

Site-contingent responses to drought of core and relict *Tetraclinis articulata* populations from Morocco and Spain

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ABSTRACT

The growth responses to climate variability are still unknown in locally threatened conifers from dry regions, but this information is necessary for improving the conservation of relict populations under increasing aridification. We characterized the radial growth patterns and responses to climate of *Tetraclinis articulata*, a Cupressaceae tree endemic to the western Mediterranean Basin, in a relict population located in southwestern Spain (Doñana) and two populations from the northern Morocco where the species core habitat is found (Tétouan, Ifarten). We assessed climate-growth relationships by using tree-ring width, climate data, drought and North Atlantic Oscillation (NAO) indices. Climate-growth analyses were refined using the *climwin* R package to select the most informative statistical models. The main climatic constraints of growth were inferred by using the process-based Vaganov-Shashkin (VS) model explicitly considering non-linear climate-growth relationships. *Tetraclinis articulata* growth was favored by wet conditions from the prior autumn to the spring of the growth year. In Doñana, warmer May conditions led to growth decline but this negative effect could be reversed by wet-warm conditions in the prior late autumn. Growth in the two Moroccan sites was constrained by 6- to 18-month long droughts peaking in summer, which account for cumulative water deficit since the previous autumn. Winter and early spring precipitation were the main climate drivers of growth in the Moroccan *T. articulata* populations, and their year-to-year variability was linked to the NAO. The VS model simulations showed that *T. articulata* growth is enhanced by wet soil conditions in late winter and early spring, probably recharging shallow soil water pools. The VS model also confirmed that warmer spring-summer conditions could amplify drought stress and threaten the long-term persistence of the relict Doñana population.

1. Introduction

Africa is the most arid continent since drylands cover 75% of its surface, representing 15% of the world drylands area (Práválie, 2016). For instance, in Saharan countries such as Morocco 90% of the total surface corresponds to arid- and semi-arid drylands (FAO, 2016). In the whole western Mediterranean Basin, climate warming is projected to rise the frequency of severe droughts amplifying water scarcity (Koutroulis, 2019). There is also evidence of strong drying trends over the Maghreb in recent decades (Hoerling et al., 2012). Such aridification trends and punctual severe droughts reduce forest productivity and tree

growth and increase tree mortality (Camarero et al., 2015, 2020a), slowing down forest cover recovery in landscapes characterized by historical overexploitation and desertification (Kouba et al., 2018; Camarero et al., 2021). These climate trends have been related to a northward shift of the North Atlantic storm track leading to increasing anticyclonic activity (Giorgi and Lionello, 2008). This shift is reflected in changes in the North Atlantic Oscillation (NAO), which is one of the major modes of atmospheric circulation affecting winter-spring climate conditions and forest growth in the western Mediterranean Basin (Camarero, 2011; Camisón et al., 2016; Camarero et al., 2020b). Therefore, investigating how drought-tolerant tree species naturally

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distributed across northwest Africa drylands respond to climate is required to better manage and preserve these degraded vegetation types (Calama et al., 2012; Sghaier et al., 2015).

The araar or Barbary thuja (*Tetraclinis articulata* (Vahl) Mast., Cupressaceae) is one of those drought-tolerant tree species, being widely distributed across northwestern African countries (Morocco, Algeria, Tunisia) (Charco, 1999; DREF, 2002; Farjon, 2005). However, it is considered to be critically endangered in semi-arid areas of south-eastern Spain and Malta due to historical human pressure on its small, fragmented populations through fire, overgrazing, urbanization and competition from invasive species (Sánchez Gómez et al., 2019). Therefore, these scattered European populations, accounting for ca. 9000 ha (0.9% of the total distribution area of the species) are regarded as highly threatened and could be menaced by further anthropogenic local pressures as well as by climate warming and increased aridification (Esteve-Selma et al., 2010, 2011). The discovery in the 1990s of a relict population located in the Doñana National Park (southwestern Spain), considered to be natural by some authors (Mañez et al., 1997; Baonza Díaz, 2010), opened a debate on the long-term viability of the species' fragmented stands in Mediterranean Europe as compared with the more extensive North African forests. If the *T. articulata* Doñana population shows a good acclimation to long-term climate variability in its local area as compared with North African populations, there are several implications: it could be used as a new dispersal focus or as an example of naturalized stand, and it should be better preserved and managed and used to improve the species' conservation status in south western Europe. In this study, we compare the climate- and drought-growth relationships of the Doñana *T. articulata* population with two Moroccan populations located in the Rif mountainous region (Tétouan, Ifarten) using dendrochronology.

Several traits make *T. articulata* resistant to the growing-season (spring, summer) water shortage typical of Mediterranean climates, including: (i) its anisohydric behavior (low sensitivity of stomatal conductance to leaf water potential) which enables it a rapid recovery of gas exchange rates in response to watering (Oliveras et al., 2003); and (ii) its cavitation-resistant xylem characterized by tracheids with small lumen and thick walls which helps to avoid embolism (Esteban et al., 2015; Román-Jordán et al., 2017). However, growth responses to changes in water availability are less studied in this species, which was considered challenging to cross-date by dendrochronologists due to the production of rings without clearly defined boundaries and missing rings (Serre-Bachet, 1969; but see Rozas et al., 2021). Addressing this research gap through tree-ring analyses would allow investigating other acclimation strategies to the variable water availability typical of Mediterranean climates, including (i) intra-annual plastic growth responses to climate such as bimodality (Camarero et al., 2010; Valeriano et al., 2023) and (ii) delayed responses to drought (Pasho et al., 2011; Gazol et al., 2020). Furthermore, better understanding climate-growth relationships in *T. articulata* would improve our knowledge on its strategies to withstand water scarcity compared to isohydric (Klein et al., 2011), drought-avoiding species such as Aleppo pine (*Pinus halepensis* Mill.) which typically show an increase of water-use efficiency in arid regions of the Maghreb (Choury et al., 2017). Hotter droughts are causing *P. halepensis* dieback (Camarero et al., 2015) which opens the question of whether species such as *T. articulata* would better tolerate the more arid conditions forecasted by climate models in some Mediterranean regions given its lower vulnerability to drought-induced xylem embolism as compared with *P. halepensis* (Oliveras et al., 2003).

Tetraclinis articulata is a slow-growing, evergreen conifer usually reaching small size (diameter at breast height, dbh, 20–40 cm, height 6–15 m) endemic to the western Mediterranean Basin, being most abundant in North West Africa (Charco, 1999; DREF, 2002; Farjon, 2005), Malta and South Eastern Spain (Esteve Selma et al., 2010, 2011) (Fig. 1). The largest part of the *T. articulata* distribution area, occupying ca. 1 million ha, is located in Morocco, where about 570,000 ha of the species are found in regions with Mediterranean, sub-humid to semi-arid

climate (Benabid, 1985; Fennane, 1988; Esteve-Selma et al., 2017). The stands of this species appear at 0–1800 m of elevation in sites with annual precipitation ranging between 300 and 550 mm and on any kind of soil type (Sghir Taleb and Fennane, 2019). It has the ability to coppice, which allows it surviving fire and moderate browsing (Sánchez Gómez et al., 2019). The main threats to the conservation of these historically exploited forests are overgrazing, habitat deterioration and timber overexploitation due to their valuable and dense wood (Calama et al., 2012; Dallahi et al., 2017). *T. articulata* has long been used by local people from the western Maghreb countries to treat digestive and respiratory disorders and has multiple ethnobotanical values (El-Hilaly et al., 2003; Khatib et al., 2022).

In this study we aimed: (i) to reconstruct the radial growth patterns of *T. articulata* populations including relict (Doñana in southwestern Spain) and core populations (Tétouan and Ifarten in northern Morocco), (ii) to evaluate their radial growth responses to climate and to a drought index using Pearson correlations and the *climwin* R package (Rubio-Cuadrado et al., 2022), (iii) and to compare and infer their climate limitations of growth by using the Vaganov-Shashkin growth model (Vaganov et al., 2006). We hypothesized that *T. articulata* growth depends on the cumulative winter-to-spring precipitation, which drives the soil moisture recharge in Mediterranean forests. We also expect that the relict Spanish population, located in the warmest site, would be the most responsive to spring maximum temperatures, which drive evapotranspiration rates and should be negatively related to *T. articulata* growth.

2. Material and methods

2.1. Study sites

Sites were selected according to the objectives of the paper, i.e., to compare relict vs. core populations subjected to different climatic conditions. We selected three study sites situated along a NW-SE geographical gradient and named thereafter: Doñana, Tétouan and Ifarten (Fig. 1). The Doñana site (6° 26' 24" W, 37° 02' 60" N, 6 m a.s.l.) is located in southwestern Spain. This is an isolated, relict *T. articulata* population discovered in the late 1990s with about 25 mature individuals with dbh of 40–85 cm and height ranging between 5 and 15 m (Baonza Díaz, 2010). The mean site slope is 1–2%. Climate is Mediterranean with mean annual temperature of 18.0° C and annual precipitation of 532 mm, with a dry period lasting from April to October (Fig. 1). The annual potential evapotranspiration is 910 mm. Soils are sandy and acid. The organic layer of soil is shallow and formed on permeable, deep sandy deposits.

The Tétouan site is located near Ben Karrich, a protected forested area due to its landscape and biodiversity values situated 15 km south from Tétouan city in northern Morocco (5° 24' 30" W, 35° 28' 5" N, 185 m a.s.l.). The mean slope is 11.5° and it varies between 5° and 18° with a main SW orientation. Climate is Mediterranean with mean annual temperature of 15.0° C and the annual precipitation is 511 mm, with a dry period lasting from April to October (Fig. 1). The annual potential evapotranspiration is 766 mm. Soils are rocky and acid.

The Ifarten site (5° 11' 33" W, 35° 20' 54" N, 81 m a.s.l.) is located in a sanctuary (termed *khaloa*), where vegetation is protected and sheltered from human use due to religious beliefs. Such vegetation refuges are mainly found in the Rif mountains (Taiqui et al., 2005). The mean slope is 27% and it ranges 3–62°, with orientations changing from NE to SW. The climate is Mediterranean with mean annual temperature of 16.0° C, annual precipitation of 562 mm and a dry period lasting from April to October (Fig. 1). The annual potential evapotranspiration is 790 mm. Soils are marly and develop on dolomitic limestones. In summary, the Spanish Doñana site is the warmest study site, whereas the Moroccan Tétouan and Ifarten sites share similar climate conditions, with a lower climatic water balance in Tétouan.

In the Moroccan sites, several tree (*P. halepensis*, *Quercus ilex* L., *Ceratonia siliqua* L.) and shrub (*Phillyrea media* L., *Rhamnus oleoides* L.,

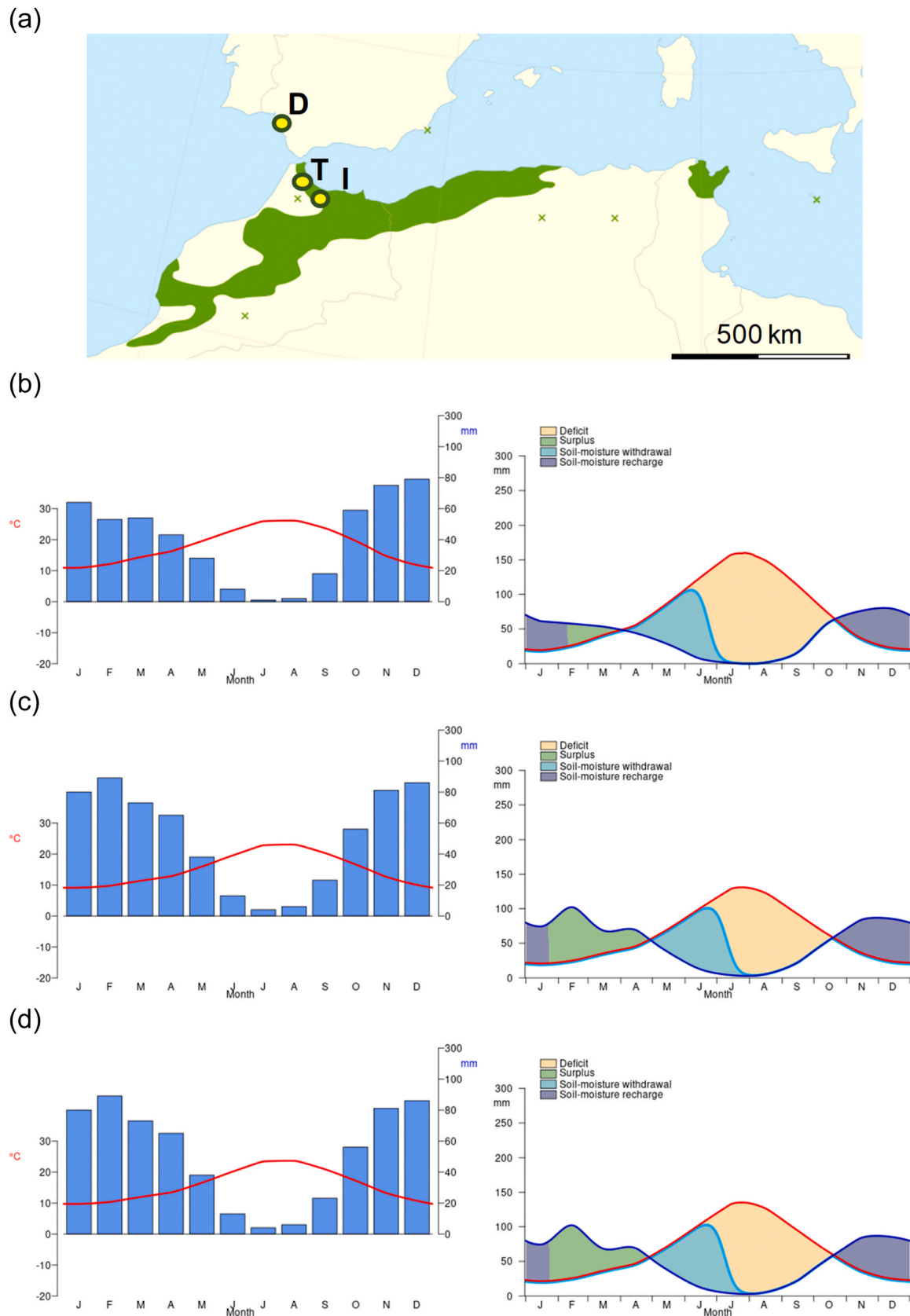


Fig. 1. Location of the study sites in southwestern Spain (D, Doñana) and northern Morocco (T, Tétouan; I, Ifarten) (a) and climate and water balance diagrams of the three study sites: (b), Doñana; (c), Tétouan; and (d), Ifarten. In plot (a), the green area shows the distribution of *T. articulata*.

Genista tricuspidata Desf., *Salvia* spp.) species were observed, whereas in the Spanish site the main tree species was *Pinus pinea* L. and the main shrub species were: *Juniperus phoenicea* L., *Phillyrea angustifolia* L., *Salvia rosmarinus* (L.) Schleidand, *Cistus salvifolius* L. and *Helianthemum* spp.

2.2. Field sampling and tree-ring analyses

The Spanish Doñana site was sampled in early 2011, whereas the two Moroccan sites were sampled in late 2020. In each site, we sampled from 8 to 17 dominant, mature trees and measured their dbh at 1.3 m using tapes. Regrettably, the conservation status of the Doñana population and its private owners did not allow further sampling to update the chronology and increase the number of sampled trees (Table 1).

We took two cores at 1.3 m, separated by 180° and perpendicular to the maximum slope, using 5-mm Pressler increment borers. Cores were air dried, glued onto wooden supports and sanded with sandpapers of increasing grain until ring boundaries were conspicuous. Then, they were visually cross-dated under the binocular scope. Cross-dated cores were scanned at 1200 dpi (Epson Expression 10000XL). The ring widths were measured with a 0.01 mm resolution on scanned images using the CooRecorder software (Larsson and Larsson, 2018). The visual cross-dating was checked using the CDendro and COFECHA programs which calculate moving correlations between individual tree-ring width series and the mean series of each site (Holmes, 1983; Larsson and Larsson, 2018). Few missing rings were found in the Moroccan chronologies (Tétouan, 2.1%; Ifarten, 1.1%), but intra-annual density fluctuations were more frequently observed in the earlywood (Tétouan, 31%; Ifarten, 22%). Tree age at 1.3 m was estimated based on the oldest cross-dated core per tree. Cores with pith were used to estimate pith offset in cores without pith. We calculated basal area increment (BAI) mean series assuming a concentric growth and using the formula:

$$BAI = \pi (r_t^2 - r_{t-1}^2) \quad (1)$$

where r is the cumulative radial length of years t and $t-1$, i.e., $r_{t-1} = r_t - w_t$ where w_t is the tree-ring width of year t .

To remove size- or disturbance-related trends in tree-ring width data and emphasize high-frequency growth variability, the series were detrended and standardized using the dplR package (Bunn, 2010) in R (R Development Core Team, 2022). We fitted 32-year cubic smoothing splines with a 50% frequency response cut-off to individual ring-width series and obtained ring-width indices by dividing observed by fitted values. Then, we fitted autoregressive models to remove most of the first-order autocorrelation in series of dimensionless ring-width indices. The residual or pre-whitened individual series were averaged using a bi-weight robust mean to obtain mean residual series for each site (Fritts, 1976).

Lastly, we calculated several statistics for a common, best-replicated period for each site. This period was defined based on the Expressed Population Signal (EPS) and we considered the period with $EPS > 0.85$ as the one in which the calculated tree-ring chronology represents the theoretically perfect chronology (Wigley et al., 1984). We also calculated several statistics to characterize the mean site chronologies (see Fritts, 1976; Briffa and Jones, 1990): the mean and standard tree-ring width values, the mean first-order autocorrelation of ring widths (AR1) which accounts for year-to-year persistence in growth, the mean sensitivity (MSx) of ring-width indices which measures relative changes in growth between consecutive years, and the mean correlation between

series (rbar), which is a measure of coherence of the site chronology.

Differences in tree diameter, tree age or tree-ring width between sites were evaluated using Mann-Whitney tests. Pearson correlations were used to compare growth series (BAI, residual chronologies) among sites.

2.3. Climate data and drought index

Due to the lack of long-term, homogeneous climate series in the study sites we used monthly 0.5°-gridded data from Climate Research Unit dataset (CRU TS 4.03; Harris et al., 2014), which were downloaded from the Climate Explorer webpage (<http://climexp.knmi.nl/>). We considered mean maximum (Tx) and minimum temperatures (Tn), based on daily means of maximum and minimum temperatures, and total precipitation (Rr) in the common period 1950–2020.

Monthly NAO data were retrieved from the CRU webpage (<https://crudata.uea.ac.uk/cru/data/nao/>) and corresponded to differences between time series of sea-level pressures recorded at Gibraltar and Reykjavik (Jones et al., 1997).

To assess drought severity and duration we used monthly, 0.5°-gridded data of the Standardized Precipitation Evapotranspiration Index (SPEI) in the same period. They were downloaded from the Spanish National Research Council SPEI webpage (<http://spei.csic.es/database>). The SPEI is a multi-scalar drought index computed from monthly rainfall, temperature and potential evapotranspiration showing cumulative changes in the water balance at multiple temporal scales (Vicente-Serrano et al., 2010). We considered 1- to 24-month long SPEI data.

Trends in monthly climate variables and NAO indices were assessed using the Kendall τ .

2.4. Climate- and drought-growth relationships: Pearson correlations

The mean series or chronologies were related to monthly climate data or drought indices using the Treeclim R package (Zang and Biondi, 2015). The relationships between monthly climate variables (Tx, Tn, Rr) or indices (NAO, SPEI) and the site chronologies were quantified using Pearson correlations (r). Correlations were calculated from October of the prior year (year $t-1$) until September of the growth year (year t). Correlations were calculated considering the 1980–2010 and 1980–2020 periods in Doñana and the Moroccan sites, respectively. These periods were included in the best-replicated ($EPS > 0.85$) period of each site chronology (Table 1). In the case of the SPEI, correlations were calculated by relating the sites chronologies and their corresponding 1- to 24-month long SPEI series. The 0.05 and 0.01 significance levels were considered in these analyses.

2.5. Climate-growth relationships: climwin

Radial growth is a continuous process and its main climate drivers may not be captured at monthly resolution (Rubio-Cuadrado et al., 2022). To address this issue, we calculated, for each climatic variable, the time period in which the growth-climate relationship peaked, i.e., the optimal climate window, using the *climwin* R package (Bailey and van de Pol, 2016; van de Pol et al., 2016). This package allows calculating several statistical models, based on multiple temporal windows relating climate and growth indices, and selecting those most informative (Bailey and van de Pol, 2016). This procedure increases the capacity to detect differences in growth responses to climate between sites

Table 1

Size and tree-ring width statistics. Age, diameter at breast height (dbh) and ring-width values are means \pm SD. Different letters indicate significant ($p < 0.05$) differences according to Mann-Whitney tests.

Site	No. trees (No. cores)	Dbh (cm)	Age at 1.3 m (years)	Tree-ring width (mm)	AR1	MSx	rbar	EPS	Period with $EPS > 0.85$
Doñana	8 (10)	58 \pm 10b	83 \pm 12b	2.75 \pm 0.68b	0.62	0.42	0.35	0.88	1959–2010
Tétouan	17 (23)	29 \pm 6a	59 \pm 9a	2.21 \pm 0.56b	0.43	0.38	0.39	0.90	1966–2020
Ifarten	16 (22)	32 \pm 5a	127 \pm 21c	0.83 \pm 0.42a	0.44	0.45	0.32	0.87	1941–2020

(Rubio-Cuadrado et al., 2022).

To select the best climatic window, all possible linear models relating series of ring-width indices and the climate variable are first fitted. In each model a different climate window is tested. Then, the model that minimizes the corrected Akaike information criterion (AICc) is chosen (Burnham and Anderson, 2004). The limits established for the beginning and closing of the climate window were October of the year prior to growth (t-1) and December of the growth year (t), respectively. The models were fitted for the same periods as the correlations, i.e., 1980–2010 in Doñana and 1980–2020 in the two Moroccan sites.

2.6. Using the Vaganov-Shashkin model to pinpoint climate limitations of growth

The use of the Vaganov-Shashkin growth model allows explicitly considering non-linear influences of climate on intra-annual tree-ring formation. We used the Vaganov-Shashkin model (further abbreviated VS-model) to assess differences in climatic controls of tree growth, particularly limitations of growth related to soil moisture, in the three study sites. This model explicitly accounts for non-linear relationships between radial growth and climate factors (Vaganov et al., 2006). The soil moisture is determined by an integrated hydrological sub-model from temperatures and precipitation totals considering several processes (interception, evaporation, transpiration, surface runoff, soil infiltration and snow dynamics). Model inputs include daily temperature and precipitation data and the site ring-width indices (standard chronology).

We parameterized the VS-model for each of our 3 local chronologies (Supporting Information, Table S1) and tuned the model parameters to maximize the Pearson correlations (r) between simulated and observed chronologies using the VS-Oscilloscope software ver. 1.37 (Shishov et al., 2016). To reduce the risk of overfitting, we set parameters related to plant water balance (e.g., rooting depth, transpiration coefficients interval) and growth phenology (e.g., minimal cambial cell growth rate) to be constant across sites (cf. Tumajer et al., 2021). We calibrated the models with different periods depending on the site series' length. In Doñana, the calibration period was 1980–1995 and the verification period was 1996–2010. In Tétouan and Ifarten, the calibration period was 1980–2000 and the verification period was 2001–2020.

The model calculates unitless partial growth rates to temperature (GrT) and soil moisture (GrM) using non-linear response functions of a specific climatic variable. GrT and GrM indicate relative suitability of temperature and soil moisture for growth with lower values representing worse conditions for growth. The lower partial growth rates are scaled by the daily photoperiod (GrE) to produce an integral growth rate (Gr), which is a proxy of the radial growth rate. Annual growth rate is defined as a standardized sum of integral growth rates during a year (Tychkov et al., 2019).

We calculated several statistics for the calibration and verification periods to quantify the similarity between observed and simulated series of ring-width indices including: Pearson correlation coefficients (r), root-mean-square error (RMSE) and Gleichläufigkeit (Glk), which evaluates the year-to-year agreement as the percentage of synchronous growth changes between two tree-ring width series (Buras and Wilmking, 2015).

3. Results

3.1. Tree-ring width data

Sampled trees were older in Ifarten than in the other two sites and the youngest trees were sampled in Tétouan (Table 1). The mean growth rates were lower in Ifarten (0.83 mm) than in the other sites. The first-order autocorrelation was the highest in Doñana, but the highest mean sensitivity was observed in Ifarten. The highest r_{bar} and EPS values were found in Tétouan.

In terms of BAI, Doñana (mean \pm SE, $10.64 \pm 0.71 \text{ cm}^2$) and Tétouan ($9.33 \pm 0.52 \text{ cm}^2$) showed significantly ($p < 0.001$) higher values than Ifarten ($0.67 \pm 0.05 \text{ cm}^2$, Fig. 2). In the period 1980–2010, the BAI series from Tétouan and Ifarten ($r = 0.80$, $p < 0.001$) or their residual chronologies ($r = 0.54$, $p = 0.002$) showed positive and significant correlations indicating common growth patterns in the Moroccan sites. In general, wide and narrow rings corresponded to wet (e.g., 1996–1998, 2010–2011, 2018) and dry (e.g., 1995, 2005 and 2012) years, respectively (Fig. S1).

3.2. Growth responses to climate and the NAO index

Correlation analyses revealed that *T. articulata* growth was enhanced by high minimum temperatures and wet conditions in the prior (year t-1) autumn (November in Doñana and Tétouan) and winter (December in Tétouan and Ifarten) (Fig. 3). High minimum temperatures and elevated precipitation in the current (year t) March were also positively related to series of ring-width indices in Tétouan and Ifarten, and also June precipitation in Ifarten. Elevated maximum temperatures in January and May were negatively related to growth indices in Ifarten and Doñana, respectively.

Analyses based on *climwin* show that growth in Doñana is more sensitive to temperature, with minimum temperatures accounting for 27% of the variability of growth, while in Tétouan and Ifarten growth is more sensitive to precipitation, which explains 35% and 17% of the variability of growth, respectively (Table 2; Figs. S2 and S3). At all three sites, precipitation and minimum temperatures in the previous autumn determine growth, although the time interval during which precipitation is related to growth is extended to June in Tétouan and Ifarten. Doñana was the only site where maximum temperatures are related to growth.

We found no significant correlation between the Doñana chronology and the NAO monthly indices. However, *T. articulata* ring-width indices significantly and negatively responded to prior winter NAO indices in the two Moroccan sites (November, $r = -0.39$ in both sites; December, Tétouan, $r = -0.50$, Ifarten, $r = -0.37$). On the contrary, we found positive correlations between the summer NAO indices and ring-width indices (July, $r = 0.32$ in both sites; August, Ifarten, $r = 0.48$). The precipitation in winter and spring months, which are very relevant to *T. articulata* growth, was tightly linked to the NAO variability (December, $r = -0.80$; March, $r = -0.60$; $p < 0.001$ in both cases).

3.3. Growth responses to drought

Mid- to long-term (6- to 18-month long) droughts peaking in summer reduced *T. articulata* growth, particularly in the two Moroccan sites. The highest correlation between the SPEI drought index and the ring-width chronologies was found in Tétouan ($r = 0.58$), followed by Ifarten ($r = 0.54$) and Doñana ($r = 0.38$) (Fig. 4). The highest correlations in the Moroccan sites corresponded to the June 8-month SPEI in Tétouan and to the August 14-month SPEI in Ifarten, whereas it corresponded to the May 7-month SPEI in Doñana (Fig. 4).

3.4. Inferred climate limitations of growth based on the VS model

The VS model successfully simulated growth variability based on the significant correlations obtained between the observed and the simulated series of ring-width indices in the full period and calibration/verification periods (Table 3, Fig. S4).

According to the VS-model simulations, growth was mainly constrained by low soil moisture levels from May to August in Doñana and from June to September in the Moroccan sites. Growth rates were enhanced by high soil moisture levels in late winter and early spring, mainly from February to April. The negative impact of warmer summer conditions, leading to high evapotranspiration rates, was strong in Doñana. The Moroccan sites also showed growth limitation due to warm

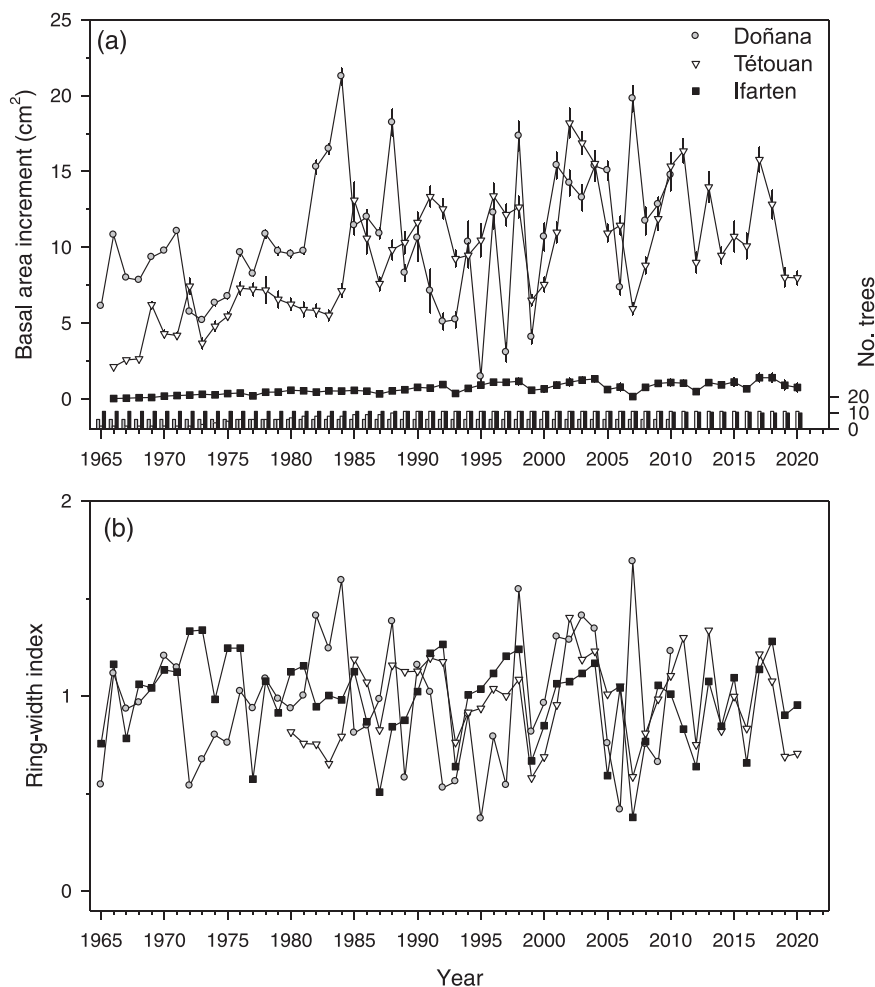


Fig. 2. (a) Mean growth series (basal area increment, means \pm SE) and (b) residual chronologies of the three *T. articulata* study sites.

summer conditions, but also in winter and early spring (December to March) due to low temperatures. The simulated growth pattern shows a possible bimodal growth pattern in Doñana, where growth was improved by wet soil conditions from September to November (Fig. 5).

4. Discussion

As expected, we found that *T. articulata* growth was favored by wet autumn (year $t-1$) to spring (year t) conditions in both the Spanish relict population (Doñana) and in the two core Moroccan populations (Tétouan, Ifarten) (Fig. 3). These findings were reached through correlation and *climwin* analyses confirming their robustness. The *T. articulata* growth was constrained by 6- to 18-month long droughts peaking in summer in the two Moroccan sites, thus corresponding to a cumulative water deficit since the previous autumn (Fig. 4). The VS model was also in agreement with drought-growth correlations highlighting that low soil moisture levels from spring to late summer reduce *T. articulata* growth. Nevertheless, longer tree-ring series would be required to reach more robust results given that the used calibration and verification periods were short, albeit they produced significant model fits. The response of *T. articulata* growth to relatively long droughts is expected for semi-arid Mediterranean sites with a clear summer drought and negative annual climate water balance (Gazol et al., 2020).

As hypothesized, warm spring conditions constrain growth in the case of the relict Spanish stand, and push this population beyond its tolerance limits if followed by severe droughts and increased water deficit in spring. Warmer spring conditions and drier-cooler conditions in the prior autumn and winter reduce growth of Doñana trees (Figs. 3

and 5). Both maximum May and minimum November temperatures have increased in southwestern Spain since 1950, according to CRU data ($\tau = 0.22$, $p < 0.05$ in both cases), which could lead to opposite effects on growth in the relict Doñana stand. In northern Morocco, the decrease of December ($\tau = -0.27$, $p = 0.03$) and March ($\tau = -0.21$, $p = 0.05$) precipitation since 1950 suggest that *T. articulata* growth could decline if climate becomes more arid in that region, particularly in slow-growing, drought-responsive sites such as Ifarten.

The main role played by elevated precipitation from prior late autumn (November) to current spring (March) for *T. articulata* growth agrees with previous findings in two sites from central and southern Morocco (Rozas et al., 2021). Wet June conditions also played a secondary role for *T. articulata* stemwood production. These findings suggest that: (i) the recharge of soil moisture in winter (Camarero, 2011) or the synthesis of carbohydrates in the previous year are main factors controlling *T. articulata* radial growth as observed in other Mediterranean areas and species such as *P. halepensis* (Camarero et al., 2020), and (ii) *T. articulata* probably shows the highest growth rate in April, as suggested the VS model (Fig. 5), when soil moisture is still adequate (Fig. 1). Therefore, the conditions during the previous winter are critical for *T. articulata* growth, similar to *J. thurifera* which is able to keep forming photo-assimilates in winter (Gimeno et al., 2012).

Although the *T. articulata* Moroccan populations we studied showed the highest growth responses to relative long droughts, as found in other Mediterranean forests (Pasho et al., 2011), they did not agree with even longer response times (26–33 months) found in other drier Moroccan populations reported by Rozas et al. (2021), who also found slightly higher *r*bar values than us. These differences may be due to the facts

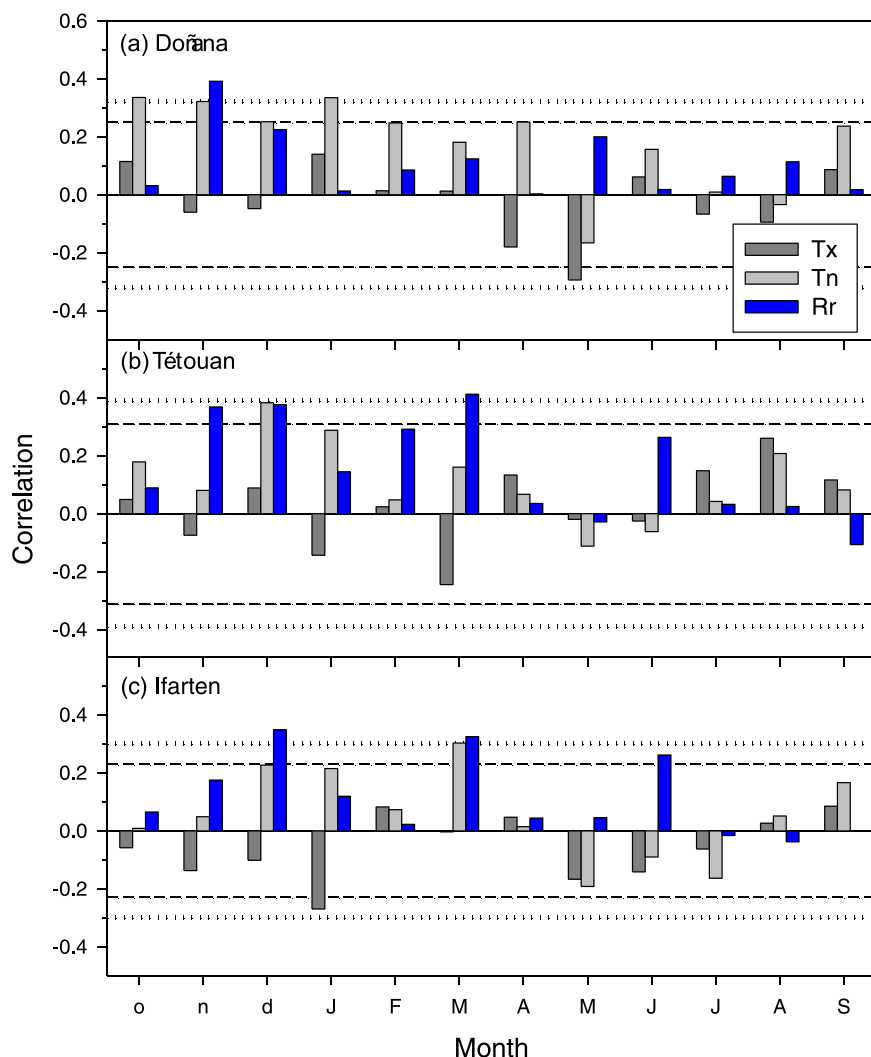


Fig. 3. Pearson correlations obtained by relating monthly climate data (Tx, mean maximum temperature; Tn, mean minimum temperature, Rr, total precipitation) and residual chronologies (ring-width indices) in the three *T. articulata* study sites: (a) Doñana, (b) Tétouan, and (c) Ifarten. Correlations were calculated from prior October (year t-1) to current September (year t) with months abbreviated by lowercase and uppercase letters corresponding to the previous and current years, respectively. The horizontal dashed and dotted lines show the 0.05 and 0.01 significance levels, respectively.

Table 2

Characteristics of the linear models fitted relating residual series of ring-width indices and the climate variable (Rr, precipitation; Tn, mean minimum temperature; Tx, mean maximum temperature) for the best time window. $\Delta AICc$ is the difference between the AICc of the fitted linear model and the null model, windows open and close show the selected climate window from the prior (t-1) to the current (t) year, p and R² refer to the model values.

Site	Climate variable	$\Delta AICc$	Windows open	Windows close	p	R ²
Doñana	Rr	-3.59	Oct. (t-1)	Dec. (t-1)	0.018	0.177
	Tn	-7.34	Oct. (t-1)	Nov. (t-1)	0.003	0.271
	Tx	-2.78	April	May	0.028	0.156
Tétouan	Rr	-15.49	Oct. (t-1)	June	0.000	0.352
	Tn	-4.16	Dec. (t-1)	Dec. (t-1)	0.014	0.146
Ifarten	Rr	-5.21	Oct. (t-1)	June	0.008	0.168

that: (i) we used pre-whitened chronologies and removed part of the first-order autocorrelation, whereas they did not, and (ii) this species may present undatable sections of wood growth with abundant missing rings as Rozas et al. (2021) illustrated. Nevertheless, results based on standard, non-pre-whitened chronologies rendered similar results to those presented here. It is also possible that drier, southern sites located near the xeric distribution limit of the species under semi-arid conditions, as those studied by Rozas et al. (2021), respond to longer droughts than wetter, northern sites such as Tétouan and Ifarten. This discrepancy could be resolved by combining tree-ring and stable carbon and oxygen

isotope data so as to infer the soil water sources and tree-rooting patterns in xeric vs. mesic sites (Sarris et al., 2013). Moroccan *T. articulata* populations from xeric sites might use deep soil moisture pools and respond to long droughts. They might be also able to tolerate chronic water shortage thanks to the elevated resistance to drought-induced xylem embolism shown by *T. articulata* (Oliveras et al., 2003). The anisohydric behavior of *T. articulata* can allow it avoiding carbon starvation during prolonged droughts, but it can also make it vulnerable to heat waves since similar Cupressaceae species show stronger coupling of growth to atmospheric water demand (Voelker et al., 2018; Camarero et al., 2020a). Xylogenesis data or continuous growth monitoring based on dendrometer data would contribute to answer these questions in *T. articulata*.

The *T. articulata* growth was also improved by high minimum temperatures in winter, in agreement with the thermophilous distribution of this conifer. Moreover, the VS model revealed that growth was limited by low winter-to-spring conditions in the more continental Moroccan sites and a bimodal pattern in the Spanish site with a main growth peak in spring and a secondary peak in autumn. Such bimodal behavior has been observed in other Mediterranean Cupressaceae species such as *Juniperus thurifera* L. (Camarero et al., 2010), suggesting that these conifers may show partial growth recovery after the summer drought in response to autumn storms. Although the three study sites form a very small northern portion of the latitudinal gradient currently occupied by the species, it should be noted that low minimum temperatures may constrain growth and impede the latitudinal migration of *T. articulata*.

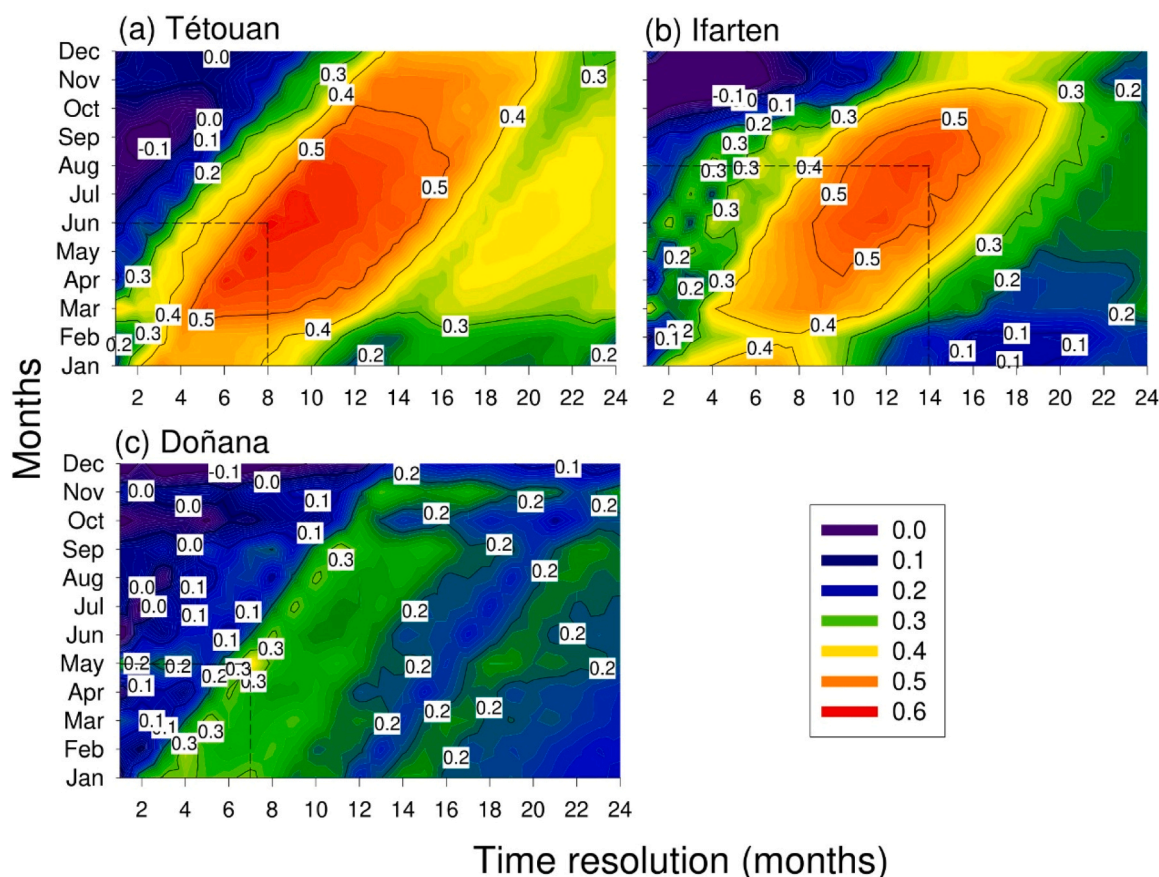


Fig. 4. Pearson correlations obtained by relating monthly SPEI data obtained at 1- to 24-month long scales (x axes) and residual chronologies (ring-width indices) in the three *T. articulata* study sites: (a) Tétouan, (b) Ifarten, and (c) Doñana. Sites are ordered in descending order of maximum SPEI-growth correlations obtained. The dashed vertical and horizontal lines indicate the monthly time resolution (x axes) and the month (y axes), respectively, when the highest correlation coefficients (color scale) were found in each site. Correlations are significant ($p < 0.05$) for coefficients higher than $r = 0.36$ and $r = 0.31$ in Doñana and Tétouan-Ifarten, respectively.

Table 3

Coherence statistics of the standard series based on the VS model and considering calibration (1980–2000/1995) and verification (1996/2001–2010/2020) periods. Statistics are Pearson correlation coefficient (r), root-mean-square error (RMSE) and Gleichläufigkeit (Glk).

Site	Period	r	Glk (%)	RMSE	r		RMSE	r		RMSE
					Calibration period			Verification period		
Doñana	1980–2010	0.64	64.52	0.339	0.71	68.75	0.322	0.54	53.33	0.371
Tétouan	1980–2020	0.47	60.98	0.296	0.42	52.38	0.334	0.51	70.00	0.281
Ifarten	1980–2020	0.61	65.85	0.427	0.52	42.86	0.501	0.75	85.00	0.356

Therefore, a shrinking in the south of its distribution area under more arid conditions and desertification could not be compensated by northward shifts due to unfavorable thermal conditions.

Low NAO indices correspond to cool-wet winter-spring conditions (Hurrell and Van Loon, 1997), which improve *T. articulata* growth (Fig. S5). The correlations found with NAO summer indices did not correspond to any significant climate-growth relationship and could be due to lagged associations between the NAO and the sea-surface temperature variability associated to longer time scales and captured by the Atlantic Multidecadal Oscillation. More arid conditions from late autumn to spring, linked to high NAO indices, could reduce growth of *T. articulata* in northern Morocco which could be outcompeted by fast-growing and drought-avoiding species such as *P. halepensis*, albeit threats due to human overuse seem to be more worrying.

The population most sensitive to water availability and the winter

NAO was Tétouan, whereas Doñana was the least responsive (Fig. 4). These differences could be explained by local factors since trees were younger and grew more in Tétouan than in the other two sites and were also growing on relatively steep, rocky sites on marly soils. In contrast, the individuals sampled in Doñana showed intermediate growth rates (Fig. 2) and were growing on deeper sandy substrates in a relatively flat area. This could explain the low coupling between drought and growth in the Spanish population.

According to a niche model, *T. articulata* suitable areas include northwestern Africa but also southeastern and southwestern Iberia (García-Castaño et al., 2021). These authors identified four genetic lineages with disparate geographical patterns: two were located in western Morocco and Algeria, respectively, and the other were highly dispersed and intermixed during post-glacial migration. Intermixing can be also explained by historical dispersal through trade routes across the

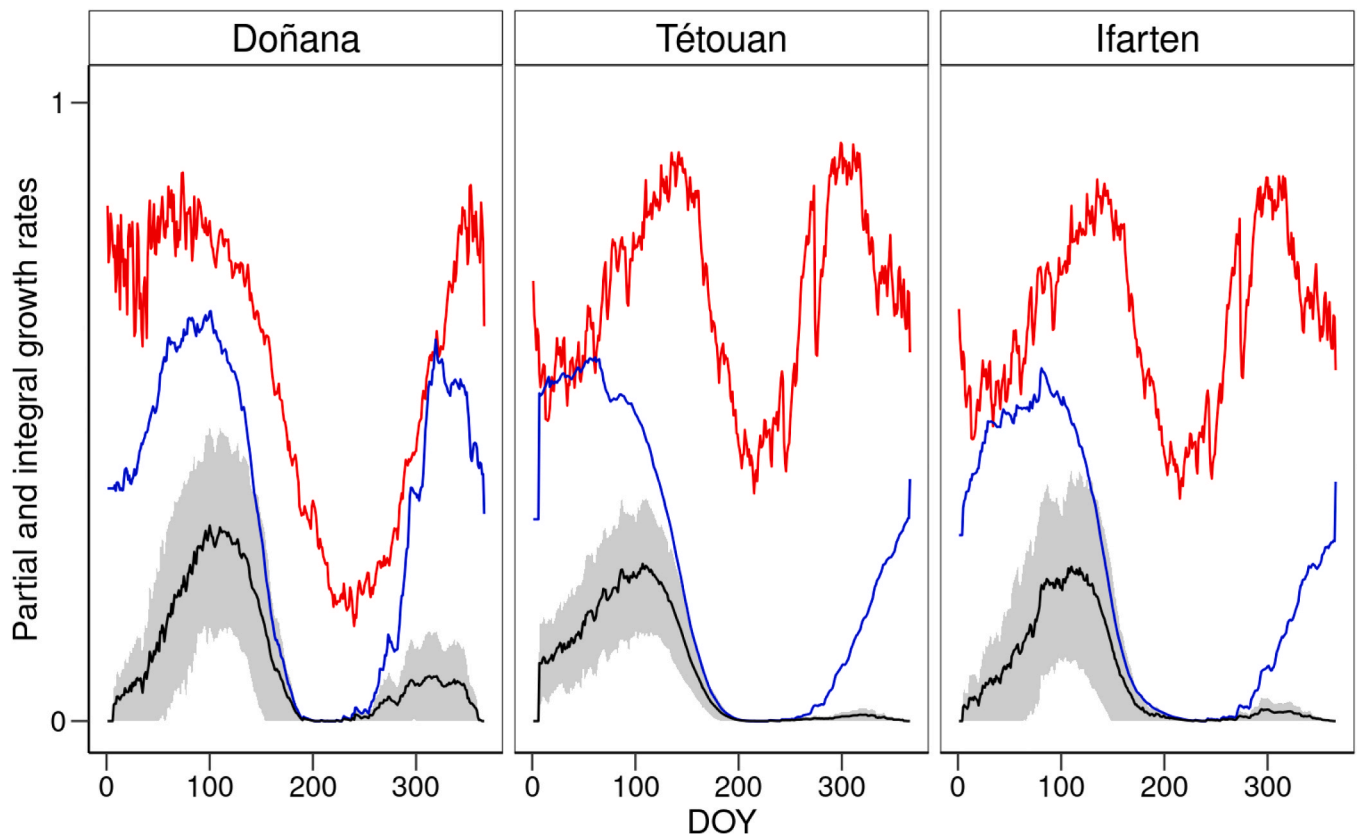


Fig. 5. Partial (blue and red lines) and integral growth rates (black lines) produced by the VS model for the three study sites. The plot shows the partial growth rates driven by soil moisture (blue lines) or temperature (red lines) with lower values indicating stronger constraints. The grey bars show the standard deviations of the modeled growth rates. The x axes show the day of the year (DOY). Note the bimodal growth pattern of the Doñana population.

Mediterranean Basin (Sánchez-Gómez et al., 2013). There is historical evidence of trade in this highly valued wood during ancient times. Such genetic data could complement tree-ring analyses to improve the knowledge on the origin and conservation of other threatened conifers.

Finally, although the studied Doñana relict population has not clearly been determined yet as autochthonous or naturalized (Baonza Díaz, 2010), our findings support the need to protect and further investigate its origin, proposing its addition to the Andalusian Red List of Threatened Species. The design and implementation of a specific conservation plan (i) promoting tree regeneration, given that the stand is subjected to a high grazing pressure, and (ii) preserving mature individuals is also needed.

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.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dendro.2023.126103.

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