹³C discrimination during CO₂ assimilation by the terrestrial biosphere. *Oecologia* 99 (3–4), 201–215.
- Lockwood, B.R., Maxwell, J.T., Robeson, S.M., Au, T.F., 2021. Assessing bias in diameter at breast height estimated from tree rings and its effects on basal area increment and biomass. *Dendrochronologia* 67, 125844. <https://doi.org/10.1016/j.dendro.2021.125844>.
- Lu, K., Chen, N., Zhang, X., Wang, J., Wang, M., Khan, S., Han, C., Zhang, C., Wang, S., Wang, L., Gao, W., Liu, Y., Zhao, C., 2019. Increased drought and atmospheric CO₂ positively impact intrinsic water use efficiency but do not promote tree growth in semi-arid areas of northwestern China. *Trees* 33 (3), 669–679. <https://doi.org/10.1007/s00468-018-1807-8>.
- Ma, W.T., Tcherkez, G., Wang, X.M., Schäufele, R., Schnyder, H., Yang, Y., Gong, X.Y., 2021. Accounting for mesophyll conductance substantially improves 13C-based estimates of intrinsic water-use efficiency. *New. Phytol.* 229 (3), 1326–1338. <https://doi.org/10.1111/nph.16958>.
- Maseyk, K., Hemming, D., Angert, A., Leavitt, S.W., Yakir, D., 2011. Increase in water-use efficiency and underlying processes in pine forests across a precipitation gradient in the dry Mediterranean region over the past 30 years. *Oecologia* 167 (2), 573–585. <https://doi.org/10.1007/s00442-011-2010-4>.
- McCarroll, D., Loader, N.J., 2004. Stable isotopes in tree rings. *Quat. Sci. Rev.* 23 (7–8), 771–801. <https://doi.org/10.1016/j.quascirev.2003.06.017>.
- McDowell, N.G., Sapes, G., Pivovarov, A., et al., 2022. Mechanisms of woody-plant mortality under rising drought, CO₂ and vapour pressure deficit. *Nat. Rev. Earth Environ.* 3, 294–308. <https://doi.org/10.1038/s43017-022-00272-1>.
- Médail, F., Quézel, P., 1999. Biodiversity Hotspots in the Mediterranean Basin: Setting Global Conservation Priorities. *Conserv. Biol.* 13, 1510–1513. <https://doi.org/10.1046/j.1523-1739.1999.98467.x>.
- Méndez-Cea, B., García-García, I., Manso-Martínez, D., Linares, J.C., Gallego, F.J., Horreo, J.L., 2025. Genetic Diversity and Risk of Non-Adaptedness in Natural North Moroccan and Planted South Spanish Atlas Cedar. *Forests* 16 (9), 1434. <https://doi.org/10.3390/f16091434>.
- Olano, J.M., Sangüesa-Barreda, G., García-López, M.A., García-Hidalgo, M., Rozas, V., García-Cervigón, A.I., Delgado-Huertas, A., Hernández-Alonso, H., 2023. Water use efficiency and climate legacies dominate beech growth at its rear edge. *J. Ecol.* 111 (10), 2160–2171. <https://doi.org/10.1111/1365-2745.14164>.
- Peñuelas, J., Hunt, J.M., Ogaya, R., Jump, A.S., 2008. Twentieth century changes of tree-ring δ¹³C at the southern range-edge of *Fagus sylvatica*: increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. *Glob. Change Biol.* 14 (5), 1076–1088. <https://doi.org/10.1111/j.1365-2486.2008.01563.x>.
- Peñuelas, J., Canadell, J.G., Ogaya, R., 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth: Tree growth in the 20th century. *Glob. Ecol. Biogeogr.* 20 (4), 597–608. <https://doi.org/10.1111/j.1466-8238.2010.00608.x>.
- Pernicová, N., Urban, O., Čáslavský, J., Kolář, T., Rybníček, M., Sochová, I., Peñuelas, J., Bošefa, M., Trnka, M., 2024. Impacts of elevated CO₂ levels and temperature on photosynthesis and stomatal closure along an altitudinal gradient are counteracted by the rising atmospheric vapor pressure deficit. *Sci. Total Environ.* 921, 171173. <https://doi.org/10.1016/j.scitotenv.2024.171173>.

- Pohlert, T. (2023). trend: Non-Parametric Trend Tests and Change-Point Detection (Versión 1.1.6) [R package]. CRAN. (<https://CRAN.R-project.org/package=trend>).
- Puchi, P.F., Camarero, J.J., Battipaglia, G., Carrer, M., 2021. Retrospective analysis of wood anatomical traits and tree-ring isotopes suggests site-specific mechanisms triggering *Araucaria araucana* drought-induced dieback. *Glob. Change Biol.* 27 (24), 6394–6408. <https://doi.org/10.1111/gcb.15881>.
- Puchi, P.F., Dalmonech, D., Vangi, E., et al., 2024. Contrasting patterns of water use efficiency and annual radial growth among European beech forests along the Italian peninsula. *Sci. Rep.* 14, 6526. <https://doi.org/10.1038/s41598-024-57293-7>.
- R Core Team, 2024. *R: A Language and Environment for Statistical Computing* (Version 4.4.1) [Computer software]. R. Found. Stat. Comput. (<https://www.R-project.org/>).
- Robertson, I., Leavitt, S.W., Loader, N.J., Buhay, W., 2008. Progress in isotope dendroclimatology. *Chem. Geol.* 252 (1–2), EX1–EX4. [https://doi.org/10.1016/S0009-2541\(08\)00177-0](https://doi.org/10.1016/S0009-2541(08)00177-0).
- Rodriguez-Caton, M., Andreu-Hayles, L., Morales, M.S., Daux, V., Christie, D.A., Coopman, R.E., Alvarez, C., Rao, M.P., Aliste, D., Flores, F., Villalba, R., 2021. Different climate sensitivity for radial growth, but uniform for tree-ring stable isotopes along an aridity gradient in *Polylepis tarapacana*, the world's highest elevation tree species. *Tree Physiol.* 41 (8), 1353–1371. <https://doi.org/10.1093/treephys/tpab021>.
- Sarmoun, M., Camarero, J.J., Abdoun, F., 2024. Aridification increases growth resistance of Atlas cedar forests in NW Algeria. *For. Ecol. Manag.* 556, 121730. <https://doi.org/10.1016/j.foreco.2024.121730>.
- Saurer, M., Siegwolf, R.T.W., Schweingruber, F.H., 2004. Carbon isotope discrimination indicates improving water-use efficiency of trees in northern Eurasia over the last 100 years. *Glob. Change Biol.* 10 (12), 2109–2120. <https://doi.org/10.1111/j.1365-2486.2004.00869.x>.
- Shestakova, T.A., Camarero, J.J., Ferrio, J.P., Knorre, A.A., Gutiérrez, E., Voltas, J., 2017. Increasing drought effects on five European pines modulate $\Delta^{13}\text{C}$ -growth coupling along a Mediterranean altitudinal gradient. *Funct. Ecol.* 31 (7), 1359–1370. <https://doi.org/10.1111/1365-2435.12857>.
- Urrutia-Jalabert, R., Malhi, Y., Barichivich, J., Lara, A., Delgado-Huertas, A., Rodríguez, C.G., Cuq, E., 2015. Increased water use efficiency but contrasting tree growth patterns in *Fitzroya cupressoides* forests of southern Chile during recent decades. *J. Geophys. Res. Biogeosciences* 120 (12), 2505–2524. <https://doi.org/10.1002/2015JG003098>.
- Van Der Sleen, P., Groenendijk, P., Vlam, M., Anten, N.P.R., Boom, A., Bongers, F., Pons, T.L., Terburg, G., Zuidema, P.A., 2015. No growth stimulation of tropical trees by 150 years of CO₂ fertilization but water-use efficiency increased. *Nat. Geosci.* 8 (1), 24–28. <https://doi.org/10.1038/ngeo2313>.
- Waterhouse, J.S., Switsur, V.R., Barker, A.C., Carter, A.H.C., Hemming, D.L., Loader, N.J., Robertson, I., 2004. Northern European trees show a progressively diminishing response to increasing atmospheric carbon dioxide concentrations. *Quat. Sci. Rev.* 23 (7–8), 803–810. <https://doi.org/10.1016/j.quascirev.2003.06.011>.
- Weiwei, L.U., Xinxiao, Y.U., Guodong, J.I.A., Hanzhi, L.I., Ziqiang, L.I.U., 2018. Responses of Intrinsic Water-use Efficiency and Tree Growth to Climate Change in Semi-Arid Areas of North China. *Sci. Rep.* 8 (1), 308. <https://doi.org/10.1038/s41598-017-18694-z>.
- Williams, A., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E. R., Gangadagamage, C., Cai, M., McDowell, N.G., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change* 3 (3), 292–297. <https://doi.org/10.1038/nclimate1693>.
- Yu, K., et al., 2024. Reconciling the tree-ring-based and leaf-level-based intrinsic water-use efficiency. *N. Phytol.* 244 (6), 2225–2238. <https://doi.org/10.1111/nph.20170>.
- Zhang, Q., Zhang, J., Adams, M.A., et al., 2026. Increased efficiency of water use does not stimulate tree productivity. *Nat. Clim. Chang* 16, 87–94. <https://doi.org/10.1038/s41558-025-02504-w>.

Supplementary Materials

Drought overrides CO₂-driven carbon sink enhancement in Moroccan Atlas cedar forests



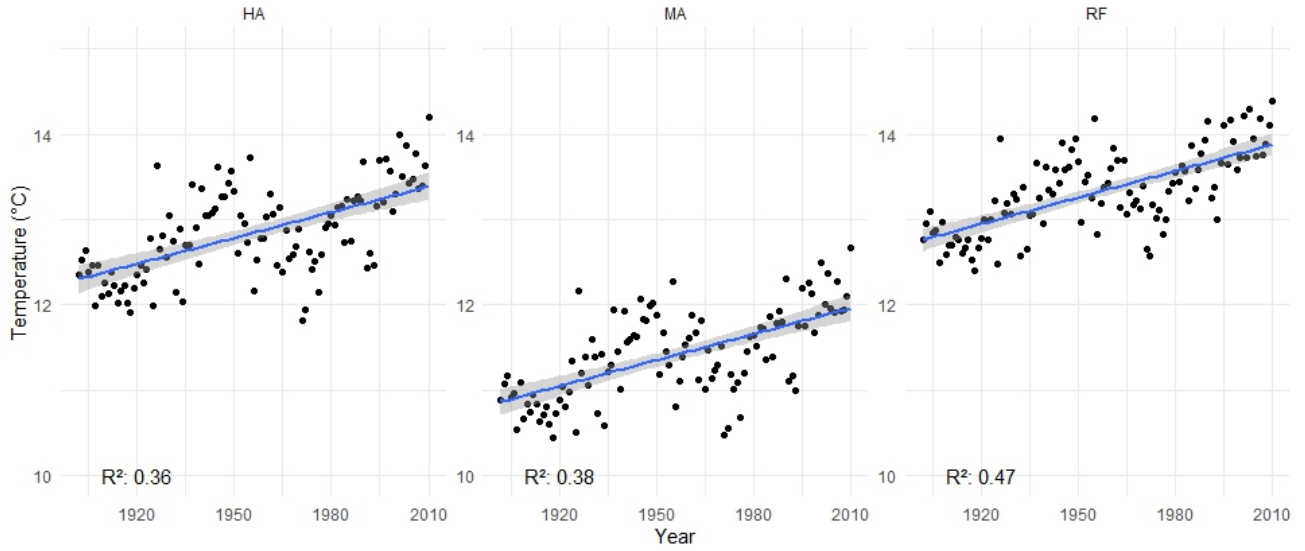


Figure S2. Trends of mean annual temperature (1902-2010) in the High Atlas (HA), Middle Atlas (MA) and Rif (RF) regions. The blue lines represent linear regressions. The three regressions were statistically significant ($p < 0.01$); R^2 values are indicated as bottom inset.

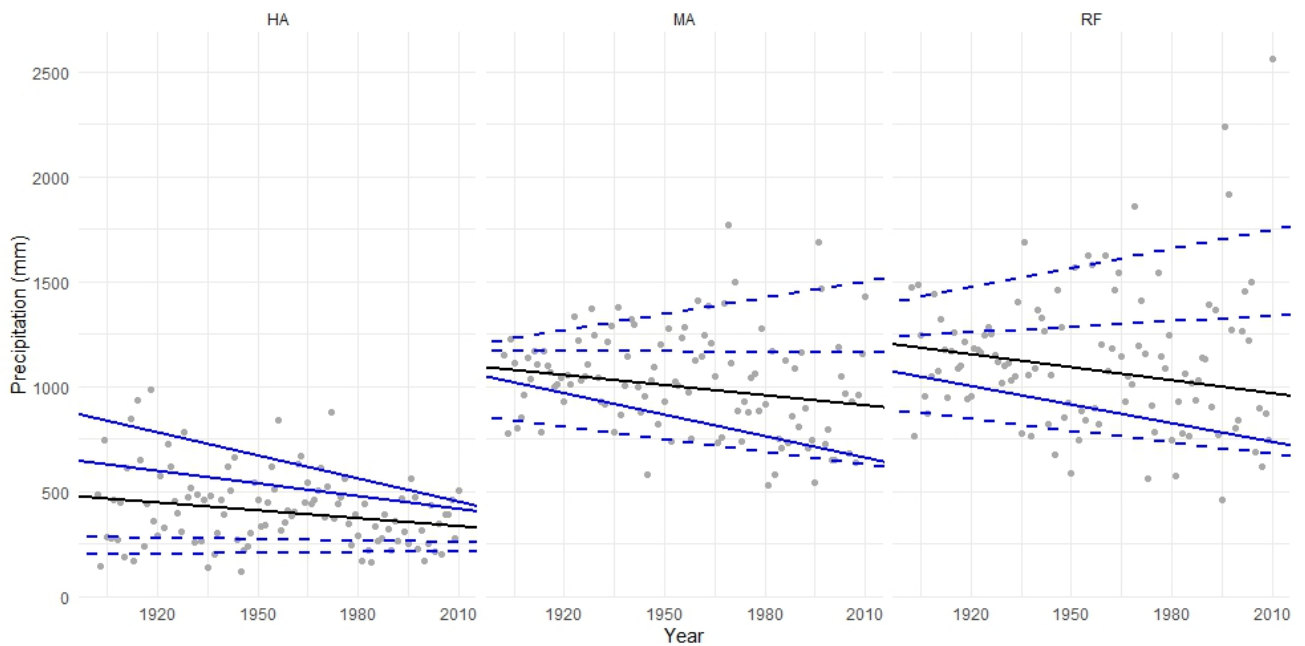


Figure S3. Quantile regression of precipitation (1902-2010) in the High Atlas (HA), Middle Atlas (MA) and Rif (RF) regions. Black lines represent the mean total annual precipitation, which was tested by Mann-Kendall test (0.5 quantile regression). Blue lines indicate 0.10, 0.25, 0.75, and 0.90 quantile regressions, with dashed lines representing non-significant trends and solid lines representing significant trends, respectively.



Figure S4. Heatmap of the frequency of annual and seasonal drought events (SPEI values below -1) in High Atlas (HA), Middle Atlas (MA) and Rif (RF) regions. Darker shades indicate higher frequency of drought events. Facets represent different seasons.

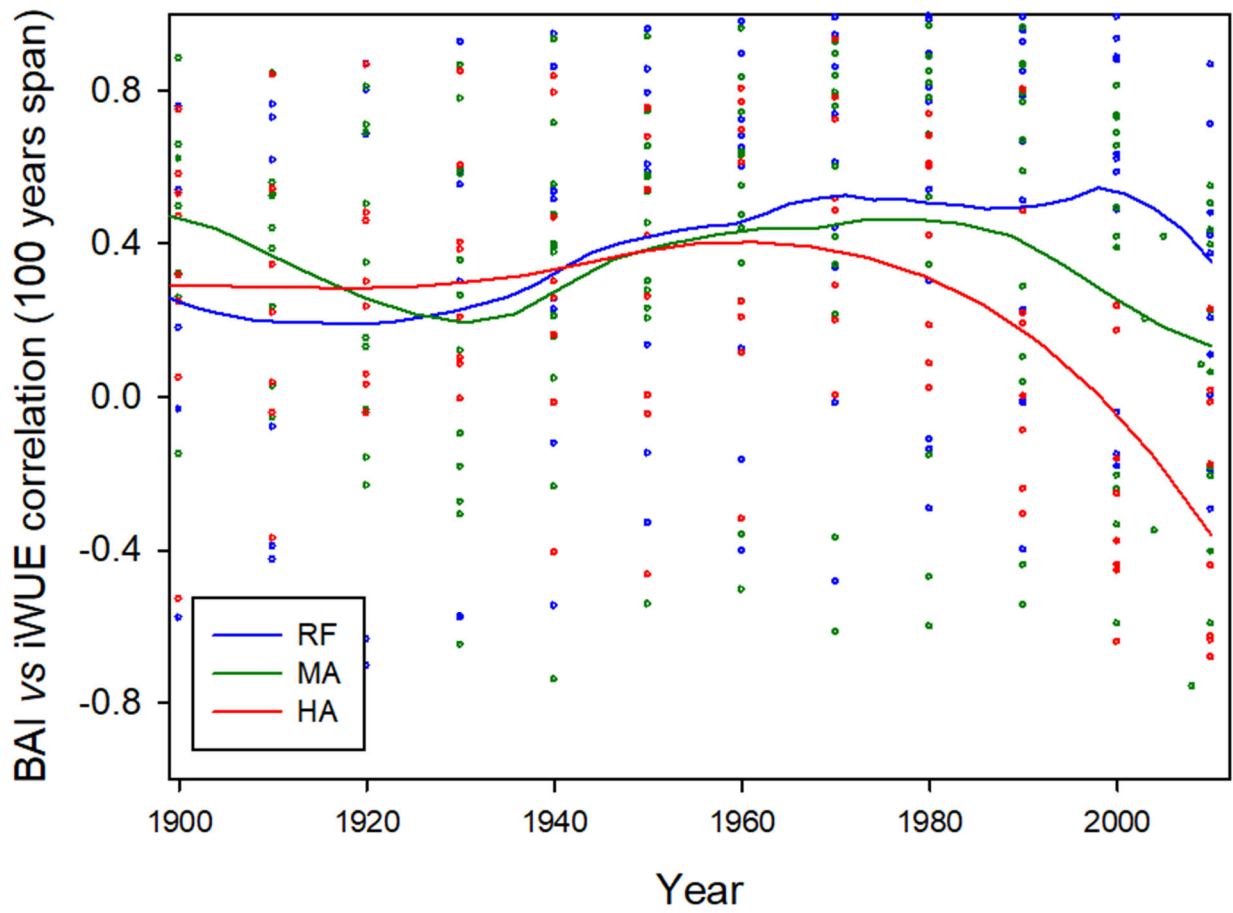


Figure S5. Running correlations calculated between decadal BAI and iWUE in High Atlas (HA), Middle Atlas (MA) and Rif (RF) study regions. Dots are individuals in each region and the lines represent the mean regional correlation.