Research paper

Enhanced growth of *Juniperus thurifera* under a warmer climate is explained by a positive carbon gain under cold and drought

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Juniperus thurifera L. is an endemic conifer of the western Mediterranean Basin where it is subjected to a severe climatic stress characterized by low winter temperatures and summer drought. Given the trend of increased warming-induced drought stress in this area and the climatic sensitivity of this species, we expect a negative impact of climate change on growth and ecophysiological performance of *J. thurifera* in the harsh environments where it dominates. To evaluate this, we measured long- and short-term radial growth using dendrochronology, photosynthesis and water-use efficiency in males, females and juveniles in three sites in Central Spain. Climate was monitored and completed with historical records. Mean annual temperature has increased +0.2 °C per decade in the study area, and the main warming trends corresponded to spring (+0.2 °C per decade) and summer (+0.3 °C per decade). Radial growth and maximum photosynthesis peaked in spring and autumn. Positive photosynthetic rates were maintained all year long, albeit at reduced rates in winter and summer. Radial growth was enhanced by wet conditions in the previous autumn and by warm springs and high precipitation in summer of the year of tree-ring formation. Cloud cover during the summer increased growth, while cloudy winters led to impaired carbon gain and reduced growth in the long term. We argue that maintenance of carbon gain under harsh conditions (low winter temperatures and dry summer months) and plastic xylogenesis underlie *J. thurifera*'s ability to profit from changing climatic conditions such as earlier spring onset and erratic summer rainfall. Our results highlight that not only the magnitude but also the sign of the impact of climate change on growth and persistence of Mediterranean trees is species specific.

Keywords: basal area increment, dendroecology, drought, *Juniperus thurifera*, Mediterranean continental biome, photosynthesis, water-use efficiency.

Introduction

Growth, photosynthesis and survival of evergreen trees in Mediterranean continental regions is constrained by multiple co-occurring climatic stresses such as extreme temperatures, low water availability and excessive irradiance (Mitrakos 1980, Martinez-Ferri et al. 2003, Valladares et al. 2008, Camarero et al. 2010, Ogaya et al. 2011). Furthermore, these climatic constraints will increase under climate change scenarios. According to the most likely climatic scenarios, the temperature rise by the end of the century will be greater during spring, increasing drought stress for the period when most Mediterranean species acquire most of their resources and grow (Christensen et al. 2007). In fact, some studies have already found that increased drought stress has negatively affected growth and altered the physiology of some tree species in the Mediterranean (Sarris et al. 2007, Linares et al. 2010, Linares and Tiscar 2010). In contrast, results from other studies are not consistent with this declining growth trend (Martin-Benito et al. 2010), or even show an increased growth

rate in response to other environmental influences (Todaro et al. 2007, Martinez-Vilalta et al. 2008). In addition to increased drought stress, the Mediterranean region will also experience increased climatic variability and modifications in light availability due to altered cloud cover (Christensen et al. 2007).

Besides climatic constraints, tree species inhabiting the Mediterranean region are subjected to other abiotic and biotic stresses such as nutrient-deprived or poorly developed soils, and competition with other woody species. Furthermore, the impact of these constraints on tree growth and physiology can be mediated by their interactions with other global change drivers (e.g., changes in land use or introduction of invasive species), including climate change (Lloret et al. 2003, Sardans et al. 2006, Matias et al. 2011). Therefore, the present global-change context imposes novel conditions for Mediterranean woodlands that are likely to alter their growth and dynamics. This is the case of Spanish juniper (*Juniperus thurifera* L.) woodlands, which are endemic formations to the western Mediterranean Basin. *Juniperus thurifera* forms open woodlands in areas with poor soils subjected to a Mediterranean continental climate, with low winter temperatures and high water deficit in summer (Gauquelin et al. 1999). These woodlands constitute a refuge for endemic and endangered species of flora and fauna and account for a high cultural and historical value (Olano et al. 2008). On the one hand, abandonment of traditional uses of these woodlands (timber harvesting and free-ranging livestock) could favour the growth and recruitment of *J. thurifera*; on the other, it could also favour the recruitment of competing *Pinus* and *Quercus* species, with faster growth rates (Olano et al. 2008, DeSoto et al. 2010).

Juniperus thurifera has several features that could make its growth, reproduction and physiology particularly sensitive to climate change. First, it is a dioecious species and previous studies have shown differences in radial growth between males and females in temporal evolution (Montesinos et al. 2006) and growth sensitivity to climate (Rozas et al. 2009). Thus, we could expect climate change to have a differential impact on growth and physiology of males and females, with potential effects on population sex ratio and reproduction. Second, it has recently been shown that both reproductive and vegetative functions of *J. thurifera* are reduced at higher altitudes (Montesinos et al. 2010), which may limit upward migration to cooler sites to avoid warming-induced stress. Besides *J. thurifera* tends to occupy high plateaus in Central Spain, which means that there are no chances for ample migration to higher locations, unlike some other species (e.g., Peñuelas et al. 2007). Finally, we could also expect *J. thurifera* growth to be negatively affected by climate change. This is because its growth depends on seasonal water availability (Bertaudiere et al. 1999), and usually the root system of *Juniper* species cannot access deep soil water (Williams and Ehleringer 2000,

Peek et al. 2006, Armas and Pugnaire 2009). Warming-induced water stress is predicted to increase during the spring, when the main peak of radial growth occurs in *J. thurifera* (Camarero et al. 2010). Although this effect could be counteracted either by the increased CO_2 fertilization effect or by CO_2-improved water-use efficiency (Huang et al. 2007), or by an extension of the growing season, since radial growth in Mediterranean continental regions is constrained not only by water availability but also by low winter temperatures (Mitrakos 1980). Without migration, persistence of perennial species relies on survival and acclimation to the novel climatic conditions (Davis et al. 2005).

In this study, we monitor the performance of *J. thurifera* to assess the main climatic factors limiting its growth and physiology. Specifically, we hypothesized that: (i) the seasonal evolution of carbon gain and water-use efficiency underlie radial growth dynamics and climate–growth relationships in *J. thurifera*, (ii) males and females have different gas-exchange dynamics and radial growth patterns, and (iii) radial growth is sensitive to the rising temperatures linked to recent climate change.

Materials and methods

Study species and sites

Juniperus thurifera L. (Cupressaceae) is a tertiary relict tree endemic to the western Mediterranean Basin. It is usually the dominant species in low-density woodlands in poor, shallow and rocky soils (both acidic and calcareous, although more abundant in the latter), at a variety of altitudes (300–3200 m a.s.l.) in climates that range from arid to sub-humid Mediterranean types. The most extensive woodlands of *J. thurifera* are found in Spain, particularly in the central high plateaus that range between 800 and 1200 m a.s.l., subjected to a continental Mediterranean climate (Gauquelin et al. 1999). It is a dioecious species and trees are usually 5–10 m tall. Males and females produce their pollen and seed cones at the end of the winter, and wind-pollinated female cones mature for 20 months (Montesinos et al. 2006).

The study was conducted at the Alto Tajo Natural Park in Central Spain. The altitude varies from 706 to 1881 m a.s.l., with most plateaus ranging from 1000 to 1200 m a.s.l. The climate is continental Mediterranean with hot and dry summers and cold and cloudless winters (see Figure S1 available as Supplementary Data at *Tree Physiology* Online). Mean annual rainfall is 499 mm, with August being the driest month (25.6 mm) and May the rainiest (66.1 mm). Mean annual temperature is 10.2 °C, with January being the coldest month (2.4 °C) and July the warmest (19.5 °C), according to climatic data of the closest meteorological station (Molina de Aragón: 40°50′40″N, 1°53′07″W, 1063 m a.s.l., 1951–2007 period,

data provided by the Spanish Agencia Estatal de Metereología). The soils are shallow, poorly developed, and formed from Cretaceous and Jurassic limestone (Ferrero et al. 2006). In this area, the lower parts (700–950 m a.s.l.) are dominated by open woodlands of *Quercus ilex* L. in south-facing slopes and by *Pinus nigra* Arn. in north-facing slopes, whereas the upper plateaus (950–1400 m a.s.l.) are dominated by open woodlands of *J. thurifera* (Valladares et al. 2008, Granda et al. 2011). Within this study area, we selected three natural woodlands, within a 10 km radius, dominated by healthy *J. thurifera* trees (Table 1). Two sites were pure *J. thurifera* woodlands [sites: Buenafuente del Sistal (BF) and Río Salado (RS)] and one was an open woodland dominated by *J. thurifera*, but where other species coexisted [*P. nigra* and *Q. ilex*; site: Transecto Alto (TA)]. Two of the sites (BF and TA) were located within the optimum distribution range of the species in this area (~1200 m a.s.l.) and one site (RS) was located at its lower distribution limit in the study area (960 m a.s.l.).

Field sampling and climatic data

To measure microclimatic conditions, we installed a HOBO® (Onset Computer Co., Bourne, MA, USA) weather station close to the study sites (40°49′08″N, 2°12′47″W, 1200 m a.s.l.) with a rain gauge (RGA-M0XX), a photosynthetically active radiation (PAR) sensor (S-LIA-M003), a temperature sensor (12-Bit Temperature Smart Sensor) and a soil moisture sensor (S-SMA-M003) located at 30 cm depth to measure relative soil volumetric water content. Readings of each sensor were recorded every 30 min with a data logger (HOBO® H21-001; Onset Computer Co.). These data were completed with long-term (1951–2007) monthly climatic records (mean temperature and total rainfall) obtained from a nearby meteorological station (Molina de Aragón) and also from interpolated data (Ninyerola et al. 2005).

At each site we randomly selected representative *J. thurifera* trees [n = 13 (BF) and 14 (TA and RS)] that had a diameter at breast height (DBH, 1.3 m height) >10 cm and showed no symptoms of decline or pathogenic infection, like most of the surrounding individuals. These were tagged, mapped, measured for DBH and gender was identified. In 7 trees from sites TA and RS and in 17 trees from site BF we installed manual band dendrometers (DB 20, Environmental Measuring Systems, Turistická, Brno, Czech Republic). Dead bark was brushed off before dendrometers were installed at 1.3 m height. Dendrometers were read at intervals of 6 weeks. Additionally, in one tree in site TA and one tree in site RS radial increment was monitored continuously with digital band dendrometers (DRL 26, Environmental Measuring Systems).

Dendrochronological methods

Standard dendrochronological methods were used to assess changes in radial growth and to quantify climate–growth relationships. In March 2008, selected trees were bored at 1.3 m height using a Pressler increment borer. Two complete radii were extracted from each tree and pith was reached in 70% of the cores. The cores were air-dried, glued onto wooden mounts and polished using sandpaper of progressively finer grain until tree rings were clearly visible. Then, the wood samples were visually cross dated (Stokes and Smiley 1968). Tree-ring width was then measured on a Lintab measuring system (Rinntech, Heidelberg, Germany) with a resolution of 0.001 mm. Tree-ring cross dating was checked using the program COFECHA (Holmes 1983). The trend of decreasing ring width with increasing tree size was removed by converting radial increment into basal area increment (BAI) using the formula: $BAI = \pi (r_t^2 - r_{t-1}^2)$; where r is the tree radius and t is the year of tree-ring formation (Jump et al. 2006). In the case of cores without pith, we used a geometric method based on the curvature of the innermost tree ring to estimate the number of missing rings up to the theoretical geometric pith.

A local tree-ring width chronology was established for each site. For each tree, its cross-dated ring-width series was detrended and standardized to remove age-related growth trends (Fritts 1976, Cook and Kairiukstis 1990). The series of raw data were processed with a double detrending. First, a negative linear or an exponential function was fitted. Second, we used cubic smoothing splines with a 50% frequency response cut-off of 30 years to keep the high-frequency variability (Cook and Peters 1981). Autoregressive modelling was performed on each detrended ring-width series to remove first-order temporal autocorrelation and they were finally averaged using a biweight robust mean to obtain residual site chronologies (Monserud 1986). This was done using the program ARSTAN (Cook 1985). To extract the relevant climatic

Table 1. Characteristics of the three study sites [means ± SE, n = 14 (TA and RS) and n = 13 (BF)]. Mean annual climatic variables were obtained from Ninyerola et al. (2005).

Site	Transecto Alto	Buenafuente del Sistal	Río Salado
Code	TA	BF	RS
Latitude (N)	40°48′56″	40°49′07″	40°51′03″
Longitude (W)	2°12′41″	2°12′50″	2°18′04″
Elevation (m a.s.l.)	1230	1220	960
Aspect	NE	NW	SE
Slope (%)	9	20	36
Basal area (m² ha⁻¹)	8.6	–	12.36
DBH (cm)	16.5 ± 1.3	17.7 ± 1.6	19.5 ± 0.6
Age[1] (years)	44 ± 3	42 ± 3	46 ± 3
Precipitation (mm)	575	594	607
Temperature[2] (°C)	10.5 (21.1–2.4)	10.5 (21.1–2.4)	11.5 (21.9–3.3)
Radiation (10 kJ m⁻² day⁻¹ μm⁻¹)	2115	2121	2043

[1]Age at breast height (1.3 m).
[2]Mean annual (mean of the hottest–coldest months) temperatures.

information on our growth series we performed all further analyses using site residual chronologies.

We calculated Pearson correlation and response function coefficients for the period 1966–2007. This period was regarded as the statistically reliable timespan, according to the expressed population signal (EPS), a measure of the statistical quality of the mean site chronology (Wigley et al. 1984). The chronology segment with EPS > 0.85 was regarded as the statistically reliable period. Pearson correlations and response functions were calculated relating each site residual chronology to monthly climatic data (mean temperature and total precipitation) derived from the Molina de Aragón station and from the Climate Research Unit (CRU, cloud cover), freely available at http://badc.nerc.ac.uk/data/cru/ and corresponding to the TS 2.1 and 3.0 gridded (0.5° resolution) datasets (Mitchell and Jones 2005). The significance of the calculated regression coefficients were estimated based on 1000 bootstrapped estimates (Guiot 1991). Response function coefficients are based on stepwise multiple regressions computed on the principal components of climatic variables to reduce the collinearity among climatic predictors of growth (Fritts 1976). Climate–growth relationships were analysed from the previous August up to October of the growth year, for the period 1966–2007. To calculate the correlation and response function coefficients we used the program Dendroclim2002 (Biondi and Waikul 2004).

Gas-exchange measurements

In addition to the 13 adult trees, 10 non-reproductive juvenile trees (height < 2 m) were tagged and mapped in August 2007 in site BF. These juveniles, together with 10 of the adult trees, were used to monitor light-saturated photosynthesis (A_{sat}), stomatal conductance to water (g_s) and instantaneous water-use efficiency (iWUE = A_{sat}/g_s, Flexas et al. 2001). These gas-exchange measurements were performed in 12 adult trees (5 females and 7 males) and 8 juveniles every 6 weeks (see Figure S2 available as Supplementary Data at *Tree Physiology* Online), in the same trees, using an LI-6400 infrared gas analyser (LI-COR, Lincoln, NE, USA). A_{sat} and g_s were measured at constant and ambient CO_2 concentration (400 μmol CO_2 mol^{-1}), using the built-in LI-6400 CO_2 controller, and saturating light intensity (1500 μmol m^{-2} s^{-1}), provided by the built-in LI-6400 blue-red light source. Monitored microclimatic values—temperature, relative humidity and vapour pressure deficit (VPD)—were kept constant and close to ambient conditions in each measuring campaign. The VPD, measured with the Li-6400, was calculated according to Campbell and Norman (1998) as VPD = $e - e_s$, the difference between the actual vapour pressure (e) and its saturation value (e_s). At each tree, we selected one mature, healthy, fully expanded photosynthetic branch completely covered by scaly leaves, always at the southern part of the canopy at 1.5 m height. Since these did

not cover completely the LI-6400 photosynthesis chamber, used sections were removed to estimate their exact area. Areas were calculated from scaled pictures, taken immediately after being removed, using the image analysis software ImageJ (Rasband 2009).

Statistical analyses

We used long-term climatic records to perform linear regressions to quantify the temporal trends using annual and seasonal data. Ecophysiological variables were tested for normality and homogeneity of variance (Quinn and Keough 2002). Non-normally distributed variables were log- or square-root transformed to achieve normality. Variables were analysed using a repeated-measures analysis of variance (ANOVA) to test for significant differences between adults and juveniles and between males and females.

The effects of time (year for BAI and day for radial increment), site and gender on BAI and radial increment were explored using hierarchical linear mixed models (LMM, Bolker et al. 2008). The three factors were included in our models as fixed effects, DBH was included as a covariate and tree (nested within site) as a random factor. The effect of the random factor was tested using the log-likelihood test (*L*-ratio, Zuur et al. 2009). We used the restricted maximum-likelihood method and Type III sum of squares. These analyses were performed in the R environment (R Development Core Team 2009) using package nlme (Pinheiro et al. 2009). Finally, we assessed the relationship between BAI and mean annual temperature and total precipitation using Pearson correlation coefficients. To account for the effects of temporal autocorrelation of the BAI series we estimated the corrected 95% confidence intervals for the correlation coefficients using stationary bootstrap estimates with an average block length proportional to the maximum estimated autocorrelation of the data (Mudelsee 2003).

Results

Climate

According to the historical record (1951–2007), mean annual temperature in the study area has increased at a rate of +0.2 °C per decade ($R^2 = 0.21$, $P < 0.001$; Figure 1). Temperature trends showed seasonal differences. Both spring and summer mean temperatures increased significantly with time ($P < 0.05$, see Table S1 available as Supplementary Data at *Tree Physiology* Online) at rates of 0.2 and 0.3 °C per decade, respectively ($R^2 = 0.11$ and 0.26; $P = 0.008$ and <0.001, respectively). Mean winter and autumn temperatures showed no significant trends with time (see Table S1 available as Supplementary Data at *Tree Physiology* Online). Annual and seasonal rainfall showed no significant trend with time for the 1951–2007 period ($P = 0.16$; Figure 1).
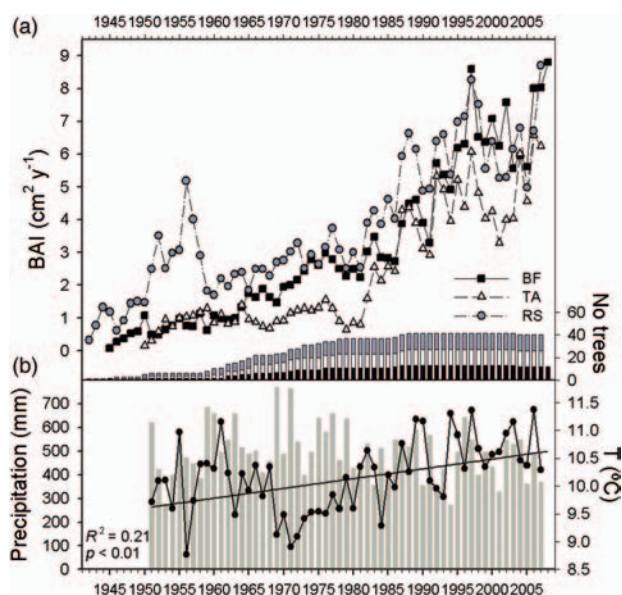
Figure 1. (a) Temporal evolution of basal area increment in the three study sites (site codes as in Table 1). Vertical bars represent the number of trees measured each year in each site. (b) Temporal evolution of mean annual temperature (T, dots and line; regression line depicts the correlation T–time; R^2 and P value are indicated) and total precipitation (grey bars, $n = 56$ years). Error bars have been omitted for clarity.

Figure 2. Cumulative radial increment dynamics in the three study sites based on discontinuous data from the three sites [dots, mean ± SE; $n = 7$ (TA and RS), $n = 17$ (BF); site codes as in Table 1] and continuous measurements (lines) in sites TA and RS.

Table 2. Results of the LMM for radial increment and basal area increment. Fixed effects were: study site (S), gender (G) and time (T, day, for radial increment and year for BAI). Diameter at breast height (DBH) was included as a covariate. Statistical parameters: F and P. Significant ($P < 0.05$) factors are in bold.

Factor	Radial increment		BAI	
	F	P	F	P
DBH	7.67	**0.009**	87.12	**< 0.001**
Site (S)	0.62	0.544	17.55	**< 0.001**
Gender (G)	0.66	0.422	1.71	0.200
Day/year (T)	209.08	**< 0.001**	2115.84	**< 0.001**
S × G	0.11	0.892	0.40	0.675
S × T	1.82	**0.032**	32.37	**< 0.001**
G × T	0.38	0.932	1.86	0.173

During the monitored period, the study area experienced a wetter than usual spring (2008) and a drier and warmer than usual spring (2009). We also found that days during the autumn–winter season of 2007–2008 were significantly brighter (mean daily PAR ± SE: 20.5 ± 0.7 mol day^{-1}) than the following autumn–winter (17.2 ± 0.8 mol day^{-1}, $F = 10.8$, $P = 0.001$, $n = 237$).

Radial increment dynamics and growth patterns

Seasonal radial increment showed a main increment period between May and June and a secondary one between September and October (Figure 2). There were no significant differences in radial increment at an intra-annual scale between males and females (Table 2). We found that there was a statistically significant effect of the interaction between measurement date and site on radial increment (Table 2), although the factor site was not significant in itself (Table 2). Diameter at breast height had a significant effect on radial increment (Table 2), and we also found significant differences among trees (L-ratio = 200.6, $P < 0.001$).

Long-term radial growth (BAI) varied significantly with time (Figure 1) and the year × site interaction also had a significant effect on BAI (Table 2). In contrast with the results of radial increment at an intra-annual scale, the factor site itself had a significant effect on BAI at an inter-annual scale (Table 2). Mean site BAI decreased in the following order: RS > BF > TA. However, this ranking changed in particular time periods (Figure 1). Similar to what was found for radial increment, there
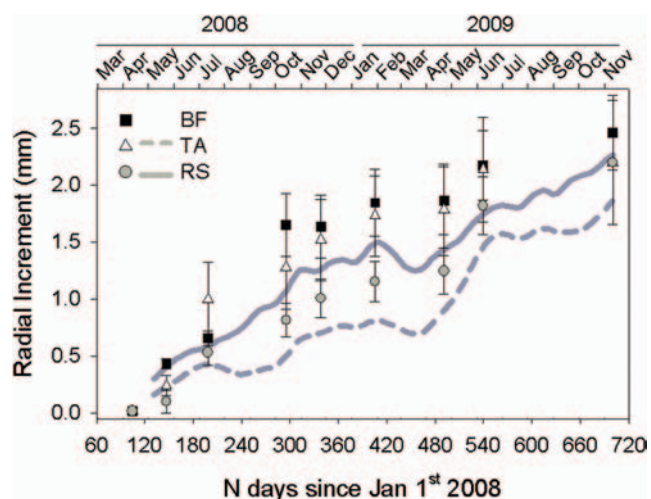
were no significant differences between males and females (Table 2). Diameter at breast height significantly affected BAI (Table 2). Again, we found significant differences among trees in BAI (L-ratio = 201.0, $P < 0.001$).

Climate–growth relationships

The EPS of the three site chronologies was above 0.85 since 1965 supporting a consistent shared growth signal among sites and age classes. The main dendrochronological statistics were similar for the three study sites, which showed mean tree-ring widths in the range 1.49–1.88 mm (see Table S2 available as Supplementary Data at *Tree Physiology* Online).

Radial growth was significantly ($P < 0.05$) and positively related to current April temperature and July rainfall, and to September rainfall of the year prior to ring formation, in all sites (Figure 3). Accordingly, radial growth was positively related to cloud cover of the current July and previous September. June
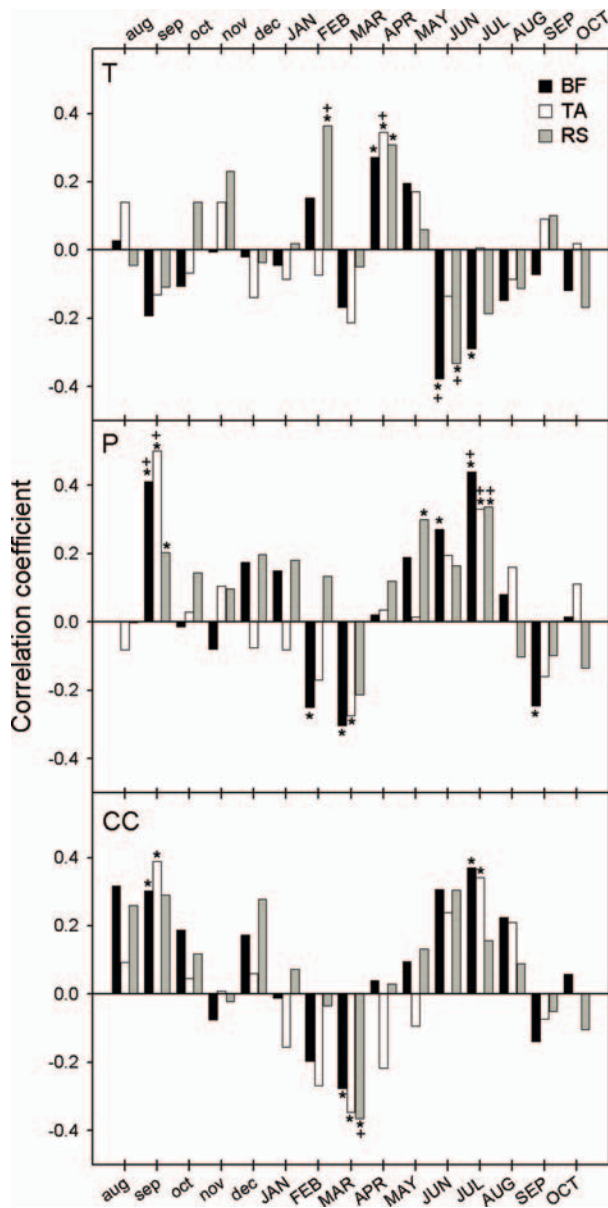
Figure 3. Relationships between climate and radial growth (residual ring-width indexes) for the three sites (site codes as in Table 1). Correlation coefficients were calculated between mean monthly temperature (T, in °C), total precipitation (P, in mm) and cloud cover (CC, in %) and the residual chronologies [$n = 14$ (RS and TA) and $n = 13$ (BF)] for the period 1966–2007 and considering the temporal window from the previous August to the current October. Significant Pearson correlations and response function coefficients ($P < 0.05$) are indicated with asterisks and crosses, respectively. Months abbreviated by lowercase letters correspond to the year previous to tree-ring formation.

Table 3. Pearson's correlation coefficients (and corrected 95% confidence intervals) between BAI and annual climatic variables. Significant values ($P < 0.05$) after taking into account temporal autocorrelation are in bold.

Site code	Temperature	Precipitation
TA	**0.36** (0.12–0.54)	−0.10 (−0.32–0.13)
BF	**0.28** (0.06–0.48)	−0.08 (−0.28–0.14)
RS	0.15 (−0.19–0.39)	−0.14 (−0.33–0.13)

that growth was negatively correlated to current June temperature (BF and RS, Figure 3).

We found that BAI series were significantly and positively correlated to mean annual temperature in sites TA and BF, but not in RS (Table 3). Basal area increment series were not significantly correlated to annual rainfall (Table 3).

Physiological data

Repeated-measures ANOVA revealed that there were significant differences between measurement dates for all physiological variables monitored (Table 4, Figure 4). Maximum A_{sat} and g_s were reached in the warm fall and winter 2007–2008, after the wet spring of 2008 and at the beginning of the fall 2008 (Figure 4). Minimum values of these variables were observed at the end of summer 2007 and 2008 and at the end of winter 2008–2009 (Figure 4). The iWUE followed a slightly different pattern: maximum values were reached in the warm fall and winter 2007–2008 and in summer 2008, and minimum values were reached at the end of the wet fall 2008 and during the cold winter of 2008–2009 (Figure 4). We did not find any significant difference between males and females based on physiological data (Table 4). However, when male and female trees were pooled together as adult trees and tested against juveniles, we found a significant age × time interaction (Figure 4). Juvenile trees had higher rates of A_{sat}, g_s and iWUE during the more favourable climatic periods, but suffered a greater decline of these variables than adults in response to adverse climatic conditions (low winter temperatures and drought stress in summer). We did not find any significant correlation between monitored gas exchange variables (g_s, A_{sat} and iWUE) and VPD ($F < 1.00$, $P > 0.40$; Figure 4c).

Discussion

Connecting seasonal gas-exchange and growth patterns

We have found that J. thurifera maintained positive carbon gain all year long, despite being subjected to a harsh continental Mediterranean climate with low winter temperatures and dry conditions in summer. For J. thurifera, which is an evergreen species with lower competitive ability and growth rates than co-existing pine and oak species (DeSoto et al. 2010),

temperature during the year of tree-ring formation was negatively related to growth in sites RS and BF. Previous winter precipitation and cloud cover were negatively correlated with growth in two of the sites (TA and BF) in the months of March (for both sites) and February (only for site BF, Figure 3). Response functions confirmed these findings and also showed

Table 4. Results of the repeated measures ANOVA (statistical parameters: F and P) for the gas-exchange variables: A_{sat}, g_s and iWUE. Categorical predictors were: gender (males vs. females) and age (adults vs. non-reproductive juveniles). Significant ($P < 0.05$) factors are in bold.

		Gender	Time	Gender × time	Age	Time	Age × time
A_{sat}	F	0.35	7.24	0.53	2.26	8.19	2.35
	P	0.584	**< 0.001**	0.887	0.184	**< 0.001**	**0.013**
g_s	F	0.11	3.15	0.56	1.38	10.43	2.25
	P	0.764	**0.004**	0.861	0.293	**< 0.001**	**0.020**
iWUE	F	0.04	7.63	0.45	0.03	14.61	2.43
	P	0.851	**< 0.001**	0.934	0.875	**< 0.001**	**0.009**

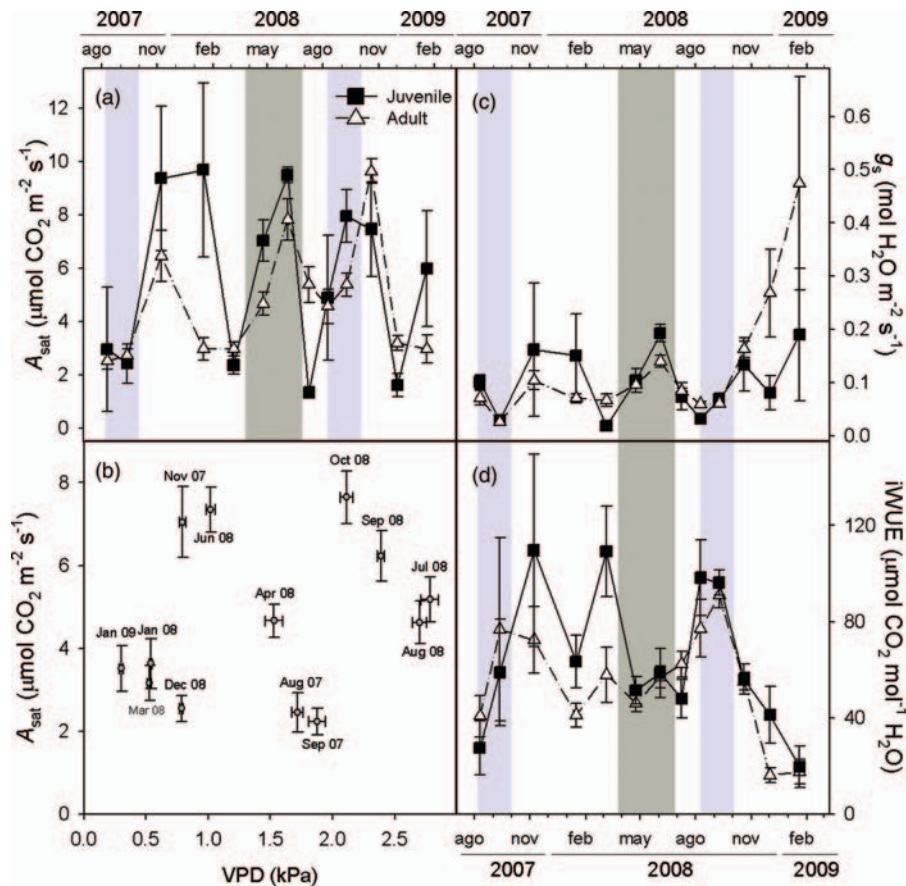
Figure 4. Gas-exchange parameters (means ± SE) monitored at Buenafuente del Sistal (BF site) from August 2007 to January 2009: (a) A_{sat}, (b) A_{sat} vs. VPD, (c) g_s and (d) instantaneous iWUE; for reproductive adults vs. non-reproductive juveniles. Shadowed periods correspond to observed main (dark) and secondary (light) radial growth peaks.

maintenance of open stomata and carbon gain could be regarded as an adaptive advantage. This could warrant greater earlywood formation in response to warmer temperatures in late winter and early spring (Kagawa et al. 2005). Furthermore, maintenance of carbon gain during the summer (when VPD increases up to 2.8 kPa in the study area) could allow for higher latewood production, first because it is linked to enhanced earlywood production (Pasho et al. 2011) and also in response to rainfall events in late summer and autumn (Camarero et al. 2010). The observed seasonal variation of monitored gas-exchange variables showed that maximum photosynthesis (A_{sat}) and stomatal conductance to water (g_s)

were reached in spring, but similarly high rates were reached in the autumn—when we registered a secondary peak of radial growth—which were similar to the rates and seasonal evolution of other junipers (Armas and Pugnaire 2009, Bendevis et al. 2010). The seasonal dynamics of A_{sat} were similar among both study years. Yet, we found that in winter 2008–2009, A_{sat} was lower than in the previous winter. This could be due to lower light availability during the autumn–winter of 2008–2009 (see Figure S2 available as Supplementary Data at *Tree Physiology* Online) compared with the previous one. This suggestion is supported by the presented climate–growth relationships, since we found that

March cloud cover and precipitation were negatively corre-
lated with growth in the three study sites. One possible inter-
pretation of this latter result is that during these months,
precipitation falls in the form of snow when climatic conditions
are cool and wet due to cyclonic activity (Rozas et al. 2009).
However, the response functions do not support that low tem-
peratures in late winter (March) constrain subsequent radial
growth the following spring. We argue that increased cloudi-
ness on its own has a direct negative effect on growth
because increased cloud cover reduces incident light, hence
limiting photosynthesis, as suggested by our data. Reduced
winter photosynthesis would negatively affect *J. thurifera*
growth as this species partly relies on winter carbon gain to
warrant carbohydrate supply for further growth. The indirect
effects of cloudiness on photosynthesis and growth seem to
be species specific, since in nearby *Pinus halepensis* Mill. for-
estswet and mild winters enhance growth (Pasho et al. 2011).

Influence of plant gender and age

Males and females differed neither in radial growth nor in gas-
exchange variables. These results agree with those of Gimeno
et al. (2011), yet this is partially in disagreement with the
results of Montesinos et al. (2006, 2012) who argued that
males had lower reproductive costs and therefore could
devote more resources to vegetative growth. Nevertheless, in
Montesinos et al. (2006) sampled trees were older (mean age
was ~150 years) than in the present study. We cannot discard
differences in the environmental conditions between that
study and our own study site, neither that differences in
growth might arise later in the ontogeny, but females in our
study did not grow less than males once the former reached
reproductive maturity (see Figure S3 available as
Supplementary Data at *Tree Physiology* Online). Lack of signifi-
cant differences between genders could be due to first, non-
negligible male reproductive effort since male *J. thurifera* trees
produce thousands of pollen cones every winter, an important
biomass and nutrient sink (Montesinos et al. 2012). This
demand occurs when photosynthetic activity is lowest, and
therefore requires mobilization of stored nutrients, an energy
expenditure that is frequently disregarded (Poot 1997, Leigh
et al. 2006). Second, it could also occur that females may
truly have a higher energy demand throughout the growing
season, but compensate for this with greater assimilation
capacity and resource-use efficiency (Lambers et al. 2000,
Montesinos et al. 2012). Our data do not support the second
hypothesis, suggesting either that gender reproductive costs
are comparable or that females compensate for greater costs
through different mechanisms.

Adults and juveniles varied over time in A_{sat} and iWUE differ-
ently. Juveniles had higher A_{sat} and iWUE in early spring and
late autumn. These results suggest juveniles were more
sensitive to varying climatic conditions, which agrees with

Rozas et al. (2009), who found that radial growth responsive-
ness to climate decreased with age in this species. Also, this
would indicate that juveniles are able to take advantage of
advanced and delayed favourable conditions over the sea-
sons. This, together with a higher plasticity of cambial activity
in juveniles than in adults (Rossi et al. 2008), would allow
juveniles to take advantage of an earlier spring cambial reacti-
vation and also to extend xylogenesis (e.g., latewood lignifica-
tion) profiting autumn rainfall. Under unfavourable climatic
conditions (summer drought and winter cold) both adults and
juveniles decreased A_{sat} and g_s but adults maintained slightly
higher rates, an extra effort which may be aimed at synthesiz-
ing carbohydrates for wood formation or for cone
development.

Climate–growth relationships and growth trends

Our results show that the climate has been getting warmer
since the 1950s in the study area, and that this trend is stron-
ger for spring and summer. For an overlapping period, we
found that basal area increment (BAI) was positively correlated
to mean annual temperature in two of the three study sites.
Our climate–growth relationships showed that *J. thurifera*
growth was favoured by warm spring (April) temperatures,
which agrees with the results from previous dendrochronologi-
cal (Bertaudiere et al. 1999, Rozas et al. 2009) and xylogen-
esis (Camarero et al. 2010) studies. Warmer spring
temperatures lead to an earlier cambial reactivation in conifers
(Deslauriers et al. 2008), which would favour *J. thurifera*
growth, since low temperatures constrain wood formation in
continental areas during the winter. This was also reflected by
the negative significant relationship found between growth and
low winter temperatures (Bertaudiere et al. 1999, Rozas et al.
2009). Given the climatic sensitivity of *J. thurifera* to warm
spring temperatures, we propose that the rise in spring tem-
peratures due to climate change could enhance *J. thurifera*
radial growth in the long term, which is also supported by the
positive relationship found between BAI and annual mean tem-
perature. Our results contrast with the significant growth
decline related to increased warming-induced water stress
observed in several Mediterranean conifer species (Sarris et al.
2007, Linares et al. 2010, Linares and Tiscar 2010) and par-
ticularly for more temperate tree species distributed in
Mediterranean areas (Tardif et al. 2003, Jump et al. 2006,
Piovesan et al. 2008). Yet, increases in radial growth have
been documented in other woody species in the Mediterranean
region. For example, Todaro et al. (2007) found that *Pinus leu-
codermis* Ant. growth and recruitment have increased since the
1970s in response to altered trends of minimum and maximum
temperatures and decreased anthropogenic pressure. Our
results concur with those from Vila et al. (2008) who found
that *Pinus sylvestris* L. and *P. halepensis* showed increasing BAI
with time, attributed to the occurrence of milder winters and

extended growing seasons. Likewise, Martinez-Vilalta et al. (2008) found a significant increase of annual BAI in Scots pine which was ascribed to a CO_2 fertilization effect, for most of the twentieth century. However, for the last quarter of the twentieth century, Martinez-Vilalta et al. (2008) found that the positive effect of CO_2 fertilization was blurred by the negative effect of occurrence of drier summers. In other biomes, growth increases have also been reported in response to an extension of the growing season, to CO_2 fertilization and to changes in management regimes (Norby et al. 2005, Huang et al. 2007, Johnson and Abrams 2009).

The positive effect of higher spring temperatures on radial growth could be counteracted by reduced growth during the summer due to increased temperature and decreased rainfall, as *J. thurifera* growth is sensitive to July rainfall and temperature. Given that we observed very low radial growth during the summer, we argue that increased summer drought is not likely to have a negative impact on growth. This suggestion is supported by Camarero et al. (2010) who showed that *J. thurifera* exhibits very low growth rates in summer both under semi-arid and sub-humid Mediterranean climates. We found that radial increment peaked between April and June and also between September and October in both studied years, and that the autumn increase was greater in 2008 under wetter conditions than in 2009. As we have not found any significant trend affecting autumn temperature or rainfall, it is likely that wet and mild autumns, in combination with earlier and warmer springs, will favour *J. thurifera* radial growth. Nevertheless, we cannot warrant that this effect will be maintained if temperatures continue to increase and cause a decrease in soil water availability under a warmer and drier future scenario.

Besides climate, other intrinsic and extrinsic factors might be influencing growth, like ontogeny, competition and management policies. In our case, ontogeny is not likely to wholly explain these trends since the sampled trees had probably overcome their juvenile radial growth phase characterized by increasing rates of BAI. Nevertheless, ontogeny cannot be completely discarded as some trees have been reported to have increasing BAI trends throughout their lives (Johnson and Abrams 2009). The role of other non-climatic factors, mostly changes in traditional management in *J. thurifera*, has been also recently explored (Olano et al. 2008, DeSoto et al. 2010). These authors highlight the importance of increasing competition with other woody species and changes in habitat use, in modulating the recent growth trends of *J. thurifera*. In fact, these additional factors are likely to be responsible for some of the observed differences in growth among sites. We found that in the TA site growth was lower than that at the other sites, which could be due to competition with other coexisting woody species (*P. nigra*, *Q. ilex*). It should be noted, though, that the lowermost site (RS) had the highest BAI, further suggesting that climate is a major factor affecting growth. It is difficult,

however, to separate the effects of different environmental and anthropogenic factors on tree growth and population dynamics (Camarero and Gutierrez 1999; Todaro et al. 2007). Furthermore, direct causal factors may not be fully ascribed as we have not quantified the effect of other factors, such as increasing CO_2 and N fertilization due to man-induced atmospheric changes (Martinez-Vilalta et al. 2008).

Final remarks

In contrast to the declining growth trends shown by other Mediterranean woody species, we found that increasingly warming temperatures enhanced *J. thurifera* growth rate. This could be partially due to increased annual and spring temperatures, as suggested by the climatic sensitiveness of radial growth in this species. Sunny and warm springs, as well as wet summers and autumns favour *J. thurifera* radial growth. This is achieved by its ability to maintain carbon gain under harsh climatic conditions (cold winter temperatures and summer drought) and to its plastic growth patterns in response to climate. However, climate change could have unexpected effects on *J. thurifera* growth trends due to altered cloud cover and light availability conditions during key periods like winter and early spring, which could impair photosynthesis and further radial growth.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Conflict of interest

None declared.

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Supplementary Information

Table S1 Results of the linear regressions calculated between annual and seasonal mean temperature (T) and total rainfall (R) *vs.* time. Significant ($P < 0.05$) regressions are in bold and non-significant associations are indicated by *ns*.

Variable	R^2	F	P	Equation
Annual T	0.210	14.54	**0.0003**	T = -24.6 + 0.018 year
Spring T	0.106	7.61	**0.0079**	T = -33.6 + 0.021 year
Summer T	0.262	19.50	**< 0.0001**	T = -41.5 + 0.030 year
Autumn T	0.012	0.67	0.4175	*ns*
Winter T	0.041	2.36	0.1300	*ns*
Annual R	0.036	2.06	0.1568	*ns*
Spring R	0.016	0.88	0.3513	*ns*
Summer R	0.144	1.17	0.2844	*ns*
Autumn R	< 0.001	< 0.01	0.9757	*ns*
Winter R	0.021	1.18	0.2823	*ns*

Table S2 Dendrochronological statistics of the site chronologies (site codes as in Table 1). All parameters refer to residual indexed chronologies excepting the mean ± SD tree-ring width (TRW) and the first-order autocorrelation (AR1) which were calculated using raw data (tree-ring width).

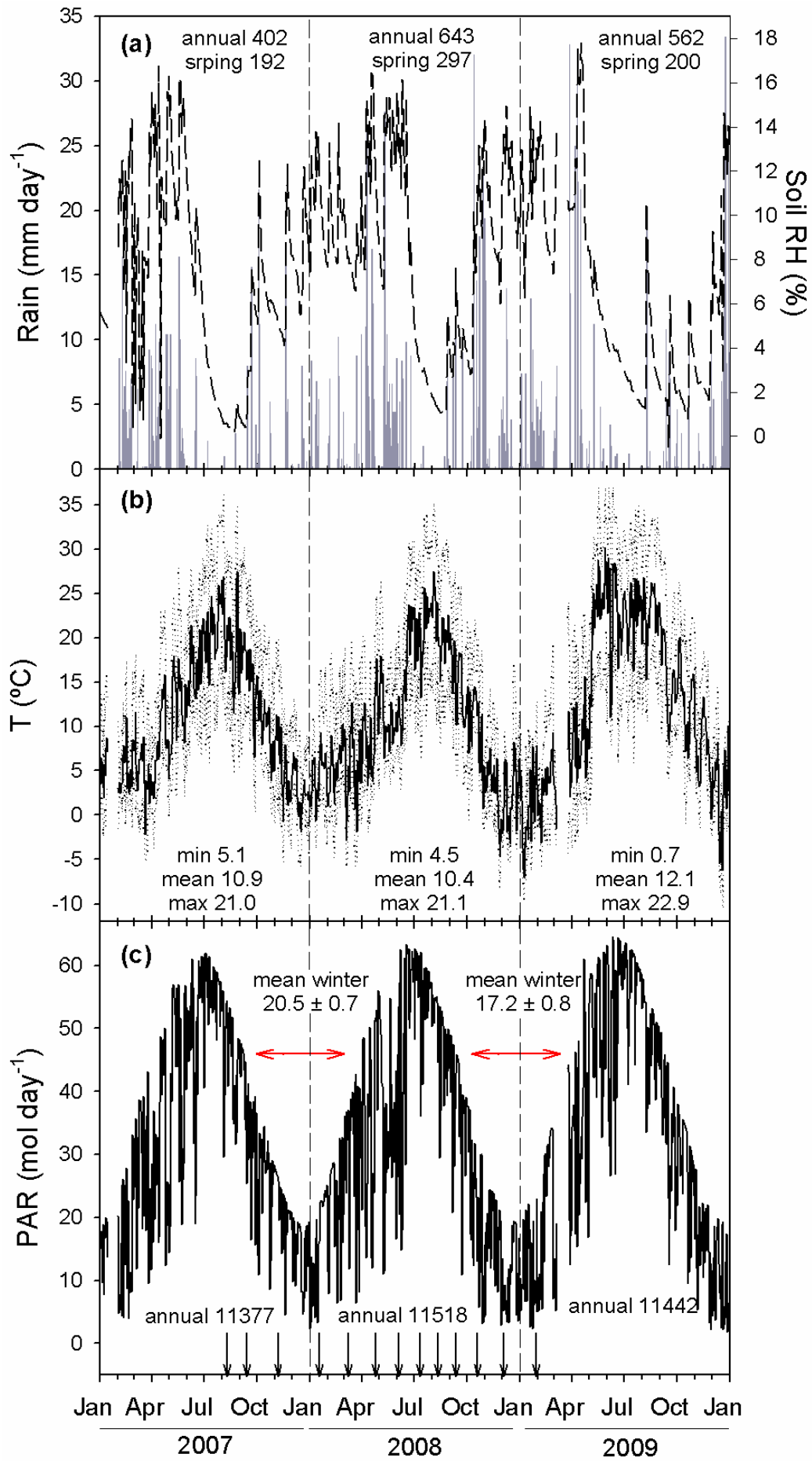| Site	TA	RS	BF
No. trees / No. radii	14/27	14 / 32	13 / 18
Time span	1949-2007	1941-2007	1944-2007
Common interval	1965-2007	1963-2007	1965-2007
TRW (mm)	1.49 ± 0.66	1.88 ± 0.64	1.78 ± 0.67
AR1	0.59	0.53	0.49
MS_x	0.19	0.24	0.29
r_{bt}	0.33	0.39	0.39
EPS	0.87	0.92	0.89
SNR	7.83	9.20	8.15
PC1 (%)	38.89	46.80	44.27

5

Abbreviations and explanations: Common interval, the statistical reliable time span (see EPS definition below); TRW, mean tree-ring width; AR1, first-order autocorrelation; MS_x, mean sensitivity; r_{bt}, mean correlation between trees; EPS, Expressed Population Signal (a measure of the tree-to-tree common growth variance used to define the common interval which is usually regarded when EPS > 0.85); SNR,

10 Signal-to-Noise ratio, an assessment of how well replicated and related are the tree-ring series in each site; PC1, variance explained by the first principal component.

Fig. S1 Climatic diagram of the meterological station closest to the study sites (Molina de Aragón, 40º 50' 40'' N, 1º 53' 07'' W, 1063 m a.s.l.) Mean monthly temperatures and total rainfall ($n = 56$, period 1951-2007). Numbers are annual mean temperature and total rainfall. Filled and dashed portions of the horizontal lower bar indicate the periods with sure and probable frost, respectively.
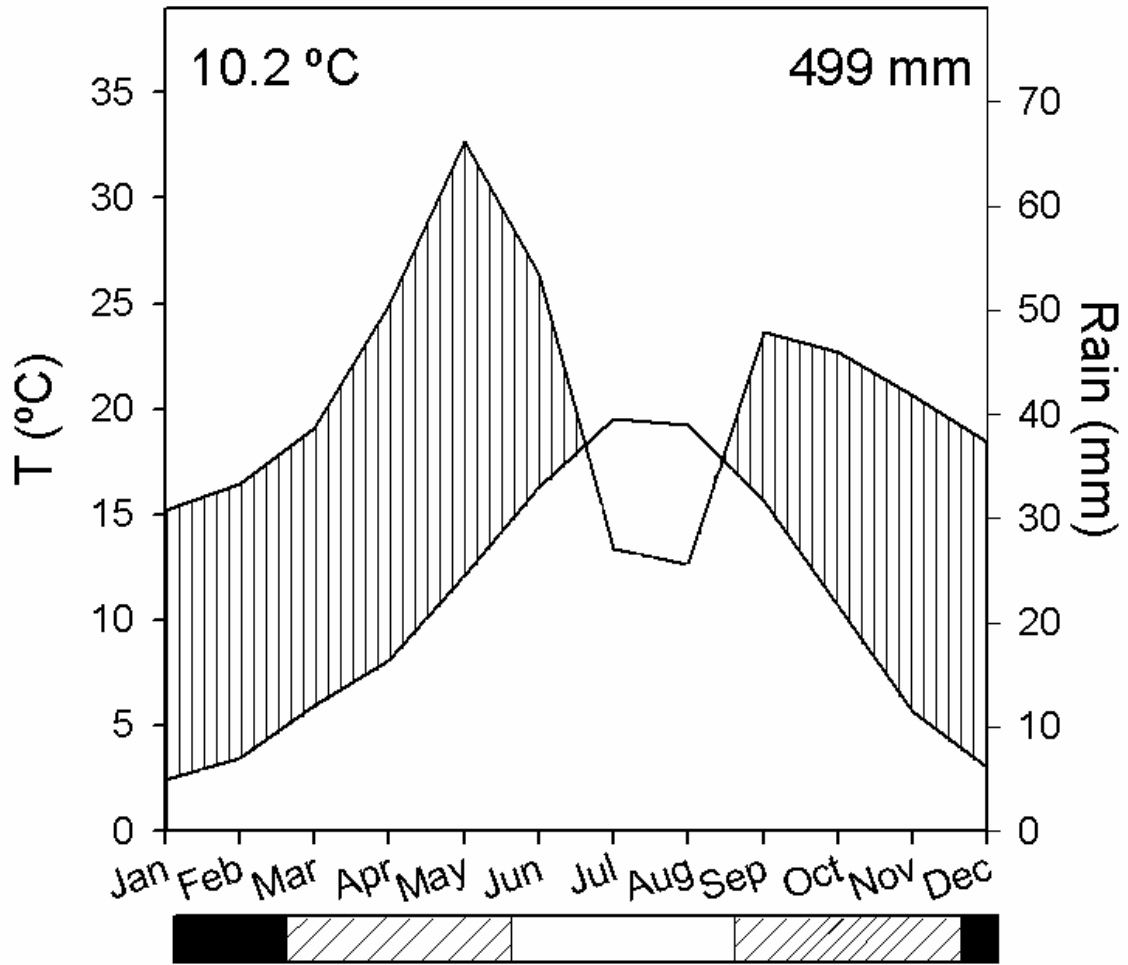
Fig. S2 Climatic conditions from 2007 to 2009 at the study area. (a) Daily rainfall (bars) and relative soil humidity (line, Soil RH), numbers are the total annual and spring rainfall in mm; (b) mean (continuous line), maximum and minimum (dotted lines) daily temperatures, numbers are the mean temperature of the coldest (January, min) and hottest month (July, max), and the annual mean in ºC; and (c) daily photosynthetically active radiation (PAR), numbers are the total annual PAR (in mol) and mean autumn-winter (October-March, red arrows) daily PAR (in mol day^{-1}). Days of the autumn-winter of 2007-2008 were significantly brighter than in 2008-2009 ($F = 10.8$, $P = 0.001$, $n = 327$). Black arrows indicate the sampling dates of the gas-exchange measurements.

(a) annual 402 srping 192   annual 643 spring 297   annual 562 spring 200

Rain (mm day^{-1})

Soil RH (%)

(b)

T (°C)

min 5.1
mean 10.9
max 21.0

min 4.5
mean 10.4
max 21.1

min 0.7
mean 12.1
max 22.9

(c)

mean winter
20.5 ± 0.7

mean winter
17.2 ± 0.8

PAR (mol day^{-1})

annual 11377   annual 11518   annual 11442

Jan Apr Jul Oct Jan Apr Jul Oct Jan Apr Jul Oct Jan

2007   2008   2009

5

Fig. S3. Mean (± SE) cumulative radial growth at the three study sites (site codes as in Table 1) of females (closed symbols) and males (open symbols). Vertical bars represent the number of trees of each sex sampled at each site. The vertical dashed lines indicate approximate maturation age according to Montesinos *et al.* (2006).