

Recent climate hiatus revealed dual control by temperature and drought on the stem growth of Mediterranean Quercus ilex

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1 RECENT CLIMATE HIATUS REVEALED DUAL CONTROL BY TEMPERATURE AND 2 DROUGHT ON THE STEM GROWTH OF MEDITERRANEAN QUERCUS ILEX 3 4 5 Running head: STEM GROWTH AND CLIMATE HIATUS 6 Morine Lempereur^{1, 2*}, Jean-Marc Limousin¹, Frédéric Guibal³, Jean-Marc Ourcival¹, Serge 7 Rambal^{1, 4}, Julien Ruffault^{1, 5, 6}, and Florent Mouillot⁷ 8 9 ¹ Centre d'Ecologie Fonctionnelle et Evolutive CEFE, UMR 5175, CNRS - Université de Montpellier -10 11 Université Paul-Valéry Montpellier – EPHE, 1919 Route de Mende, 34293 Montpellier Cedex 5, France 12 ² Agence de l'Environnement et de la Maîtrise de l'Energie, 20, avenue du Grésillé- BP 90406, 49004 13 Angers Cedex 01, France 14 ³ Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE), UMR 7263 15 CNRS, Aix-Marseille Université – IRD – Avignon Université, Europôle de l'Arbois, BP 8013545, Aix-16 en-Provence Cedex 4, France 17 ⁴ Universidade Federal de Lavras, Departamento de Biologia, CP 3037, CEP 37200-000, Lavras, MG, 18 Brazil 19 ⁵ Irstea, UR REVOVER, 3275 route Cézanne, CS 40061, 13182 Aix-en-Provence cedex 5, France ⁶ CEREGE UMR 7330, CNRS – Aix-Marseille Université, Europôle de l'Arbois, BP 8013545, Aix-en-20 21 Provence Cedex 4, France 22 ⁷ Centre d'Ecologie Fonctionnelle et Evolutive CEFE, UMR 5175, CNRS - Université de Montpellier -23 Université Paul-Valéry Montpellier – EPHE - IRD, 1919 Route de Mende, 34293 Montpellier Cedex 5, 24 France 25 *Author for correspondence: Morine Lempereur 26 27 Tel: +33(0)467613292 28 Email: morine.lempereur@cefe.cnrs.fr 29 30 **Keywords**: Basal area increment, climate change, climate-growth response, climate hiatus, 31 drought, growth duration, growth phenology, Quercus ilex 32 33 **Type of Paper**: Primary Research Article

Abstract

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36 A better understanding of stem growth phenology and its climate drivers would improve 37 projections of the impact of climate change on forest productivity. Under a Mediterranean 38 climate, tree growth is primarily limited by soil water availability during summer, but cold 39 temperatures in winter also prevent tree growth in evergreen forests. In the widespread 40 Mediterranean evergreen tree species *Quercus ilex*, the duration of stem growth has been shown 41 to predict annual stem increment, and to be limited by winter temperatures on the one hand, and by the summer drought onset on the other. We tested how these climatic controls of Q. ilex 42 43 growth varied with recent climate change by correlating a 40-year tree ring record and a 30year annual diameter inventory against winter temperature, spring precipitation, and simulated 44 45 growth duration. Our results showed that growth duration was the best predictor of annual tree 46 growth. We predicted that recent climate changes have resulted in earlier growth onset (-10 47 days) due to winter warming and earlier growth cessation (-26 days) due to earlier drought 48 onset. These climatic trends partly offset one another, as we observed no significant trend of 49 change in tree growth between 1968 and 2008. A moving-window correlation analysis revealed 50 that in the past, Q. ilex growth was only correlated with water availability, but that since the 51 2000s, growth suddenly became correlated with winter temperature in addition to spring 52 drought. This change in the climate-growth correlations matches the start of the recent 53 atmospheric warming pause also known as the 'climate hiatus'. The duration of growth of Q. 54 *ilex* is thus shortened because winter warming has stopped compensating for increasing drought 55 in the last decade. Decoupled trends in precipitation and temperature, a neglected aspect of climate change, might reduce forest productivity through phenological constraints and have 56 57 more consequences than climate warming alone.

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LIST OF ABBREVIATIONS USE IN PAPER

- 60 **FS**: Long-term field survey of diameter at breast height (DBH), measured from 1986 to 2013.
- **RW**: Ring-width series, measured from 1942 to 2008.
- **AD**: Automatic dendrometer series, measured from 2004 to 2013.
- Puéchabon station: weather station located in the study site since 1984.
- 64 **SML station**: weather station located in St Martin-de-Londres, 12 km away from the study site,
- data available from 1966 to 2013 (Meteo France).
- 66 **T**_{JFM}: Mean of daily temperature from January to March (°C).
- 67 **P**_{AMJ}: Sum of precipitation from April to June (mm).
- 68 **WSI**: Water stress integral, a time-cumulated drought severity index (MPa day)
- 69 **t**₀: Day of year when stem growth starts

- t_1 : Day of year when stem growth stops in early summer Δt_{t0-t1} : Duration of the period between t_0 and t_1 computed for each set of simulated phenological
- thresholds.

- **BAI**: Basal area increment of the stems, expressed in mm² year⁻¹ **PET**: Potential evapotranspiration (mm)

Introduction

Stem growth, recorded in annual tree rings, is a synthetic surrogate of carbon input in standing biomass (Babst *et al.*, 2014) and an index for tree vitality and fitness (Bigler & Bugmann 2003; Benito-Garzon *et al.*, 2013). In return, it is the record of the yearly climatic conditions that have enabled stem growth over a period lasting from decades to centuries (Fritts 1976; Briffa *et al.*, 2002). Understanding the factors that control stem growth is therefore crucial to assess the impact of past and future climate change on forests, but remains a major scientific issue due to a series of currently unresolved uncertainties.

First, the climate sensitivity of tree growth is generally considered to depend on photosynthesis and respiration fluxes because most process-based models assume that tree growth is carbon limited (Davi *et al.*, 2006; Gaucherel *et al.*, 2008; Keenan *et al.*, 2011). Carbon allocation to sapwood is therefore the key process driving the carbon sink, and is at the heart of tree growth simulations in most terrestrial biosphere models (e.g. Sitch *et al.*, 2003; Friedlingstein *et al.*, 2006; Fisher *et al.*, 2010). Several allocation schemes exist (e.g. fixed allocation, the pipe model, and hierarchical allocation between plant organs, Schippers *et al.*, 2015), but there is accumulating experimental evidence that cambial activity (sink limitation) is more sensitive to environmental stressors than carbon assimilation (source limitation; Körner 2003; Fatichi *et al.*, 2014; Guillemot *et al.*, 2015; Körner 2015; Delpierre *et al.*, 2016a). Taking sink limitation into account in terrestrial biosphere models is thus likely to improve their ability to simulate past and future forest productivity (Leuzinger *et al.*, 2013; Fatichi *et al.*, 2014), but a better characterization of the phenology and climate sensitivity of wood formation is a prerequisite (Rossi *et al.*, 2011; Rossi *et al.*, 2014; Lempereur *et al.*, 2015; Delpierre *et al.*, 2016a; Delpierre *et al.*, 2016b).

Second, global climate change may simultaneously exert opposing influences on forest functioning, and these impacts are difficult to disentangle. For example, increased water use efficiency due to atmospheric CO₂ enrichment is sometime reported to increase tree growth in spite of concurrently increasing aridity (Martinez-Vilalta *et al.*, 2008; Koutouvas 2013), but the opposite finding is far more common (Peñuelas *et al.*, 2011). Warming also exerts opposing impacts on tree growth: on one hand it increases the length of the growing season (Keeling *et al.*, 1996; Dragoni *et al.*, 2011) while on the other hand it exacerbates atmospheric evaporative demand and hence water limitation (Angert *et al.*, 2005; Zhao & Running, 2010). Warming may therefore affect tree growth positively (e.g. Rossi *et al.*, 2014) or negatively (e.g. Brzostek *et al.*, 2014) depending on the ecosystem under consideration.

Third, relationships between tree growth and climate may change under the influence of climate change (e.g. Briffa *et al.*, 1998; Büntgen *et al.*, 2006; Carrer & Urbinati 2006; D'Arrigo *et al.*, 2008). A classic example of this phenomenon is the so-called 'divergence problem' in northern forests, which is a weakening of the positive temperature response of tree growth in strongly temperature limited ecosystems since the middle of the 20th century (D'Arrigo *et al.*, 2008). The consequence of such temporal variations in tree growth sensitivity to climate is that empirical dendrochronological models based on statistical links between tree growth and climate cannot be extrapolated to long term historical and future climate conditions with confidence (e.g. Gea-Izquierdo *et al.*, 2013; Subedi & Sharma 2013).

Fourth, climate change itself is a complex phenomenon that may result in changes in the mean climate (IPCC 2014), in the frequency of extreme climatic events (Meehl & Tebaldi 2004) and in seasonality (Giorgi *et al.*, 2011; Ruffault *et al.*, 2013), all of which may have contrasted impacts on tree growth and function. In addition, climate change is not monotonous and the recent slowing down of the warming trend, early identified by Easterling & Wehner (2009) and later called the 'climate hiatus' (Trenberth & Fasullo, 2013), is currently a topic of increasing scientific interest. But if most scientific studies have focused on explaining the causes and processes behind this 'climate hiatus' or pause in atmospheric warming (Meehl *et al.*, 2011; Balmaseda *et al.*, 2013; England *et al.*, 2014; Steinman *et al.*, 2015), few have attempted to assess its ecological consequences, especially for processes that are highly sensitive to climate, such as tree growth.

In water limited ecosystems, where forest productivity is primarily limited by drought (Churkina & Running 1998; Zhao & Running 2010), the supply of water from rainfall appears to be the key variable to explain tree growth (Babst *et al.*, 2013). In the case of the Mediterranean species *Quercus ilex*, the conclusions of dendrochronological studies converge more specifically to identify winter and spring rainfall amounts as the key drivers of annual stem growth (Gutiérrez *et al.*, 2011). In contrast, *Q. ilex* stem growth is generally poorly correlated with winter and spring temperatures. Daily measurements of basal area increment over an eight year period (2004-2011) with automatic dendrometers in a *Q. ilex* forest, demonstrated that the duration of spring growth was an accurate predictor of annual stem growth (Lempereur *et al.*, 2015). After observing that the duration of spring growth was determined by winter temperature for growth start and a lower threshold of predawn plant water potential of -1.1 MPa for growth cessation, Lempereur *et al.* (2015) proposed a new hypothesis wherein the annual growth of *Q. ilex* is under the dual control of winter temperature and spring water limitation.

In this contextual framework, we used both tree ring records over a 40-year period and an annual diameter inventory over a 30-year period to (i) test whether the stem growth phenology approach proposed by Lempereur *et al.* (2015) can explain *Q. ilex* growth over a long retrospective period with different growth estimation methods, (ii) assess the relative importance of drought and temperature in limiting *Q. ilex* growth under a Mediterranean climate, and (iii) evaluate the stationarity of these limitations in recent decades. In particular, we aimed to identify whether any temporal shift in the climate controls of *Q. ilex* growth (drought or temperature plus drought) are concomitant to, and the functional consequence of, the recent pause in atmospheric warming.

MATERIALS AND METHODS

Site description

The study site is located 35 km north-west of Montpellier (southern France), on a flat plateau, in the Puéchabon state forest (43°44′29″N, 3°35′45″E, 270 m a.s.l.). This forest has been managed as a coppice for centuries and the last clearcut took place in 1942. Vegetation is largely dominated by a dense overstory of the evergreen oak *Quercus ilex*. In 2014, the average top canopy height was 5.5 m and the stem density was 4700 (±700) stems ha⁻¹. Understory evergreen species, *Buxus sempervirens*, *Phyllirea latifolia*, *Pistacia lentiscus* and *Juniperus oxycedrus*, compose a sparse shrubby layer (height < 2 m) with less than 25% cover. The climate is Mediterranean, with 80% of the rainfall occurring between September and April. Average annual precipitation for the 1984-2013 period was 916 mm (550 to 1549 mm). Mean annual temperature over the same period was 13.2 °C with a minimum in January (5.5 °C) and a maximum in July (22.9 °C). The very shallow bedrock has a hard Jurassic limestone origin. The volumetric fraction of stones and rocks averages 0.75 in the top 0-50 cm and 0.90 below. The stone free fine fraction of the soil in the 0-50 cm layer is a homogeneous silty clay loam (USDA texture triangle) comprising 38.8% clay, 35.2% silt and 26% sand.

Monitoring annual stem growth

Stem diameter at breast height (DBH) was measured annually from 1986 to 2013 on 319 trees distributed in eight circular plots (diameter 20 m) within an area of 2 ha. The 319 trees used in this field survey (hereafter FS, Fig. 1) were selected so as to include all the diameter

size classes in 1986. DBH was measured every winter under dry conditions using a diameter tape at a height identified by a paint mark on the stem. In January 2008, the stem diameters were distributed as follows: 58% < 8 cm DBH, 24% between 8 and 10 cm and 18% >10 cm. Because the smaller size classes exhibited a very low growth and a high mortality rate, we restricted our analysis to the 125 trees with a DBH > 8 cm in 2008 to obtain a stronger growth signal (Table 1). From 2004 to 2013, stem growth was measured more frequently and with greater accuracy using automatic band dendrometers on a subset of trees in two neighboring plots (for more details, see Lempereur *et al.*, 2015). Automatic dendrometers (ELPA-98, University of Oulu, Finland; hereafter AD) were set up at a height of 1.3 m above the ground on 6 to 12 trees with DBH > 7 cm. The two datasets (FS and AD) were strongly correlated during their overlapping period (Table 1), thus demonstrating the relative accuracy of FS in estimating the annual growth of the largest trees.



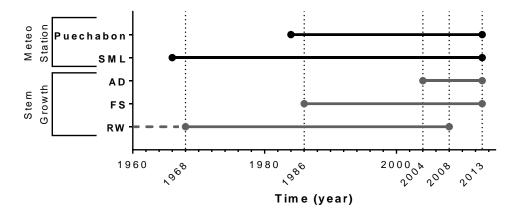


Fig. 1 Chronological timeline of the main data sources used in this study. Stem growth series: automatic dendrometers (AD), field survey (FS) of stem diameter at breast height (DBH) and ring width series (RW). Climatic data: Puéchabon meteorological station and St Martin-de-Londres (SML) meteorological station.

Dendrochronological procedures

In 2005 and 2008, 15 and 12 stems, respectively, were selected among the largest size classes of the field survey (FS) sample (10 cm < DBH < 16 cm) and cut down to measure ring-width chronology. Cross sections were collected at stump height, air dried, sanded and polished (40 to 400 grit). The longest growth radii in each cross section were selected and compared pairwise under a binocular magnifier. In old coppiced oaks, rings are narrow and sometimes not clearly visible after 40 years of cambial age; consequently only 12 of the sampled stems could be cross dated with confidence, seven stems in 2005 and five stems in 2008. The first ring was formed in 1942 after the clearcut in winter 1941-1942, so data in the ring width series

(hereafter RW) were obtained from 1942 to 2008 (Table 1, Fig. 1). Cross dating was facilitated by the presence of frost rings corresponding to the severe winters of 1963, 1985 and 1987. These rings, typical for years with severe freezing episodes, were abnormally wide because the cells of their initial area were crushed and dislocated, a typical constraint on tree ring interpretation in woody species under a Mediterranean climate (Cherubini *et al.*, 2003). This particular feature made them useful as markers for cross dating but prevented the reliable measurement of annual stem growth, so these years were excluded from subsequent analyses. Cross correlation coefficients on annual tree ring indices calculated among the 12 individual series were all higher than 0.6 (P-value<0.05). The ring width measured at stump height and along the longest growth radius was then rescaled to the tree DBH at the time of the cut. This required correction for the tapering between stump height (20 cm) and breast height (130 cm) as well as correction for the bark thickness (see Fig. S1 for details). The average tree ring width after rescaling, which was used to calculate the basal area increment (BAI), was 954 μ m (CV = 48%) between 1942 and 2008, and 792 μ m (CV = 38%) over the period 1968-2008 used in our study.

Table 1 Main characteristics of the three growth series used in the study, automatic dendrometer (AD), field survey (FS) and ring width (RW), over their respective complete temporal series and their overlap periods. Coefficients of correlation (r) between FS and AD over the period 2004-2013 and between RW and FS over the period 1987-2008 are given (P-value < 0.05: *; P-value < 0.001: ***).

Characteristics of the growth series								
	Method	Period	Mean BAI (mm²)	DBH 2008 (cm)	Sample size			
AD	Auto Dendro	2004-2013	$185.8(\pm 70,00)$	11.1 (±2.45)	12			
FS	Diameter tape	1987-2013	154.4 (±44,47)	$10.5~(\pm 1.85)$	125			
\mathbf{RW}	Ring width	1968-2008	204.6 (±55,39)	12.7 (±1.75)	12			
Correlations of	on overlap periods							
	Ovelap period	Growth series	Mean BAI (mm²)	r				
AD vs. FS	2004-2013	AD	$185.8(\pm 70.00)$	0.90 (***)				
		FS	142.3 (±55.37)	0.90 (****)				
FS vs. RW	1987-2008	FS	158.2 (±44.68)	0.55 (*)				
		DIII	1060(45.00)	0.55 (*)				

 $196.2(\pm 45.00)$

Climate variables

The Puéchabon meteorological station (hereafter Puéchabon) is located in a clearing 200 m away from the study plot and has provided daily on-site climate data since 1984 (Fig. 1). Precipitation was measured with a tipping bucket rain gauge (ARG100; Environmental Measurements, Sunderland, UK) calibrated to 0.2 mm per tip and placed 1 m above the ground, air temperature was recorded with a MP100 sensor (Rotronic, Bassersdorf, Switzerland) at a

RW

height of 2 m, and net radiation was measured with a pyranometer (SKS1110; Skye Instruments, UK) at a height of 2 m above the ground.

To extend our analysis before 1984, we used climate variables (daily rainfall, daily minimum and maximum temperature) from the St Martin-de-Londres meteorological station (hereafter SML; 43°47′06′′N; 3°43′48′′E, altitude 194 m a.s.l., located about 12 km away from the study site; source Meteo-France) over the period 1966-2013 (Fig. 1). The mean daily temperature was calculated as the average of the minimum and maximum daily temperature. The climate data from SML station were compared to on-site measurements in the overlap period 1984-2013 (Table S1 and Fig. S2). The comparison showed close agreement for temperature but a higher rainfall amount in SML than in Puéchabon. No significant biases (slope not different from 1, and distance to origin not different from 0) were observed between the two meteorological stations in the two crucial variables related to stem growth: the mean temperature from January to March (T_{JFM}) and the sum of precipitation from April to June (P_{AMJ}. Fig. S2).

Daily solar radiation at the SML station was calculated from the processing chain described in Kumar *et al.* (1997). In the first step, theoretical clear sky solar radiation (R_a) was calculated from the daily timing of sunrise and sunset, the bi-hourly sun azimuthal angle and the atmospheric transmittance according to longitude using R Cran Packages 'RAtmosphere' and 'oce'. No topographical effects were taken into consideration. Actual solar radiation (R_s, in MJ m⁻² day⁻¹) was then calculated from maximum and minimum daily temperature (T_{max} and T_{min}, respectively) and the clear sky theoretical radiation following the Hargreaves equation: $R_s = k_{Rs} \sqrt{(T_{max} - T_{min})} R_a$, where the adjustment coefficient k_{Rs} was set to 0.16 for interior location (Allen *et al.*, 1998). Results of the Hargreaves equation were validated against solar radiation measured in Puéchabon since 1998.

Modeling predawn leaf water potential and water stress integral

Soil water storage integrated over the rooting depth, c.a. 4.5 m, was measured during the vegetative periods of 1984-1986 and from July 1998 to August 2009 at approximately monthly intervals, using a neutron moisture gauge (503DR Hydroprobe, CPN, Concord, CA, USA). Discrete measurements were interpolated at a daily time step using the soil water balance model described by Rambal (1993) and further used by Rambal *et al.* (2014). The model was driven by daily values of incoming solar radiation, minimum and maximum temperatures, and rainfall amount. Potential evapotranspiration was computed using the Priestley-Taylor equation

(Priestley & Taylor, 1972). The reduced major axis (RMA) regression between neutron moisture gauge measurements and model simulations yielded an R² of 0.93, the slope was 0.94 ± 0.05 (P < 0.0001, n = 91) and the intercept not significantly different from 0. Soil water storage and soil water potential were linked by a Campbell-type retention curve (Campbell, 1985) whose parameters are strongly dependent on soil texture (Saxton et al., 1986; Rambal et al., 2003). Predawn leaf water potential used for model validation was measured about eight times a year between April and October from 2003 to 2009 on a subsample of four trees among those equipped with automatic dendrometers (see Limousin et al., 2012). RMA regressions between measured and simulated values of predawn leaf water potential yielded an R² of 0.84, the slope was 0.93 ± 0.05 (P < 0.0001, n = 54), and the intercept was not significantly different from 0. We used the simulations of predawn water potential rather than soil water content, as the former is more closely linked with plant functioning (Rambal et al., 2003). The daily simulations of predawn water potential were performed with the climate data from the Puéchabon and SML stations for the periods 1984-2012 and 1966-2012, respectively. The water stress integral (WSI), defined by Myers (1988) as the seasonally or yearly sum of predawn water potential, was used as a drought severity index to quantify annual or seasonal water stress.

Duration of spring basal area increment: calculations of dates t_0 and t_1

The dates of stem growth phenology that bounded the spring growth period, the DOY (day of the year) when stem growth starts (hereafter t_0) and the DOY when stem growth stops in early summer (hereafter t_1 , Fig. S3), were estimated for each year. The relationships between t_0 or t_1 and climate variables were calibrated by Lempereur *et al.* (2015) on observations of t_0 and t_1 obtained with automatic dendrometers from 2004 to 2011. Briefly, t_0 was defined as the first day at which basal area exceeded the culmination of the previous year, and t_1 as the first day when BAI became null or negative (see Lempereur *et al.*, 2015 for methodological details). t_0 and t_1 were estimated using climate data from both Puéchabon and the nearby SML station over their corresponding timeframes. t_0 was predicted by a nonlinear relationship with the mean temperature from January to March (T_{JFM}). The relationships were fitted between t_0 and T_{JFM} measured in Puéchabon ($t_0 = 849.2*exp(-0.6436 T_{JFM})+121$; $R^2 = 0.95$; RMSE = 2.6 days; Lempereur *et al.*, 2015) and between t_0 and T_{JFM} measured in SML ($t_0 = 4300*exp(-0.943 T_{JFM})+124.4$; $R^2 = 0.95$; RMSE = 2.3 days; Fig. S4). t_1 was predicted by the DOY when the plant water potential simulated using climate data from Puéchabon reached a threshold of $t_0 = 1.1$ MPa ($t_0 = 0.75$; t_0

the plant water potential simulated using climate data from SML reached a threshold of - 1.1 MPa + ϵ (with ϵ = -0.1; R² = 0.73; RMSE = 13.5 days) due to the slight differences in temperature and precipitation between the two stations (see Fig. S5). The duration Δt_{t0-t1} corresponds to the duration of the period between t_0 and t_1 and was computed for each pair of simulated phenological thresholds.

Data processing and statistical analyses

Annual stem growth (DBH and ring widths) was converted into annual basal area increments (BAI, expressed in mm² year¹) for the two data series. Analyses were performed with averaged BAI values of 125 and 5-12 individual trees for FS and RW, respectively. The year 1992 presented two periods when predawn plant water potential fell below the threshold of -1.1 MPa, in spring and autumn (Fig. S6). This unusual bi-modal drought prevented us from determining the duration Δt_{t0t1} so 1992 was excluded from subsequent analyses. The growth series BAI_{FS} included measurements that appeared to be outliers compared to BAI_{RW} or BAI_{AD} for the years 2002 and 2010 (see Fig. S7). In 2002, BAI_{FS} was particularly low when BAI_{RW} was close to the expected value, and in 2010, BAI_{FS} was clearly higher than the BAI_{AD} value. Because BAI_{FS} is less accurate than the other two methods, and was calculated as the difference between two subsequent measurements of DBH, these two values were considered to be unreliable and excluded from the analyses performed on BAI_{FS}.

To investigate the links between tree growth and climate, we computed the correlations between our two different growth datasets (FS and RW) and a set of relevant climate predictors. For each correlation tested, we reported the Pearson's correlation coefficient and its significance based on the standard bootstrap method with 1000 samples taken from the original distribution of climate and tree ring data. Within each sample, the number of observations was random and followed a geometric distribution. We used the 'treeclim' R package built upon the DENDROCLIM2002 statistical tool dedicated to tree ring analysis (Biondi & Waikul, 2004; Zang & Biondi, 2015). Climate predictors were derived from temperature and precipitation at monthly, seasonal and annual time scales, and from our functional index of spring growth duration (Δt_{1011}). To test for the stationarity of the drought and temperature controls over the studied period, we also performed the same bootstrap sampling Pearson correlation analysis on a 10-year moving window along the whole series.

The temporal trends in stem growth and climate variables were characterized using both trend tests and breakpoint analyses. Temporal trends in time series were estimated using the

Theil-Sen test (Sen 1968) from the 'openair' R cran package, applied on a 1000 block bootstrap simulations to account for auto-correlated variables (Kunsch 1989), with the block length set to n/3, n being the length of the time series. Temporal breakpoints in the time series were assessed by computing the yearly F-statistic (sequential F-test) and the *supF* statistic was then used to test for their significance.

RESULTS

Sensitivity of stem growth to the dual temperature-drought drivers

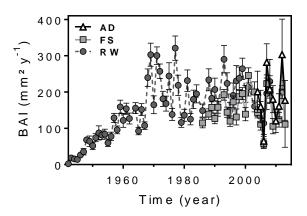


Fig. 2 Time series of annual stem basal area increment (BAI) for the ring width series (RW; 1942-2008), the long-term field survey (FS; 1986-2013) and the automatic dendrometer series (AD; 2004-2013). Error bars are standard errors among the sampled trees (see Table 1 for sample size).

Annual stem growth (BAI_{RW}) from 1942 to 2008 exhibited two distinct phases, with a significant breakpoint around 1967 (Fstat = 81.96; P-value<0.0001; Fig. 2). The first phase (1942-1967) lasted 25 years after the clearcut and showed a linear increase of 5.5 (±0.62) mm² y⁻¹ in annual BAI. This phase, which corresponds approximately to the cut frequency formerly used in the traditional management of this *Q. ilex* coppice (Floret *et al.*, 1992), was characterized by incomplete canopy cover and notable self-thinning. The second phase (1968-2008) showed a stabilization of BAI_{RW} around a mean value of 203.8 (±54.84) mm² y⁻¹. The influence of climate on stem growth was consequently only considered from 1968 on, to avoid the confounding effects caused by changes in competition, space-filling and self-thinning during the first phase.

The two long-term growth series BAI_{RW} and BAI_{FS} were significantly correlated with each other during their overlap period 1986-2008 (r = 0.55, P-value < 0.05, Table 1). Both series of BAI exhibited large between year variations (coefficient of variation, CV = 27% and 29% for

BAI_{RW} and BAI_{FS}, respectively). The minimum value of BAI was recorded in 2006 for both series: BAI_{RW} = 114 mm² y⁻¹ (SE = 36.5 mm² y⁻¹) and BAI_{FS} = 58 mm² y⁻¹ (SE = 13.2 mm² y⁻¹). The maximum BAI was recorded in 1977 for RW (BAI_{RW} = 348 mm² y⁻¹, SE = 22.1 mm² y⁻¹) and in 2001 for FS (BAI_{FS} = 246 mm² y⁻¹; SE = 20.8 mm² y⁻¹, vs. BAI_{RW} = 213 mm² y⁻¹; SE = 24 mm² y⁻¹.2).



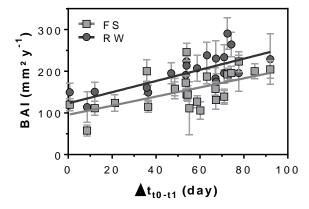


Fig. 3 Relationship between yearly basal area increment (BAI) and the duration of the spring growth period (Δt_{t0}). Ring width (RW, dark grey circle) is shown for the period 1984-2008 and field survey (FS, light grey square) for the period 1986-2013. The linear relationships between Δt_{t0-t1} and BAI_{RW} (dark grey line; BAI_{RW} = 1.34* Δt_{t0-t1} + 122.9; R² = 0.56; P-value < 0.001) or BAI_{FS} (light grey line; BAI_{FS} = 1.09* Δt_{t0-t1} + 95.5; R² = 0.35; P-value < 0.01) are represented. Error bars are standard errors.

The DOY of the start (t_0) and stop (t_1) of the spring stem growth, simulated over the period 1984-2013 using climate data from the Puéchabon station, occurred on average in mid-May (DOY 133, SD = 9.9 days) and early July (DOY 184, SD = 23.5 days), respectively. The growth duration Δt_{t0-t1} varied considerably among years (CV = 50%) with values ranging from 2 days in 1995 to 95 days in 2008 (Fig. 3). BAI was linearly correlated with Δt_{t0-t1} for both stem growth series (R^2 = 0.56; P-value < 0.0001 and R^2 = 0.35; P-value < 0.01 for RW and FS respectively; Fig. 3). Moreover, Δt_{t0-t1} was the best explanatory variable for the inter-annual variations in BAI_{RW} compared to other climate variables over the period 1984-2008 (Table 2; 3). We thus concluded that the dual control of annual stem growth by temperature and precipitation, stated by Lempereur *et al.* (2015) for the period 2004-2011, remained valid for a longer retrospective period and when growth is measured with less accuracy than with automatic dendrometers. The intercepts of the linear relationships between BAI and Δt_{t0-t1} , which represent the residual autumnal growth (Lempereur *et al.*, 2015), differed significantly between the two BAI series (F = 17.97; P-value < 0.001), with 122.9 (±34.42) mm² y⁻¹ and 95.5 (±39.09) mm² y⁻¹ for RW and FS, respectively (Fig. 3). By contrast, the slopes of these relationships did not differ

significantly between RW and FS (F = 0.46; P-value > 0.05), and the common slope equals $1.23 \text{ mm}^2 \text{ day}^{-1}$. The sensitivity of BAI_{RW} to $\Delta t_{t0\text{-}t1}$ was thus identical to the sensitivity of BAI_{FS}. Furthermore, neither the extension of the study period to 1968-2008 nor the switch in meteorological stations from Puéchabon to SML, removed the significant correlation between BAI_{RW} and $\Delta t_{t0\text{-}t1}$ (R² = 0.31; P-value < 0.001; Table 2).

Table 2 Mean Pearson's correlation coefficients (and significance derived from a 1000 classical bootstrap sampling) between chronologies of annual stem growth (BAI) and the main phenology explanatory variables. The correlations are given using climate variables measured in Puéchabon field surveys (FS) over the period 1986-2013 and ring width (RW) over the period 1984-2008, and climate data from the SML meteorological station over the period 1968-2008 for RW (see Fig. 1). The explanatory variables tested were the start and stop growth dates (t_0 and t_1 , respectively) and the duration of stem growth ($\Delta t_{t_0-t_1}$). The coefficient of correlation (r) and the level of statistical significance (*P-value < 0.05; **P-value < 0.01; ***P-value < 0.001) are given. Significant correlations are in bold.

	FS	RW	RW
Period	1986-2013	1984-2008	1968-2008
t_0	-0.43**	-0.51***	0.18
t_1	0.56***	0.68***	0.66***
$\Delta t_{\text{t0-t1}}$	0.60***	0.73***	0.56***

Stem growth response to climate trends from 1968 to 2013

Over the longer period 1968-2008, Δt_{t0-t1} was not a better predictor of BAI than the sum of spring precipitation (P_{AMJ}) or t_1 alone (r = 0.75; P-value < 0.001 and r = 0.66; P-value < 0.001 respectively; Table 2, 3), and we also observed a loss of correlation between BAI and t_0 (r = 0.18; P-value = 0.31; Table 2).

P_{AMJ} was the main explanatory climate variable for t₁ (over the period 1968-2008: r = 0.80; P-value<0.001) and it exhibited no temporal trend between 1968 and 2013 (P-value = 0.31; Fig. 4b). However, spring water limitation increased (WSI in spring: -0.48 MPa day y⁻¹; P-value<0.001; Fig. 4d, Table S3) as a result of increasing spring potential evapotranspiration (PET; +0.028 mm day⁻¹ y⁻¹; P-value<0.001; Fig. 4c, Table S3). This trend in PET was mainly due to the significant warming trend in spring temperatures throughout the period 1968-2013 (+0.07°C y⁻¹; P-value<0.001; Fig. 4a, Table S3). As a result, drought onset t₁ exhibited a temporal trend toward earlier dates (-0.57 day y⁻¹; P-value<0.01; Fig. 5). The correlation between BAI_{RW} and P_{AMJ} remained significant, however, throughout most of the 1968-2008 period (Fig. 6a).

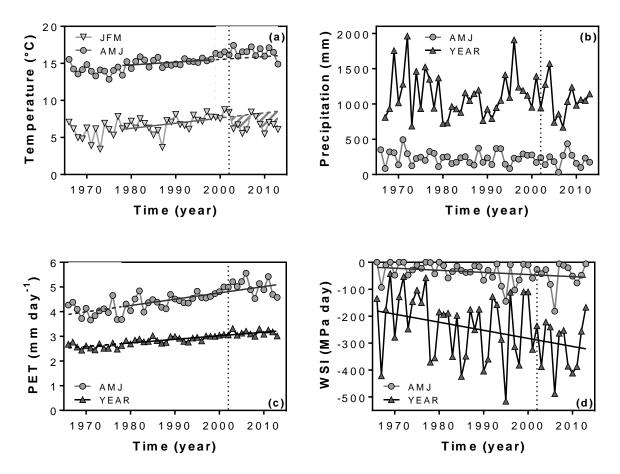


Fig. 4 Temporal trends in (a) spring (AMJ) temperature (grey circles) and winter (JFM) temperature (light grey inverted triangles), (b) mean annual precipitation (dark grey triangles) and AMJ precipitation (grey circles), (c) mean annual potential evapotranspiration (ETP; dark grey triangles) and AMJ ETP (grey circles) and (d) annual water stress integral (WSI, dark grey triangles) and AMJ three months WSI (grey circles). The solid lines represent significant temporal trends (P-value<0.05). The dashed lines represent the extended trend for temperature after 1998, or before 1978 for PET. The effect of the warming pause on the JFM temperature (panel a) is shown by the hatched area between the points and the regression line, the vertical dotted lines indicate the start of the winter warming pause in 2002.

In parallel, T_{JFM} increased significantly throughout the period (+0.04 °C y⁻¹; P-value<0.05; Fig. 4a) which led to a significant trend of t₀ toward earlier dates (-0.21 day y⁻¹; P-value<0.05; Fig. 5). However, a pause in the atmospheric winter warming occurred in the last decade. This warming pause is apparent in the discrepancy between actual and expected T_{JFM} obtained from the temporal trend built over the period 1978-1998. The year 1978 was chosen because it corresponds to the onset of a rapid warming phase in the Northern Hemisphere (Mann *et al.*, 1999). Similarly, the year 1998 was considered as the onset of the climate hiatus observations (IPCC 2014). We used the period 1978-1998 to build the reference trend line and extrapolate expected T_{JFM} values over the 1999-2013 period. We then tested for a breakpoint in the anomalies between observed and expected T_{JFM} over the whole period. Such a breakpoint was identified in 2002, indicating a significant slowing down in winter warming after this date

(Fstat = 21.52; P<0.001; Fig. 4a). This temporal pattern was also observed at seven other meteorological stations in the region surrounding our study site (Table S4 and Fig. S8), thus confirming the regional occurrence of the globally observed climate hiatus (Trenberth & Fasullo, 2013). The date of growth onset (t₀) was very sensitive to the warming pause in T_{JFM} and a breakpoint in the t₀ trend was observed in 2002 (Fstat = 21.52; P<0.001; Fig. 5). We also observed that the start of the winter warming pause coincided with a change in the climate controls on annual stem growth. Indeed, the correlation between BAI and T_{JFM}, which was only significant over one 10-year window between 1968 and 1994, became constantly significant from the time window 1995-2004 on (Fig. 6b).

Table 3 Mean Pearson's correlation coefficients and significance (derived from a 1000 classical bootstrap sampling) between annual stem growth (BAI) or spring growth duration (Δt_{t0t1}) and monthly or seasonal precipitation (P, in mm) and temperature (T, in °C) for RW data series. The climate data from Puéchabon and Saint Martin-de-Londres meteorological stations were used for the periods 1984-2013 and 1966-2013, respectively. The coefficients of correlation (r) and the level of statistical significance (*P-value < 0.05; **P-value < 0.01; ***P-value < 0.001) are given. Significant correlations are in bold.

	BAI				$\Delta { m t}_{ m t0t1}$			
	1984-2008		1968-2008		1984-2013		1966-2013	
	T	P	T	P	T	P	T	P
November (t-1)	0.06	-0.08	-0.23*	-0.03	0.07	0.24	-0.31*	-0.03
December (t-1)	0.30**	0.08	-0.07	-0.04	0.25	0.04	-0.06	-0.03
January	0.50***	-0.06	0.02	0.15	0.51***	0.03	0.34***	0.14
February	0.37*	-0.27*	-0.02	0.06	0.20	-0.16	0.22	0.02
March	0.34**	-0.17	-0.10	0.21	0.41***	-0.10	0.11	0.19*
April	0.05	0.23	0.00	0.33*	-0.11	0.48***	-0.07	0.24*
May	0.12	0.47***	-0.23	0.57***	0.08	0.37	-0.25*	0.48**
June	-0.46**	0.21	-0.65***	0.44***	-0.01	0.00	-0.24*	0.22
July	-0.56***	0.32**	-0.54***	0.36**	-0.26	-0.13	-0.42***	0.01
August	-0.08	-0.04	-0.30**	0.07	0.03	0.24*	-0.37***	0.08
September	-0.39*	-0.39*	-0.42***	-0.25*	-0.18	-0.35	-0.34***	-0.10
October	-0.13	-0.13	-0.14	-0.04	-0.18	-0.34**	-0.22	-0.15
Jan. Feb. March	0.48***	-0.20	-0.05	0.18	0.47*	-0.11	0.32**	0.15
Apr. May June	-0.15	0.53***	-0.38***	0.75***	-0.02	0.49*	-0.23	0.55***
June Aug. Sept.	-0.42**	-0.34	-0.51*	-0.14	-0.18	-0.30	-0.45***	-0.05
from Nov(t-1) to Oct	0.04	-0.11	-0.37*	0.25*	0.15	0.01	-0.21*	0.17

The temporal trends in t_0 and t_1 , both toward earlier dates (-10 and -26 days, respectively) offset each other to some extent until 2002 and resulted in a non-significant trend in Δt_{t0-t1} . After 2002, the prolonged trend in t_1 continued to decrease while t_0 stabilized, thereby leading to a sudden shortening of the growing season (Fig. 5). The timing of this phenological reduction was concomitant with the appearance of a significant relationship between T_{JFM} and

BAI (Fig. 6b). The decline in Δt_{t0-t1} induced by the winter warming pause resulted in a decrease in BAI_{RW} after 2002. This decreasing trend over time become significant after the 10-year time window 1997-2006 (Fig. 7a,b). BAI_{FS} exhibited a similar decreasing trend in the same period, but of lower amplitude and not significant.

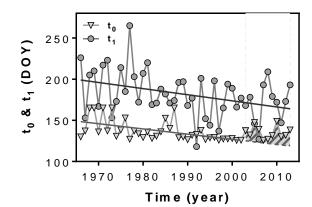
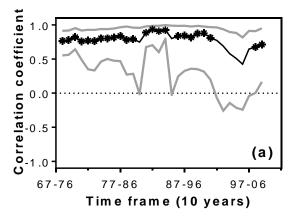


Fig. 5 Onset of phenological stem growth (t_0 , pale grey inverted triangles) and end of stem growth (t_1 , grey circles) from 1966 to 2013, expressed as day of the year (DOY). The effect of the warming pause on t_0 is shown by the hatched area between the points and the regression line over the 1978-1998 period.



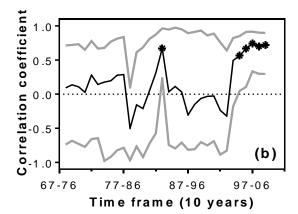
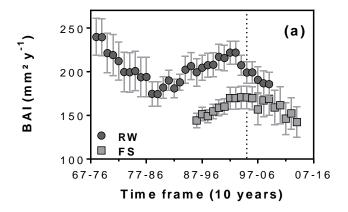


Fig. 6 Temporal variations in the bootstrapped Pearson's correlation coefficients between (a) BAI_{RW} and P_{AMJ} , and (b) BAI_{RW} and T_{JFM} over 10-year moving windows. The black curve represents the correlation coefficient and the grey curves the upper and lower confidence intervals at a significance level $\alpha=0.05$. Asterisks identify the time windows with significant correlations.



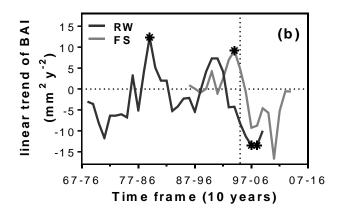


Fig. 7 Temporal trend over 10-year moving windows of (a) mean annual stem growth from 1968 to 2008 and from 1987 to 2013 for ring width (RW, dark grey circles) and field surveys (FS, grey squares), respectively. Error bars are standard errors. (b) Slopes of the linear trends of BAI for the two series. The asterisks indicate time windows with a significant trend (p<0.05). The dotted vertical lines in both panels indicate the first time window with a significant relationship between BAI_{RW} and T_{JFM} after the warming pause.

DISCUSSION

Growth duration as a predictor of annual stem growth

The duration of spring stem growth (Δt_{t0-t1}) was the best explanatory variable of yearly basal area increment for both BAI_{FS} and BAI_{RW} after 1984. This confirms earlier results obtained with automatic dendrometers over a shorter period and a smaller sample of trees (Lempereur *et al.*, 2015), and therefore validates Δt_{t0-t1} as a robust estimator of *Q. ilex* annual stem growth over long time scales and large samples. The two independent samplings we used here differed markedly in the number of trees measured, the measurement method and its precision. FS corresponds to a large number of trees (125 trees) representing a broader tree size distribution but measured with a less precise resolution (0.3 mm of DBH), while RW was measured on a small sample of large dominant trees (12 trees) but with a better resolution

(0.01 mm of radius). Average stem growth was lower for BAI_{FS} than for BAI_{RW}, but both responded linearly and with the same sensitivity to Δt_{t0-t1} (Fig. 3).

The spring stem growth duration Δt_{t0-t1} is defined as the length of the period between the

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onset of spring stem growth (t₀) and the date of growth cessation caused by summer drought (t₁). Lempereur et al. (2015) observed that t₀ was well predicted by winter temperature, and that t₁ occurred when the leaf predawn water potential dropped below a threshold of -1.1 MPa. A similar approach was used by Rossi et al. (2011, 2014) who linked the stem growth of boreal black spruce with the duration of xylem growth delimited by cold temperatures in spring and autumn, and by Delpierre et al. (2016a) who linked the growth of temperate oak to the timing of the summer growth cessation controlled by water limitation. By identifying the climatic limits for cell division and elongation, the temporal delimitation of tree growth duration is an innovative way of improving simulation of forest carbon sink response to climate change (Fatichi et al., 2014). Tree growth has generally been simulated using two types of models: statistical dendroclimatological models, which are empirical and may lead to marked uncertainties when extrapolated to future climate scenarios (e.g. Gea-Izquierdo et al., 2013; Babst et al., 2014); and process based models that link tree growth to carbon assimilation (e.g. Sitch et al., 2003; Friedlingstein et al., 2006; Gaucherel et al., 2008; Keenan et al., 2011), ignoring experimental evidence showing a direct, and generally more limiting, climate control of plant growth (Körner, 2003; Muller et al., 2011). Projecting tree growth based on growth phenology as in Rossi et al. (2011) and Lempereur et al. (2015) merges the biological realism of the first approach, i.e. a direct link between climate and growth, with the mechanistic understanding of tree physiology used in process based models, and be a significant step forward in projecting the response of forest ecosystems to climate change (Delpierre et al., 2016b). Showing that growth duration is an adequate predictor of tree growth for long time series datasets (40 years in our study) and coarse temporal resolution (annual diameter measurements) is thus an important preliminary. Nevertheless, the spring growth duration approach remains limited by both its conditions of applicability and the large proportion of the growth variability not explained by Δt_{t0-t1} . The particular case of the year 1992, with its bi-modal drought in spring and autumn and its wellwatered summer (Fig. S6), suggests that Δt_{t0-t1} can only be used as a descriptor of stem growth phenology in years with typical Mediterranean seasonality and a drought period occurring in summer. While the lowest threshold of predawn water potential below which stem growth is prevented certainly remains valid for any drought seasonality (Hsiao & Xu, 2000; Muller et al., 2011; Lempereur et al., 2015), we hypothesize that the relationship between stem growth and

the duration of periods with adequate growth conditions (the rate of growth) varies in years with peculiar phenology. Variations in the rate of growth may also account for the unexplained variability in the BAI against Δt_{t0-t1} relationships (44% and 65% for RW and FS, respectively; Fig. 3). Finally, the relative extent of autumn growth compared to spring growth would deserve more detailed investigation. Lempereur *et al.* (2015) observed that autumn growth explained only approximately 30% of annual stem growth and was strongly determined by spring conditions, but its magnitude over long time periods and under climate change conditions remains to be described.

Dual limitation of growth by winter cold and spring-summer drought

Summers in the Mediterranean region are typically characterized by the concomitance of low rainfall, high temperature and high solar radiation, while winters are cold and humid. Consequently, vegetation functioning is limited by water deficit in summer and by low temperatures in winter (Mitrakos, 1980; Terradas & Savé, 1992). A cessation of growth during cold and dry periods is frequently observed in Mediterranean trees which display a bi-phasic growth pattern over the year (Cherubini *et al.*, 2002; Campelo *et al.*, 2007; Montserrat-Marti *et al.*, 2009; Camarero *et al.*, 2009, Gutiérrez *et al.*, 2011).

The sensitivity of growth to water deficit is well established in the literature (Lockhart 1965; Hsiao & Xu, 2000; Muller et al., 2011), as is the negative impact of drought on ring width (Fritts, 1976). Previous dendroclimatological studies generally stated that spring to earlysummer precipitation was the main driver of annual stem growth of Q. ilex (Gutiérrez et al., 2011). More precisely, it is the start of the dry season, defined by a threshold of soil water deficit that was identified as the main determinant of variations in inter-annual growth (Maselli et al., 2014; Lempereur et al., 2015). The predominant effect of the timing of drought induced growth cessation on annual stem growth is not limited to Mediterranean ecosystems, as a similar effect has been observed in mesic temperate forests (Brzostek et al., 2014; Delpierre et al., 2016a). In our study, we defined the start of the dry season as a critical threshold of predawn plant water potential of -1.1 MPa. This threshold is biologically meaningful because water potential affects the cell turgor pressure necessary for cell growth (Hsiao & Xu, 2000), and it has the other advantage of comprehensively accounting for climate and local soil conditions in a single metric (Ruffault et al., 2013). It is, however, a more complex index to calculate than climatic indices of drought as it requires substantial knowledge of soil and vegetation characteristics, and accurate meteorological data at the daily time scale. Consequently, the

uncertainty on t_1 was higher than the uncertainty on t_0 , especially when meteorological data from SML (located at a distance of 12 km from the study site) was used instead of on-site data, but t_1 nonetheless remained a good predictor of annual stem growth for whichever period (Table 2).

Depending on the species and on the local bio-climate, a minimum temperature threshold ranging from +4 °C to +7 °C is required for stem growth to occur (Körner, 2003; Rossi *et al.*, 2007; Deslauriers *et al.*, 2008; Gruber *et al.*, 2010; Swidrak *et al.*, 2011; Lempereur *et al.*, 2015). The onset of stem growth can be assessed from winter temperature (Delpierre *et al.*, 2016b), thus the mean winter temperature directly impacts the duration of cambium activity and wood formation (Rossi *et al.*, 2011). However, there is no consensus in dendrochronological studies of the Mediterranean *Q. ilex* that winter temperature is a good predictor of annual BAI, and both negative (Zhang & Romane 1990; Paton *et al.*, 2009; Gea-Izquierdo *et al.*, 2009) and positive correlations (Campelo *et al.*, 2009; Nijland *et al.*, 2011; Gea-Izquierdo *et al.*, 2011) between annual stem growth and winter temperature have been reported. In our study, a positive correlation between growth and winter temperature was observed over the period 1984-2008 (r = 0.48, P<0.001; Table 3), in accordance with Lempereur *et al.* (2015), but the relationship was not significant for the period 1968-2008, either with t₀ or with T_{JFM}.

Taken together, these results suggest that summer drought is the main limiting factor for *Q. ilex* growth, which is to be expected under the dry Mediterranean climate. Nevertheless, the contrasted growth responses to winter temperature depending on the study concerned, or on the period of interest, led us to investigate the impact of recent climate change on *Q. ilex* growth in more detail.

Can warmer winter temperature compensate for earlier summer drought under climate change?

From 1968 to 2008, the annual and spring amounts of precipitation were stable (Fig. 4b), but water limitation increased (Fig. 4d) due to increasing potential evapotranspiration with rising temperature in spring and summer (Fig. 4a and c), in accordance with regional observations (Ruffault *et al.*, 2013). Consequently, we simulated an earlier occurrence of drought onset (t₁, -26 days on average) along with an earlier growth onset, although to a lesser extent (t₀, -10 days; Fig. 5), which, taken together resulted in a non-significant decrease in growth duration. The positive effect of warming on ecosystem functioning and tree growth

through a longer growing season has been widely observed in temperature limited boreal and temperate forests (Keeling *et al.*, 1996; Menzel *et al.*, 2006; D'Arrigo *et al.*, 2008; Dragoni *et al.*, 2011). However, in water limited regions, like the Mediterranean, warming is generally considered to be an aggravating factor for drought, mainly because of increased evaporative demand (Angert *et al.*, 2005; Zhao & Running, 2010; Park *et al.*, 2012). Consequently, climate warming in the Mediterranean usually reduces tree growth (Jump *et al.*, 2006; Sarris *et al.*, 2007; Peñuelas *et al.*, 2008; Piovesan *et al.*, 2008; Martin-Benito *et al.*, 2010). Our results thus mitigate this widely accepted conclusion and illustrate the peculiar parallel controls driven by temperature, such that the benefit of an earlier stem growth is cancelled out by earlier drought onset mostly caused by increasing evaporative demand.

The effect of temperature on t_1 , mediated by PET, may also explain why the correlation with growth was better for t_1 than for P_{AMJ} over the period 1984-2008, when temperatures increased significantly, but not over the longer period 1968-2008. Actually, spring PET, like temperature, did not increase significantly until the early 1980s (Fig. 4a, c), suggesting that, in the past, inter-annual variability in precipitation may have been a stronger driver of drought onset. Alternatively, the lack of on-site precipitation measurements before 1984 may mean that t_1 estimates based on SML are less closely linked to on-site conditions than three-month cumulated precipitation. The correlation in precipitation amounts between Puéchabon and SML actually increases with longer temporal resolutions.

Winter warming may also have a positive impact on stem growth by delaying growth cessation in autumn, thereby partly compensating for earlier drought onset. However, the phenology of autumn growth cessation appears to be less variable than that of t₀ (Lempereur *et al.*, 2015), possibly because it is concurrently driven by photoperiod. Moreover, warm winters may even impact *Q. ilex* growth negatively if the species requires winter chilling, as is the case of the deciduous *Quercus* species (Fu *et al.*, 2015).

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A Mediterranean "divergence problem"

When looking at the temporal variations in the correlations between stem growth and climate variables, we observed an abrupt and significant increase in the sensitivity of stem growth to temperature in the early 2000s, while at the same time, its response to precipitation weakened (Fig. 6a, b). Temporal changes in the response of tree growth to climate have been observed in a wide range of climates and tree species in recent decades (e.g. Briffa *et al.*, 1998; Büntgen *et al.*, 2006; Carrer & Urbinati 2006; Jump *et al.*, 2007; D'Arrigo *et al.*, 2008). The

'divergence problem' in northern forests has been defined as the tendency for tree growth at previously temperature limited sites to undergo a weakening of their temperature response concurrent with an increasing sensitivity to drought (D'Arrigo *et al.*, 2008). Our results suggest a Mediterranean 'divergence problem' according to which tree growth in water limited Mediterranean ecosystems undergo a weakening of their response to spring-summer precipitation and an increasing sensitivity to winter temperatures. Similar reports of temporal changes from water driven to increasingly temperature driven tree growth in water limited ecosystems have already been reported for beech forests in northeast Spain (Jump *et al.*, 2007), black pine forests in Spain (Martin-Benito *et al.*, 2010), and Scots pine, European larch and black pine in Switzerland (Feichtinger *et al.*, 2014). These observations differ from ours by reporting an increase of the overall negative effect of warming on tree growth. Nevertheless, they collectively point to the increasing influence of temperature on the growth of previously water limited trees.

Concurrent increase in drought and warming: a keystone aspect of climate change revealed during the recent warming hiatus

A keystone result of our study is the sudden significance of the growth-temperature relationship occurring from the 1995-2004 time window on (Fig. 6b). In parallel, we observed lower winter temperatures than would have been expected on the basis of continuous climate warming (Fig. 4a). This regional pattern is therefore comparable to the globally observed "warming hiatus" (Easterling & Wehner 2009; Trenberth & Fasullo 2013). Our results suggest that these recent cooler winter temperatures resulted in later growth onset and led to an increased temperature constraint on the duration of stem growth. In the meantime, the constraint exerted by the water deficit increased constantly from 1968 onward with neither breakpoints nor changes in the trend line (Fig. 4d, 5). As a result, the stem growth of *Q. ilex* was significantly correlated only with water deficit in the past, but the shorter growth period after the 2000s revealed the dual control by winter temperatures and spring-summer water deficit. The pause in climate warming in turn disrupted the precarious balance between increasing winter temperatures and increasing spring-summer water deficit, which temporarily sustained stem growth until the end of the 1990s (Fig. 7). This is, to our knowledge, the first example of a 'divergence problem' in the tree growth-climate relationship triggered not by a continuous climate change but instead by the warming pause. This recent warming pause, a still controversial aspect of climate change (Lewandowsky et al., 2015; Wehner & Easterling 2015),

654 is mainly caused by the variations in Atlantic and Pacific multidecadal oscillations (Steinman 655 et al., 2015), and produced globally heterogeneous patterns of breakpoint in the recent warming trend (Ying et al., 2015), with an enhanced effect on winter temperature in Eurasia (Li et al., 656 657 2015). It is however, likely to be reversed in the coming decades (Steinman et al., 2015). 658 Whether a future re-acceleration of climate warming in the Mediterranean would compensate 659 for increasing water deficit by phenological stimulation of earlier tree growth again, or on the 660 contrary, further exacerbate drought stress remains an open and important question. Studying trends in targeted and concurrent climate variables such as temperature and drought should fully 661 662 capture the complexity of climate change impacts (Mazdiyani & Aghakouchak 2015). Climate 663 projections for the Mediterranean region forecast an increase in potential evapotranspiration and a decrease in summer precipitation by the end of the 21th century (Gao & Giorgi 2008; 664 Ruffault et al., 2014), which are likely to move the onset of drought forward more strongly than 665 666 the onset of spring growth (Lempereur et al., 2015). Together with the current growth limiting 667 winter temperatures, these future trends in drought features could lead to a sharp reduction in 668 forest productivity and an increase in tree mortality in Mediterranean Q. ilex forests.

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SUPPORTING INFORMATION

- 952 **Fig. S1** Relationships used to rescale the ring width series to the tree DBH at the time of the
- cut: tree tapering (base diameter minus DBH) against DBH, and bark thickness against DBH.
- **Table S1** Summary of climate data for Puéchabon and St Martin-de-Londres meteorological
- 955 stations.

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- 956 **Fig. S2** Relationships between the meteorological data of Puéchabon and St Martin-de-Londres
- 957 for the overlap period 1984-2013.
- 958 **Fig. S3** Characteristic example of annual stem growth showing the main phenological events
- 959 for stem growth.
- 960 Fig. S4 Relationship between the spring onset of growth (t₀) and the January to March
- temperature (T_{JFM}) for the meteorological station of St Martin-de-Londres.
- Fig. S5 Relationship between observed and predicted day of the year of growth cessation due
- 963 to drought (t₁) when simulating plant water potential with the meteorological data from St
- 964 Martin-de-Londres.
- 965 **Fig. S6** Seasonal variations of simulated predawn leaf water in Puéchabon in 1992.
- 966 **Fig. S7** Relationship between yearly basal area increment (BAI) and the duration of the spring
- basal growth period (Δt_{t0-t1}) showing the years 2002 and 2010 that are outliers for the series
- 968 BAI_{ES}.
- 969 **Table S3** Results of the Theil-Sen tests for the trends of temperature, precipitation,
- evapotranspiration and drought index.

- 971 **Fig. S8** Temporal trends in winter temperature for seven meteorological stations in the region
- 972 Languedoc-Roussillon.
- 973 **Table S4** Breakpoints and changes in mean winter temperature for seven meteorological
- 974 stations in the region Languedoc-Roussillon.