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1 RECENT CLIMATE HIATUS REVEALED DUAL CONTROL BY TEMPERATURE AND  
2 DROUGHT ON THE STEM GROWTH OF MEDITERRANEAN *QUERCUS ILEX*

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4  
5 **Running head:** STEM GROWTH AND CLIMATE HIATUS

6  
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31 drought, growth duration, growth phenology, *Quercus ilex*

32  
33 **Type of Paper:** Primary Research Article

34

35 **Abstract**

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  
42 by the summer drought onset on the other. We tested how these climatic controls of *Q. ilex*  
43 growth varied with recent climate change by correlating a 40-year tree ring record and a 30-  
44 year annual diameter inventory against winter temperature, spring precipitation, and simulated  
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  
56 climate change, might reduce forest productivity through phenological constraints and have  
57 more consequences than climate warming alone.

58

59 **LIST OF ABBREVIATIONS USE IN PAPER**

60 **FS:** Long-term field survey of diameter at breast height (DBH), measured from 1986 to 2013.  
61 **RW:** Ring-width series, measured from 1942 to 2008.  
62 **AD:** Automatic dendrometer series, measured from 2004 to 2013.  
63 **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,  
65 data available from 1966 to 2013 (Meteo France).  
66 **T<sub>JFM</sub>:** Mean of daily temperature from January to March (°C).  
67 **P<sub>AMJ</sub>:** Sum of precipitation from April to June (mm).  
68 **WSI:** Water stress integral, a time-cumulated drought severity index (MPa day)  
69 **to:** Day of year when stem growth starts

70 **t<sub>1</sub>**: Day of year when stem growth stops in early summer  
71 **Δt<sub>0-t1</sub>**: Duration of the period between t<sub>0</sub> and t<sub>1</sub> computed for each set of simulated phenological  
72 thresholds.  
73 **BAI**: Basal area increment of the stems, expressed in mm<sup>2</sup> year<sup>-1</sup>  
74 **PET**: Potential evapotranspiration (mm)  
75

## 76 INTRODUCTION

77 Stem growth, recorded in annual tree rings, is a synthetic surrogate of carbon input in  
78 standing biomass (Babst *et al.*, 2014) and an index for tree vitality and fitness (Bigler &  
79 Bugmann 2003; Benito-Garzon *et al.*, 2013). In return, it is the record of the yearly climatic  
80 conditions that have enabled stem growth over a period lasting from decades to centuries (Fritts  
81 1976; Briffa *et al.*, 2002). Understanding the factors that control stem growth is therefore crucial  
82 to assess the impact of past and future climate change on forests, but remains a major scientific  
83 issue due to a series of currently unresolved uncertainties.

84 First, the climate sensitivity of tree growth is generally considered to depend on  
85 photosynthesis and respiration fluxes because most process-based models assume that tree  
86 growth is carbon limited (Davi *et al.*, 2006; Gaucherel *et al.*, 2008; Keenan *et al.*, 2011). Carbon  
87 allocation to sapwood is therefore the key process driving the carbon sink, and is at the heart of  
88 tree growth simulations in most terrestrial biosphere models (e.g. Sitch *et al.*, 2003;  
89 Friedlingstein *et al.*, 2006; Fisher *et al.*, 2010). Several allocation schemes exist (e.g. fixed  
90 allocation, the pipe model, and hierarchical allocation between plant organs, Schippers *et al.*,  
91 2015), but there is accumulating experimental evidence that cambial activity (sink limitation)  
92 is more sensitive to environmental stressors than carbon assimilation (source limitation; Körner  
93 2003; Fatichi *et al.*, 2014; Guillemot *et al.*, 2015; Körner 2015; Delpierre *et al.*, 2016a). Taking  
94 sink limitation into account in terrestrial biosphere models is thus likely to improve their ability  
95 to simulate past and future forest productivity (Leuzinger *et al.*, 2013; Fatichi *et al.*, 2014), but  
96 a better characterization of the phenology and climate sensitivity of wood formation is a  
97 prerequisite (Rossi *et al.*, 2011; Rossi *et al.*, 2014; Lempereur *et al.*, 2015; Delpierre *et al.*,  
98 2016a; Delpierre *et al.*, 2016b).

99 Second, global climate change may simultaneously exert opposing influences on forest  
100 functioning, and these impacts are difficult to disentangle. For example, increased water use  
101 efficiency due to atmospheric CO<sub>2</sub> enrichment is sometime reported to increase tree growth in  
102 spite of concurrently increasing aridity (Martinez-Vilalta *et al.*, 2008; Koutouvas 2013), but the  
103 opposite finding is far more common (Peñuelas *et al.*, 2011). Warming also exerts opposing  
104 impacts on tree growth: on one hand it increases the length of the growing season (Keeling *et al.*  
105 *et al.*, 1996; Dragoni *et al.*, 2011) while on the other hand it exacerbates atmospheric evaporative  
106 demand and hence water limitation (Angert *et al.*, 2005; Zhao & Running, 2010). Warming  
107 may therefore affect tree growth positively (e.g. Rossi *et al.*, 2014) or negatively (e.g. Brzostek  
108 *et al.*, 2014) depending on the ecosystem under consideration.

109 Third, relationships between tree growth and climate may change under the influence of  
110 climate change (e.g. Briffa *et al.*, 1998; Büntgen *et al.*, 2006; Carrer & Urbinati 2006; D'Arrigo  
111 *et al.*, 2008). A classic example of this phenomenon is the so-called 'divergence problem' in  
112 northern forests, which is a weakening of the positive temperature response of tree growth in  
113 strongly temperature limited ecosystems since the middle of the 20<sup>th</sup> century (D'Arrigo *et al.*,  
114 2008). The consequence of such temporal variations in tree growth sensitivity to climate is that  
115 empirical dendrochronological models based on statistical links between tree growth and  
116 climate cannot be extrapolated to long term historical and future climate conditions with  
117 confidence (e.g. Gea-Izquierdo *et al.*, 2013; Subedi & Sharma 2013).

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

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

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

152

## 153 **MATERIALS AND METHODS**

### 154 *Site description*

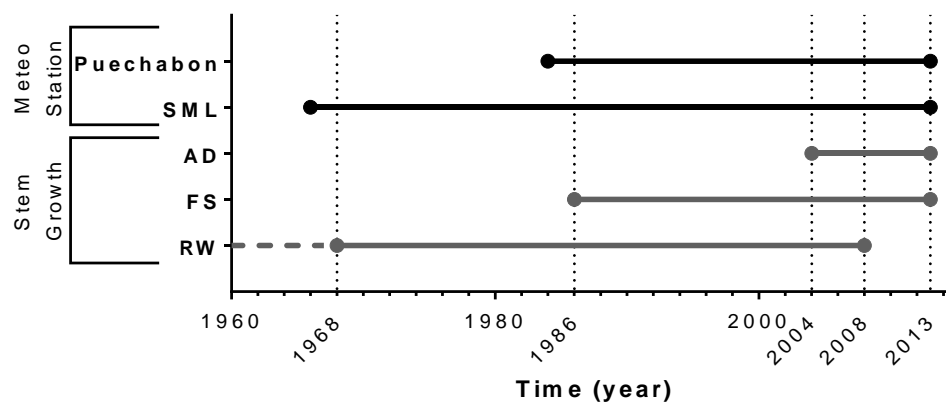
155 The study site is located 35 km north-west of Montpellier (southern France), on a flat  
156 plateau, in the Puéchabon state forest (43°44'29"N, 3°35'45"E, 270 m a.s.l.). This forest has  
157 been managed as a coppice for centuries and the last clearcut took place in 1942. Vegetation is  
158 largely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

169

### 170 *Monitoring annual stem growth*

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

174 size classes in 1986. DBH was measured every winter under dry conditions using a diameter  
 175 tape at a height identified by a paint mark on the stem. In January 2008, the stem diameters  
 176 were distributed as follows: 58% < 8 cm DBH, 24% between 8 and 10 cm and 18% >10 cm.  
 177 Because the smaller size classes exhibited a very low growth and a high mortality rate, we  
 178 restricted our analysis to the 125 trees with a DBH > 8 cm in 2008 to obtain a stronger growth  
 179 signal (Table 1). From 2004 to 2013, stem growth was measured more frequently and with  
 180 greater accuracy using automatic band dendrometers on a subset of trees in two neighboring  
 181 plots (for more details, see Lempereur *et al.*, 2015). Automatic dendrometers (ELPA-98,  
 182 University of Oulu, Finland; hereafter AD) were set up at a height of 1.3 m above the ground  
 183 on 6 to 12 trees with DBH > 7 cm. The two datasets (FS and AD) were strongly correlated  
 184 during their overlapping period (Table 1), thus demonstrating the relative accuracy of FS in  
 185 estimating the annual growth of the largest trees.  
 186



187  
 188 **Fig. 1** Chronological timeline of the main data sources used in this study. Stem growth series: automatic  
 189 dendrometers (AD), field survey (FS) of stem diameter at breast height (DBH) and ring width series (RW).  
 190 Climatic data: Puechabon meteorological station and St Martin-de-Londres (SML) meteorological station.  
 191

## 192 *Dendrochronological procedures*

193 In 2005 and 2008, 15 and 12 stems, respectively, were selected among the largest size  
 194 classes of the field survey (FS) sample (10 cm < DBH < 16 cm) and cut down to measure ring-  
 195 width chronology. Cross sections were collected at stump height, air dried, sanded and polished  
 196 (40 to 400 grit). The longest growth radii in each cross section were selected and compared  
 197 pairwise under a binocular magnifier. In old coppiced oaks, rings are narrow and sometimes  
 198 not clearly visible after 40 years of cambial age; consequently only 12 of the sampled stems  
 199 could be cross dated with confidence, seven stems in 2005 and five stems in 2008. The first  
 200 ring was formed in 1942 after the clearcut in winter 1941-1942, so data in the ring width series



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

216

217 **Table 1** Main characteristics of the three growth series used in the study, automatic dendrometer (AD), field survey  
 218 (FS) and ring width (RW), over their respective complete temporal series and their overlap periods. Coefficients  
 219 of correlation (r) between FS and AD over the period 2004-2013 and between RW and FS over the period 1987-  
 220 2008 are given (P-value < 0.05: \*; P-value < 0.001: \*\*\*).

*Characteristics of the growth series*

	Method	Period	Mean BAI (mm <sup>2</sup> )	DBH 2008 (cm)	Sample size
<b>AD</b>	Auto Dendro	2004-2013	185.8(±70,00)	11.1 (±2.45)	12
<b>FS</b>	Diameter tape	1987-2013	154.4 (±44,47)	10.5 (±1.85)	125
<b>RW</b>	Ring width	1968-2008	204.6 (±55,39)	12.7 (±1.75)	12

*Correlations on overlap periods*

	Overlap period	Growth series	Mean BAI (mm <sup>2</sup> )	r
<b>AD vs. FS</b>	2004-2013	AD	185.8(±70.00)	0.90 (***)
		FS	142.3 (±55.37)	
<b>FS vs. RW</b>	1987-2008	FS	158.2 (±44.68)	0.55 (*)
		RW	196.2(±45.00)	

221

222 **Climate variables**

223 The Puéchabon meteorological station (hereafter Puéchabon) is located in a clearing  
 224 200 m away from the study plot and has provided daily on-site climate data since 1984 (Fig. 1).  
 225 Precipitation was measured with a tipping bucket rain gauge (ARG100; Environmental  
 226 Measurements, Sunderland, UK) calibrated to 0.2 mm per tip and placed 1 m above the ground,  
 227 air temperature was recorded with a MP100 sensor (Rotronic, Bassersdorf, Switzerland) at a

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

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

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

252

### 253 ***Modeling predawn leaf water potential and water stress integral***

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

261 (Priestley & Taylor, 1972). The reduced major axis (RMA) regression between neutron  
262 moisture gauge measurements and model simulations yielded an  $R^2$  of 0.93, the slope was  
263  $0.94 \pm 0.05$  ( $P < 0.0001$ ,  $n = 91$ ) and the intercept not significantly different from 0. Soil water  
264 storage and soil water potential were linked by a Campbell-type retention curve (Campbell,  
265 1985) whose parameters are strongly dependent on soil texture (Saxton *et al.*, 1986; Rambal *et*  
266 *al.*, 2003). Predawn leaf water potential used for model validation was measured about eight  
267 times a year between April and October from 2003 to 2009 on a subsample of four trees among  
268 those equipped with automatic dendrometers (see Limousin *et al.*, 2012). RMA regressions  
269 between measured and simulated values of predawn leaf water potential yielded an  $R^2$  of 0.84,  
270 the slope was  $0.93 \pm 0.05$  ( $P < 0.0001$ ,  $n = 54$ ), and the intercept was not significantly different  
271 from 0. We used the simulations of predawn water potential rather than soil water content, as  
272 the former is more closely linked with plant functioning (Rambal *et al.*, 2003). The daily  
273 simulations of predawn water potential were performed with the climate data from the  
274 Puéchabon and SML stations for the periods 1984-2012 and 1966-2012, respectively. The water  
275 stress integral (WSI), defined by Myers (1988) as the seasonally or yearly sum of predawn  
276 water potential, was used as a drought severity index to quantify annual or seasonal water stress.  
277

### 278 ***Duration of spring basal area increment: calculations of dates $t_0$ and $t_1$***

279 The dates of stem growth phenology that bounded the spring growth period, the DOY  
280 (day of the year) when stem growth starts (hereafter  $t_0$ ) and the DOY when stem growth stops  
281 in early summer (hereafter  $t_1$ , Fig. S3), were estimated for each year. The relationships between  
282  $t_0$  or  $t_1$  and climate variables were calibrated by Lempereur *et al.* (2015) on observations of  $t_0$   
283 and  $t_1$  obtained with automatic dendrometers from 2004 to 2011. Briefly,  $t_0$  was defined as the  
284 first day at which basal area exceeded the culmination of the previous year, and  $t_1$  as the first  
285 day when BAI became null or negative (see Lempereur *et al.*, 2015 for methodological details).  
286  $t_0$  and  $t_1$  were estimated using climate data from both Puéchabon and the nearby SML station  
287 over their corresponding timeframes.  $t_0$  was predicted by a nonlinear relationship with the mean  
288 temperature from January to March ( $T_{JFM}$ ). The relationships were fitted between  $t_0$  and  $T_{JFM}$   
289 measured in Puéchabon ( $t_0 = 849.2 * \exp(-0.6436 T_{JFM}) + 121$ ;  $R^2 = 0.95$ ; RMSE = 2.6 days;  
290 Lempereur *et al.*, 2015) and between  $t_0$  and  $T_{JFM}$  measured in SML ( $t_0 = 4300 * \exp(-0.943$   
291  $T_{JFM}) + 124.4$ ;  $R^2 = 0.95$ ; RMSE = 2.3 days; Fig. S4).  $t_1$  was predicted by the DOY when the  
292 plant water potential simulated using climate data from Puéchabon reached a threshold of -  
293 1.1 MPa ( $R^2 = 0.75$ ; RMSE = 7 days, Lempereur *et al.*, 2015), corresponding to a DOY when

294 the plant water potential simulated using climate data from SML reached a threshold of -  
295 1.1 MPa +  $\epsilon$  (with  $\epsilon = -0.1$ ;  $R^2 = 0.73$ ; RMSE = 13.5 days) due to the slight differences in  
296 temperature and precipitation between the two stations (see Fig. S5). The duration  $\Delta t_{t_0-t_1}$   
297 corresponds to the duration of the period between  $t_0$  and  $t_1$  and was computed for each pair of  
298 simulated phenological thresholds.

299

### 300 *Data processing and statistical analyses*

301 Annual stem growth (DBH and ring widths) was converted into annual basal area  
302 increments (BAI, expressed in  $\text{mm}^2 \text{ year}^{-1}$ ) for the two data series. Analyses were performed  
303 with averaged BAI values of 125 and 5-12 individual trees for FS and RW, respectively. The  
304 year 1992 presented two periods when predawn plant water potential fell below the threshold  
305 of -1.1 MPa, in spring and autumn (Fig. S6). This unusual bi-modal drought prevented us from  
306 determining the duration  $\Delta t_{t_0-t_1}$  so 1992 was excluded from subsequent analyses. The growth  
307 series  $\text{BAI}_{\text{FS}}$  included measurements that appeared to be outliers compared to  $\text{BAI}_{\text{RW}}$  or  $\text{BAI}_{\text{AD}}$   
308 for the years 2002 and 2010 (see Fig. S7). In 2002,  $\text{BAI}_{\text{FS}}$  was particularly low when  $\text{BAI}_{\text{RW}}$   
309 was close to the expected value, and in 2010,  $\text{BAI}_{\text{FS}}$  was clearly higher than the  $\text{BAI}_{\text{AD}}$  value.  
310 Because  $\text{BAI}_{\text{FS}}$  is less accurate than the other two methods, and was calculated as the difference  
311 between two subsequent measurements of DBH, these two values were considered to be  
312 unreliable and excluded from the analyses performed on  $\text{BAI}_{\text{FS}}$ .

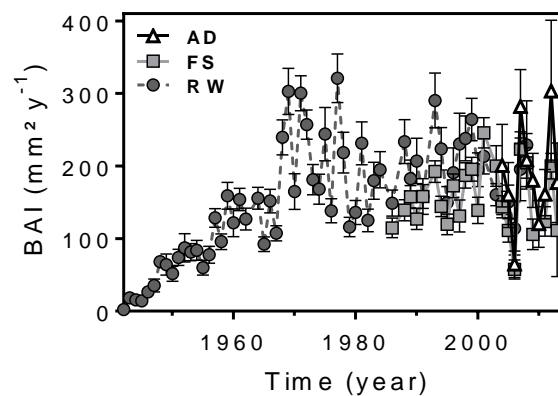
313 To investigate the links between tree growth and climate, we computed the correlations  
314 between our two different growth datasets (FS and RW) and a set of relevant climate predictors.  
315 For each correlation tested, we reported the Pearson's correlation coefficient and its  
316 significance based on the standard bootstrap method with 1000 samples taken from the original  
317 distribution of climate and tree ring data. Within each sample, the number of observations was  
318 random and followed a geometric distribution. We used the 'treeclim' R package built upon the  
319 DENDROCLIM2002 statistical tool dedicated to tree ring analysis (Biondi & Waikul, 2004;  
320 Zang & Biondi, 2015). Climate predictors were derived from temperature and precipitation at  
321 monthly, seasonal and annual time scales, and from our functional index of spring growth  
322 duration ( $\Delta t_{t_0-t_1}$ ). To test for the stationarity of the drought and temperature controls over the  
323 studied period, we also performed the same bootstrap sampling Pearson correlation analysis on  
324 a 10-year moving window along the whole series.

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

327 Theil-Sen test (Sen 1968) from the ‘openair’ R cran package, applied on a 1000 block bootstrap  
328 simulations to account for auto-correlated variables (Kunsch 1989), with the block length set to  
329  $n/3$ ,  $n$  being the length of the time series. Temporal breakpoints in the time series were assessed  
330 by computing the yearly F-statistic (sequential F-test) and the *supF* statistic was then used to  
331 test for their significance.  
332

## 333 RESULTS

### 334 *Sensitivity of stem growth to the dual temperature-drought drivers*

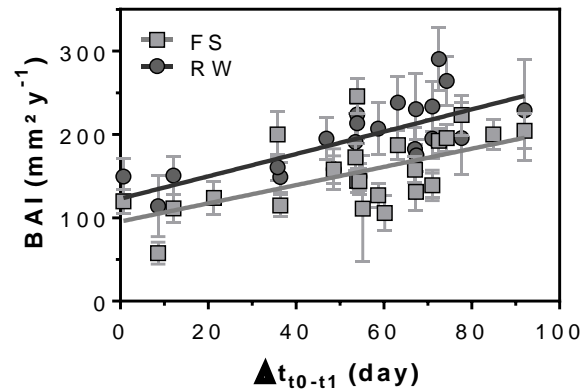


335  
336 **Fig. 2** Time series of annual stem basal area increment (BAI) for the ring width series (RW; 1942-2008), the long-  
337 term field survey (FS; 1986-2013) and the automatic dendrometer series (AD; 2004-2013). Error bars are standard  
338 errors among the sampled trees (see Table 1 for sample size).  
339

340 Annual stem growth ( $BAI_{RW}$ ) from 1942 to 2008 exhibited two distinct phases, with a  
341 significant breakpoint around 1967 ( $F_{stat} = 81.96$ ;  $P\text{-value} < 0.0001$ ; Fig. 2). The first phase  
342 (1942-1967) lasted 25 years after the clearcut and showed a linear increase of  $5.5 (\pm 0.62) \text{ mm}^2$   
343  $\text{y}^{-1}$  in annual BAI. This phase, which corresponds approximately to the cut frequency formerly  
344 used in the traditional management of this *Q. ilex* coppice (Floret *et al.*, 1992), was  
345 characterized by incomplete canopy cover and notable self-thinning. The second phase (1968-  
346 2008) showed a stabilization of  $BAI_{RW}$  around a mean value of  $203.8 (\pm 54.84) \text{ mm}^2 \text{ y}^{-1}$ . The  
347 influence of climate on stem growth was consequently only considered from 1968 on, to avoid  
348 the confounding effects caused by changes in competition, space-filling and self-thinning  
349 during the first phase.

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

353 BAI<sub>RW</sub> and BAI<sub>FS</sub>, respectively). The minimum value of BAI was recorded in 2006 for both  
 354 series: BAI<sub>RW</sub> = 114 mm<sup>2</sup> y<sup>-1</sup> (SE = 36.5 mm<sup>2</sup> y<sup>-1</sup>) and BAI<sub>FS</sub> = 58 mm<sup>2</sup> y<sup>-1</sup> (SE = 13.2 mm<sup>2</sup> y<sup>-1</sup>)  
 355 <sup>1</sup>). The maximum BAI was recorded in 1977 for RW (BAI<sub>RW</sub> = 348 mm<sup>2</sup> y<sup>-1</sup>, SE = 22.1 mm<sup>2</sup> y<sup>-1</sup>)  
 356 <sup>1</sup>) and in 2001 for FS (BAI<sub>FS</sub> = 246 mm<sup>2</sup> y<sup>-1</sup>; SE = 20.8 mm<sup>2</sup> y<sup>-1</sup>, vs. BAI<sub>RW</sub> = 213 mm<sup>2</sup> y<sup>-1</sup>;  
 357 SE = 24 mm<sup>2</sup> y<sup>-1</sup>.2).  
 358



359  
 360 **Fig. 3** Relationship between yearly basal area increment (BAI) and the duration of the spring growth period ( $\Delta t_{t_0-t_1}$ ). Ring width (RW, dark grey circle) is shown for the period 1984-2008 and field survey (FS, light grey square)  
 361 for the period 1986-2013. The linear relationships between  $\Delta t_{t_0-t_1}$  and BAI<sub>RW</sub> (dark grey line; BAI<sub>RW</sub> = 1.34\* $\Delta t_{t_0-t_1}$  + 122.9; R<sup>2</sup> = 0.56; P-value < 0.001) or BAI<sub>FS</sub> (light grey line; BAI<sub>FS</sub> = 1.09\* $\Delta t_{t_0-t_1}$  + 95.5; R<sup>2</sup> = 0.35; P-  
 362 value < 0.01) are represented. Error bars are standard errors.  
 363  
 364  
 365

366 The DOY of the start ( $t_0$ ) and stop ( $t_1$ ) of the spring stem growth, simulated over the period  
 367 1984-2013 using climate data from the Puéchabon station, occurred on average in mid-May  
 368 (DOY 133, SD = 9.9 days) and early July (DOY 184, SD = 23.5 days), respectively. The growth  
 369 duration  $\Delta t_{t_0-t_1}$  varied considerably among years (CV = 50%) with values ranging from 2 days  
 370 in 1995 to 95 days in 2008 (Fig. 3). BAI was linearly correlated with  $\Delta t_{t_0-t_1}$  for both stem growth  
 371 series (R<sup>2</sup> = 0.56; P-value < 0.0001 and R<sup>2</sup> = 0.35; P-value < 0.01 for RW and FS respectively;  
 372 Fig. 3). Moreover,  $\Delta t_{t_0-t_1}$  was the best explanatory variable for the inter-annual variations in  
 373 BAI<sub>RW</sub> compared to other climate variables over the period 1984-2008 (Table 2; 3). We thus  
 374 concluded that the dual control of annual stem growth by temperature and precipitation, stated  
 375 by Lempereur *et al.* (2015) for the period 2004-2011, remained valid for a longer retrospective  
 376 period and when growth is measured with less accuracy than with automatic dendrometers. The  
 377 intercepts of the linear relationships between BAI and  $\Delta t_{t_0-t_1}$ , which represent the residual  
 378 autumnal growth (Lempereur *et al.*, 2015), differed significantly between the two BAI series  
 379 (F = 17.97; P-value < 0.001), with 122.9 ( $\pm$ 34.42) mm<sup>2</sup> y<sup>-1</sup> and 95.5 ( $\pm$ 39.09) mm<sup>2</sup> y<sup>-1</sup> for RW  
 380 and FS, respectively (Fig. 3). By contrast, the slopes of these relationships did not differ

381 significantly between RW and FS ( $F = 0.46$ ;  $P\text{-value} > 0.05$ ), and the common slope equals  
 382  $1.23 \text{ mm}^2 \text{ day}^{-1}$ . The sensitivity of  $\text{BAI}_{\text{RW}}$  to  $\Delta t_{t_0-t_1}$  was thus identical to the sensitivity of  $\text{BAI}_{\text{FS}}$ .  
 383 Furthermore, neither the extension of the study period to 1968-2008 nor the switch in  
 384 meteorological stations from Puéchabon to SML, removed the significant correlation between  
 385  $\text{BAI}_{\text{RW}}$  and  $\Delta t_{t_0-t_1}$  ( $R^2 = 0.31$ ;  $P\text{-value} < 0.001$ ; Table 2).

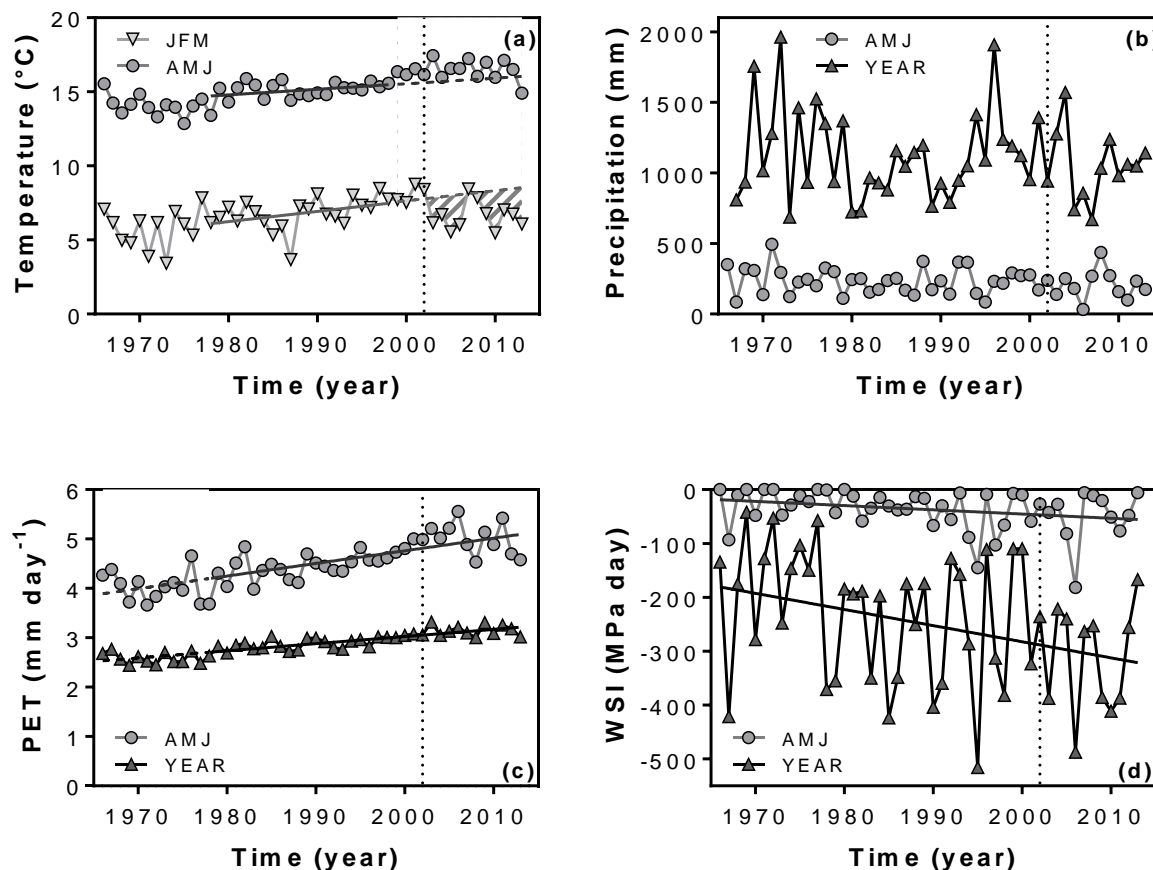
386  
 387 **Table 2** Mean Pearson's correlation coefficients (and significance derived from a 1000 classical bootstrap  
 388 sampling) between chronologies of annual stem growth (BAI) and the main phenology explanatory variables. The  
 389 correlations are given using climate variables measured in Puéchabon field surveys (FS) over the period 1986-  
 390 2013 and ring width (RW) over the period 1984-2008, and climate data from the SML meteorological station over  
 391 the period 1968-2008 for RW (see Fig. 1). The explanatory variables tested were the start and stop growth dates  
 392 ( $t_0$  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  
 393 statistical significance (\* $P\text{-value} < 0.05$ ; \*\* $P\text{-value} < 0.01$ ; \*\*\* $P\text{-value} < 0.001$ ) are given. Significant correlations  
 394 are in bold.

	FS	RW	RW
Period	1986-2013	1984-2008	1968-2008
$t_0$	<b>-0.43**</b>	<b>-0.51***</b>	0.18
$t_1$	<b>0.56***</b>	<b>0.68***</b>	<b>0.66***</b>
$\Delta t_{t_0-t_1}$	<b>0.60***</b>	<b>0.73***</b>	<b>0.56***</b>

395  
 396 ***Stem growth response to climate trends from 1968 to 2013***  
 397 Over the longer period 1968-2008,  $\Delta t_{t_0-t_1}$  was not a better predictor of BAI than the sum  
 398 of spring precipitation ( $P_{\text{AMJ}}$ ) or  $t_1$  alone ( $r = 0.75$ ;  $P\text{-value} < 0.001$  and  $r = 0.66$ ;  $P\text{-value} < 0.001$   
 399 respectively; Table 2, 3), and we also observed a loss of correlation between BAI and  $t_0$   
 400 ( $r = 0.18$ ;  $P\text{-value} = 0.31$ ; Table 2).

401  $P_{\text{AMJ}}$  was the main explanatory climate variable for  $t_1$  (over the period 1968-2008:  
 402  $r = 0.80$ ;  $P\text{-value} < 0.001$ ) and it exhibited no temporal trend between 1968 and 2013 ( $P\text{-}$   
 403  $\text{value} = 0.31$ ; Fig. 4b). However, spring water limitation increased (WSI in spring: -  
 404  $0.48 \text{ MPa day } y^{-1}$ ;  $P\text{-value} < 0.001$ ; Fig. 4d, Table S3) as a result of increasing spring potential  
 405 evapotranspiration (PET;  $+0.028 \text{ mm day}^{-1} y^{-1}$ ;  $P\text{-value} < 0.001$ ; Fig. 4c, Table S3). This trend  
 406 in PET was mainly due to the significant warming trend in spring temperatures throughout the  
 407 period 1968-2013 ( $+0.07^\circ\text{C } y^{-1}$ ;  $P\text{-value} < 0.001$ ; Fig. 4a, Table S3). As a result, drought onset  
 408  $t_1$  exhibited a temporal trend toward earlier dates ( $-0.57 \text{ day } y^{-1}$ ;  $P\text{-value} < 0.01$ ; Fig. 5). The  
 409 correlation between  $\text{BAI}_{\text{RW}}$  and  $P_{\text{AMJ}}$  remained significant, however, throughout most of the  
 410 1968-2008 period (Fig. 6a).

411



412 **Fig. 4** Temporal trends in (a) spring (AMJ) temperature (grey circles) and winter (JFM) temperature (light grey  
 413 inverted triangles), (b) mean annual precipitation (dark grey triangles) and AMJ precipitation (grey circles), (c)  
 414 mean annual potential evapotranspiration (ETP; dark grey triangles) and AMJ ETP (grey circles) and (d) annual  
 415 water stress integral (WSI, dark grey triangles) and AMJ three months WSI (grey circles). The solid lines represent  
 416 significant temporal trends ( $P$ -value $<0.05$ ). The dashed lines represent the extended trend for temperature after  
 417 1998, or before 1978 for PET. The effect of the warming pause on the JFM temperature (panel a) is shown by the  
 418 hatched area between the points and the regression line, the vertical dotted lines indicate the start of the winter  
 419 warming pause in 2002.

420

421 In parallel,  $T_{JFM}$  increased significantly throughout the period ( $+0.04 \text{ } ^\circ\text{C y}^{-1}$ ;  $P$ -  
 422 value $<0.05$ ; Fig. 4a) which led to a significant trend of  $t_0$  toward earlier dates ( $-0.21 \text{ day y}^{-1}$ ;  $P$ -  
 423 value $<0.05$ ; Fig. 5). However, a pause in the atmospheric winter warming occurred in the last  
 424 decade. This warming pause is apparent in the discrepancy between actual and expected  $T_{JFM}$   
 425 obtained from the temporal trend built over the period 1978-1998. The year 1978 was chosen  
 426 because it corresponds to the onset of a rapid warming phase in the Northern Hemisphere (Mann  
 427 *et al.*, 1999). Similarly, the year 1998 was considered as the onset of the climate hiatus  
 428 observations (IPCC 2014). We used the period 1978-1998 to build the reference trend line and  
 429 extrapolate expected  $T_{JFM}$  values over the 1999-2013 period. We then tested for a breakpoint in  
 430 the anomalies between observed and expected  $T_{JFM}$  over the whole period. Such a breakpoint  
 431 was identified in 2002, indicating a significant slowing down in winter warming after this date



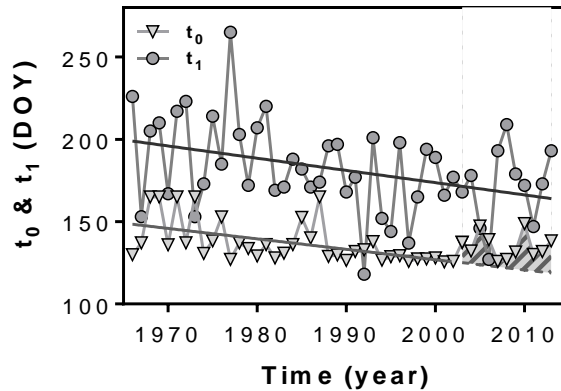
432 (Fstat = 21.52; P<0.001; Fig. 4a). This temporal pattern was also observed at seven other  
433 meteorological stations in the region surrounding our study site (Table S4 and Fig. S8), thus  
434 confirming the regional occurrence of the globally observed climate hiatus (Trenberth &  
435 Fasullo, 2013). The date of growth onset ( $t_0$ ) was very sensitive to the warming pause in  $T_{JFM}$   
436 and a breakpoint in the  $t_0$  trend was observed in 2002 (Fstat = 21.52; P<0.001; Fig. 5). We also  
437 observed that the start of the winter warming pause coincided with a change in the climate  
438 controls on annual stem growth. Indeed, the correlation between BAI and  $T_{JFM}$ , which was only  
439 significant over one 10-year window between 1968 and 1994, became constantly significant  
440 from the time window 1995-2004 on (Fig. 6b).

441  
442 **Table 3** Mean Pearson's correlation coefficients and significance (derived from a 1000 classical bootstrap  
443 sampling) between annual stem growth (BAI) or spring growth duration ( $\Delta t_{t_0 t_1}$ ) and monthly or seasonal  
444 precipitation (P, in mm) and temperature (T, in °C) for RW data series. The climate data from Puéchabon and  
445 Saint Martin-de-Londres meteorological stations were used for the periods 1984-2013 and 1966-2013,  
446 respectively. The coefficients of correlation (r) and the level of statistical significance (\*P-value < 0.05; \*\*P-  
447 value < 0.01; \*\*\*P-value < 0.001) are given. Significant correlations are in bold.

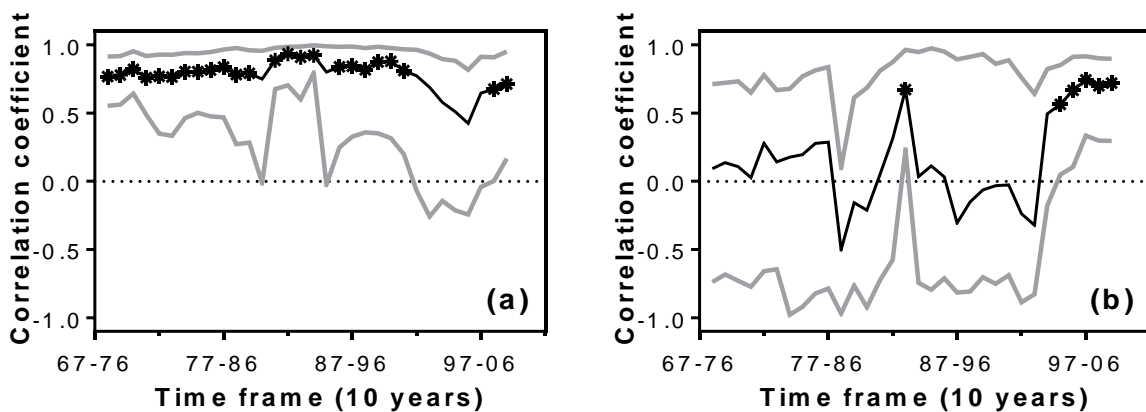
	BAI				$\Delta t_{t_0 t_1}$			
	1984-2008		1968-2008		1984-2013		1966-2013	
	T	P	T	P	T	P	T	P
November (t-1)	0.06	-0.08	<b>-0.23*</b>	-0.03	0.07	0.24	<b>-0.31*</b>	-0.03
December (t-1)	<b>0.30**</b>	0.08	-0.07	-0.04	0.25	0.04	-0.06	-0.03
January	<b>0.50***</b>	-0.06	0.02	0.15	<b>0.51***</b>	0.03	<b>0.34***</b>	0.14
February	<b>0.37*</b>	<b>-0.27*</b>	-0.02	0.06	0.20	-0.16	0.22	0.02
March	<b>0.34**</b>	-0.17	-0.10	0.21	<b>0.41***</b>	-0.10	0.11	<b>0.19*</b>
April	0.05	0.23	0.00	<b>0.33*</b>	-0.11	<b>0.48***</b>	-0.07	<b>0.24*</b>
May	0.12	<b>0.47***</b>	-0.23	<b>0.57***</b>	0.08	0.37	<b>-0.25*</b>	<b>0.48**</b>
June	<b>-0.46**</b>	0.21	<b>-0.65***</b>	<b>0.44***</b>	-0.01	0.00	<b>-0.24*</b>	0.22
July	<b>-0.56***</b>	<b>0.32**</b>	<b>-0.54***</b>	<b>0.36**</b>	-0.26	-0.13	<b>-0.42***</b>	0.01
August	-0.08	-0.04	<b>-0.30**</b>	0.07	0.03	<b>0.24*</b>	<b>-0.37***</b>	0.08
September	<b>-0.39*</b>	<b>-0.39*</b>	<b>-0.42***</b>	<b>-0.25*</b>	-0.18	-0.35	<b>-0.34***</b>	-0.10
October	-0.13	-0.13	-0.14	-0.04	-0.18	<b>-0.34**</b>	-0.22	-0.15
Jan. Feb. March	<b>0.48***</b>	-0.20	-0.05	0.18	<b>0.47*</b>	-0.11	<b>0.32**</b>	0.15
Apr. May June	-0.15	<b>0.53***</b>	<b>-0.38***</b>	<b>0.75***</b>	-0.02	<b>0.49*</b>	-0.23	<b>0.55***</b>
June Aug. Sept.	<b>-0.42**</b>	-0.34	<b>-0.51*</b>	-0.14	-0.18	-0.30	<b>-0.45***</b>	-0.05
from Nov(t-1) to Oct	0.04	-0.11	<b>-0.37*</b>	0.25*	0.15	0.01	<b>-0.21*</b>	0.17

448  
449 The temporal trends in  $t_0$  and  $t_1$ , both toward earlier dates (-10 and -26 days,  
450 respectively) offset each other to some extent until 2002 and resulted in a non-significant trend  
451 in  $\Delta t_{t_0 t_1}$ . After 2002, the prolonged trend in  $t_1$  continued to decrease while  $t_0$  stabilized, thereby  
452 leading to a sudden shortening of the growing season (Fig. 5). The timing of this phenological  
453 reduction was concomitant with the appearance of a significant relationship between  $T_{JFM}$  and

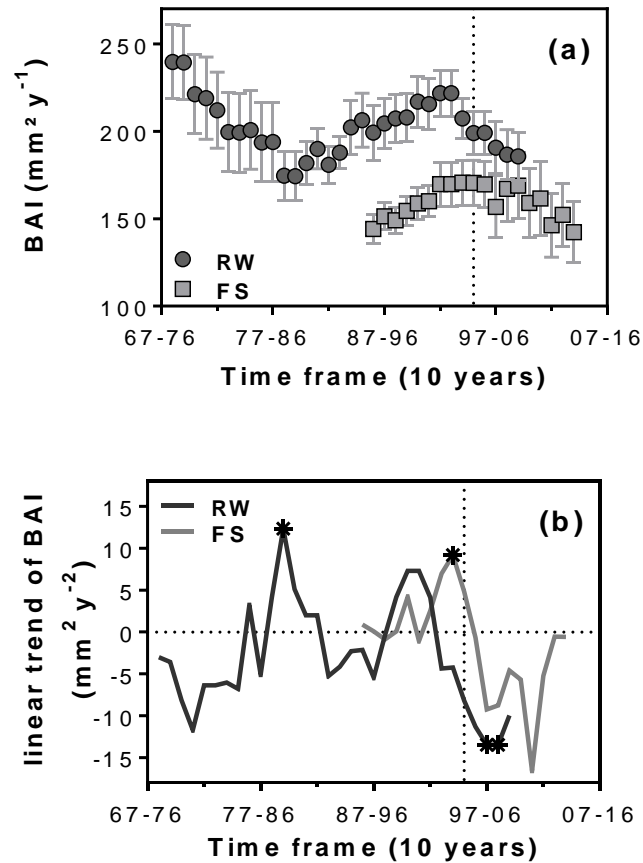
454 BAI (Fig. 6b). The decline in  $\Delta t_{t_0-t_1}$  induced by the winter warming pause resulted in a decrease  
 455 in  $BAI_{RW}$  after 2002. This decreasing trend over time become significant after the 10-year time  
 456 window 1997-2006 (Fig. 7a,b).  $BAI_{FS}$  exhibited a similar decreasing trend in the same period,  
 457 but of lower amplitude and not significant.  
 458



459 **Fig. 5** Onset of phenological stem growth ( $t_0$ , pale grey inverted triangles) and end of stem growth ( $t_1$ , grey circles)  
 460 from 1966 to 2013, expressed as day of the year (DOY). The effect of the warming pause on  $t_0$  is shown by the  
 461 hatched area between the points and the regression line over the 1978-1998 period.  
 462  
 463



464  
 465 **Fig. 6** Temporal variations in the bootstrapped Pearson's correlation coefficients between (a)  $BAI_{RW}$  and  $P_{AMJ}$ ,  
 466 and (b)  $BAI_{RW}$  and  $T_{JFM}$  over 10-year moving windows. The black curve represents the correlation coefficient and  
 467 the grey curves the upper and lower confidence intervals at a significance level  $\alpha = 0.05$ . Asterisks identify the  
 468 time windows with significant correlations.  
 469  
 470



471 **Fig. 7** Temporal trend over 10-year moving windows of (a) mean annual stem growth from 1968 to 2008 and from  
 472 1987 to 2013 for ring width (RW, dark grey circles) and field surveys (FS, grey squares), respectively. Error bars  
 473 are standard errors. (b) Slopes of the linear trends of BAI for the two series. The asterisks indicate time windows  
 474 with a significant trend ( $p < 0.05$ ). The dotted vertical lines in both panels indicate the first time window with a  
 475 significant relationship between  $\text{BAI}_{\text{RW}}$  and  $T_{\text{JFM}}$  after the warming pause.  
 476

## 477 DISCUSSION

### 478 *Growth duration as a predictor of annual stem growth*

479 The duration of spring stem growth ( $\Delta t_{t_0-t_1}$ ) was the best explanatory variable of yearly  
 480 basal area increment for both  $\text{BAI}_{\text{FS}}$  and  $\text{BAI}_{\text{RW}}$  after 1984. This confirms earlier results  
 481 obtained with automatic dendrometers over a shorter period and a smaller sample of trees  
 482 (Lempereur *et al.*, 2015), and therefore validates  $\Delta t_{t_0-t_1}$  as a robust estimator of *Q. ilex* annual  
 483 stem growth over long time scales and large samples. The two independent samplings we used  
 484 here differed markedly in the number of trees measured, the measurement method and its  
 485 precision. FS corresponds to a large number of trees (125 trees) representing a broader tree size  
 486 distribution but measured with a less precise resolution (0.3 mm of DBH), while RW was  
 487 measured on a small sample of large dominant trees (12 trees) but with a better resolution

488 (0.01 mm of radius). Average stem growth was lower for  $BAI_{FS}$  than for  $BAI_{RW}$ , but both  
489 responded linearly and with the same sensitivity to  $\Delta t_{t_0-t_1}$  (Fig. 3).

490 The spring stem growth duration  $\Delta t_{t_0-t_1}$  is defined as the length of the period between the  
491 onset of spring stem growth ( $t_0$ ) and the date of growth cessation caused by summer drought  
492 ( $t_1$ ). Lempereur *et al.* (2015) observed that  $t_0$  was well predicted by winter temperature, and that  
493  $t_1$  occurred when the leaf predawn water potential dropped below a threshold of -1.1 MPa. A  
494 similar approach was used by Rossi *et al.* (2011, 2014) who linked the stem growth of boreal  
495 black spruce with the duration of xylem growth delimited by cold temperatures in spring and  
496 autumn, and by Delpierre *et al.* (2016a) who linked the growth of temperate oak to the timing  
497 of the summer growth cessation controlled by water limitation. By identifying the climatic  
498 limits for cell division and elongation, the temporal delimitation of tree growth duration is an  
499 innovative way of improving simulation of forest carbon sink response to climate change  
500 (Fatichi *et al.*, 2014). Tree growth has generally been simulated using two types of models:  
501 statistical dendroclimatological models, which are empirical and may lead to marked  
502 uncertainties when extrapolated to future climate scenarios (e.g. Gea-Izquierdo *et al.*, 2013;  
503 Babst *et al.*, 2014); and process based models that link tree growth to carbon assimilation (e.g.  
504 Sitch *et al.*, 2003; Friedlingstein *et al.*, 2006; Gaucherel *et al.*, 2008; Keenan *et al.*, 2011),  
505 ignoring experimental evidence showing a direct, and generally more limiting, climate control  
506 of plant growth (Körner, 2003; Muller *et al.*, 2011). Projecting tree growth based on growth  
507 phenology as in Rossi *et al.* (2011) and Lempereur *et al.* (2015) merges the biological realism  
508 of the first approach, i.e. a direct link between climate and growth, with the mechanistic  
509 understanding of tree physiology used in process based models, and be a significant step  
510 forward in projecting the response of forest ecosystems to climate change (Delpierre *et al.*,  
511 2016b). Showing that growth duration is an adequate predictor of tree growth for long time  
512 series datasets (40 years in our study) and coarse temporal resolution (annual diameter  
513 measurements) is thus an important preliminary.

514 Nevertheless, the spring growth duration approach remains limited by both its conditions of  
515 applicability and the large proportion of the growth variability not explained by  $\Delta t_{t_0-t_1}$ . The  
516 particular case of the year 1992, with its bi-modal drought in spring and autumn and its well-  
517 watered summer (Fig. S6), suggests that  $\Delta t_{t_0-t_1}$  can only be used as a descriptor of stem growth  
518 phenology in years with typical Mediterranean seasonality and a drought period occurring in  
519 summer. While the lowest threshold of predawn water potential below which stem growth is  
520 prevented certainly remains valid for any drought seasonality (Hsiao & Xu, 2000; Muller *et al.*,  
521 2011; Lempereur *et al.*, 2015), we hypothesize that the relationship between stem growth and

522 the duration of periods with adequate growth conditions (the rate of growth) varies in years  
523 with peculiar phenology. Variations in the rate of growth may also account for the unexplained  
524 variability in the BAI against  $\Delta t_{0-t1}$  relationships (44% and 65% for RW and FS, respectively;  
525 Fig. 3). Finally, the relative extent of autumn growth compared to spring growth would deserve  
526 more detailed investigation. Lempereur *et al.* (2015) observed that autumn growth explained  
527 only approximately 30% of annual stem growth and was strongly determined by spring  
528 conditions, but its magnitude over long time periods and under climate change conditions  
529 remains to be described.

530

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

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

539 The sensitivity of growth to water deficit is well established in the literature (Lockhart  
540 1965; Hsiao & Xu, 2000; Muller *et al.*, 2011), as is the negative impact of drought on ring width  
541 (Fritts, 1976). Previous dendroclimatological studies generally stated that spring to early-  
542 summer precipitation was the main driver of annual stem growth of *Q. ilex* (Gutiérrez *et al.*,  
543 2011). More precisely, it is the start of the dry season, defined by a threshold of soil water  
544 deficit that was identified as the main determinant of variations in inter-annual growth (Maselli  
545 *et al.*, 2014; Lempereur *et al.*, 2015). The predominant effect of the timing of drought induced  
546 growth cessation on annual stem growth is not limited to Mediterranean ecosystems, as a similar  
547 effect has been observed in mesic temperate forests (Brzostek *et al.*, 2014; Delpierre *et al.*,  
548 2016a). In our study, we defined the start of the dry season as a critical threshold of predawn  
549 plant water potential of -1.1 MPa. This threshold is biologically meaningful because water  
550 potential affects the cell turgor pressure necessary for cell growth (Hsiao & Xu, 2000), and it  
551 has the other advantage of comprehensively accounting for climate and local soil conditions in  
552 a single metric (Ruffault *et al.*, 2013). It is, however, a more complex index to calculate than  
553 climatic indices of drought as it requires substantial knowledge of soil and vegetation  
554 characteristics, and accurate meteorological data at the daily time scale. Consequently, the

555 uncertainty on  $t_1$  was higher than the uncertainty on  $t_0$ , especially when meteorological data  
556 from SML (located at a distance of 12 km from the study site) was used instead of on-site data,  
557 but  $t_1$  nonetheless remained a good predictor of annual stem growth for whichever period (Table  
558 2).

559 Depending on the species and on the local bio-climate, a minimum temperature  
560 threshold ranging from +4 °C to +7 °C is required for stem growth to occur (Körner, 2003;  
561 Rossi *et al.*, 2007; Deslauriers *et al.*, 2008; Gruber *et al.*, 2010; Swidrak *et al.*, 2011; Lempereur  
562 *et al.*, 2015). The onset of stem growth can be assessed from winter temperature (Delpierre *et al.*  
563 *et al.*, 2016b), thus the mean winter temperature directly impacts the duration of cambium activity  
564 and wood formation (Rossi *et al.*, 2011). However, there is no consensus in  
565 dendrochronological studies of the Mediterranean *Q. ilex* that winter temperature is a good  
566 predictor of annual BAI, and both negative (Zhang & Romane 1990; Paton *et al.*, 2009; Gea-  
567 Izquierdo *et al.*, 2009) and positive correlations (Campelo *et al.*, 2009; Nijland *et al.*, 2011;  
568 Gea-Izquierdo *et al.*, 2011) between annual stem growth and winter temperature have been  
569 reported. In our study, a positive correlation between growth and winter temperature was  
570 observed over the period 1984-2008 ( $r = 0.48$ ,  $P < 0.001$ ; Table 3), in accordance with  
571 Lempereur *et al.* (2015), but the relationship was not significant for the period 1968-2008, either  
572 with  $t_0$  or with  $T_{JFM}$ .

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

578

### 579 ***Can warmer winter temperature compensate for earlier summer drought under climate*** 580 ***change?***

581 From 1968 to 2008, the annual and spring amounts of precipitation were stable (Fig. 4b),  
582 but water limitation increased (Fig. 4d) due to increasing potential evapotranspiration with  
583 rising temperature in spring and summer (Fig. 4a and c), in accordance with regional  
584 observations (Ruffault *et al.*, 2013). Consequently, we simulated an earlier occurrence of  
585 drought onset ( $t_1$ , -26 days on average) along with an earlier growth onset, although to a lesser  
586 extent ( $t_0$ , -10 days; Fig. 5), which, taken together resulted in a non-significant decrease in  
587 growth duration. The positive effect of warming on ecosystem functioning and tree growth

588 through a longer growing season has been widely observed in temperature limited boreal and  
589 temperate forests (Keeling *et al.*, 1996; Menzel *et al.*, 2006; D'Arrigo *et al.*, 2008; Dragoni *et*  
590 *al.*, 2011). However, in water limited regions, like the Mediterranean, warming is generally  
591 considered to be an aggravating factor for drought, mainly because of increased evaporative  
592 demand (Angert *et al.*, 2005; Zhao & Running, 2010; Park *et al.*, 2012). Consequently, climate  
593 warming in the Mediterranean usually reduces tree growth (Jump *et al.*, 2006; Sarris *et al.*,  
594 2007; Peñuelas *et al.*, 2008; Piovesan *et al.*, 2008; Martin-Benito *et al.*, 2010). Our results thus  
595 mitigate this widely accepted conclusion and illustrate the peculiar parallel controls driven by  
596 temperature, such that the benefit of an earlier stem growth is cancelled out by earlier drought  
597 onset mostly caused by increasing evaporative demand.

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

607 Winter warming may also have a positive impact on stem growth by delaying growth  
608 cessation in autumn, thereby partly compensating for earlier drought onset. However, the  
609 phenology of autumn growth cessation appears to be less variable than that of  $t_0$  (Lempereur *et*  
610 *al.*, 2015), possibly because it is concurrently driven by photoperiod. Moreover, warm winters  
611 may even impact *Q. ilex* growth negatively if the species requires winter chilling, as is the case  
612 of the deciduous *Quercus* species (Fu *et al.*, 2015).

613

#### 614 ***A Mediterranean “divergence problem”***

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

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

634

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

637 A keystone result of our study is the sudden significance of the growth-temperature  
638 relationship occurring from the 1995-2004 time window on (Fig. 6b). In parallel, we observed  
639 lower winter temperatures than would have been expected on the basis of continuous climate  
640 warming (Fig. 4a). This regional pattern is therefore comparable to the globally observed  
641 “warming hiatus” (Easterling & Wehner 2009; Trenberth & Fasullo 2013). Our results suggest  
642 that these recent cooler winter temperatures resulted in later growth onset and led to an  
643 increased temperature constraint on the duration of stem growth. In the meantime, the constraint  
644 exerted by the water deficit increased constantly from 1968 onward with neither breakpoints  
645 nor changes in the trend line (Fig. 4d, 5). As a result, the stem growth of *Q. ilex* was significantly  
646 correlated only with water deficit in the past, but the shorter growth period after the 2000s  
647 revealed the dual control by winter temperatures and spring-summer water deficit. The pause  
648 in climate warming in turn disrupted the precarious balance between increasing winter  
649 temperatures and increasing spring-summer water deficit, which temporarily sustained stem  
650 growth until the end of the 1990s (Fig. 7). This is, to our knowledge, the first example of a  
651 ‘divergence problem’ in the tree growth-climate relationship triggered not by a continuous  
652 climate change but instead by the warming pause. This recent warming pause, a still  
653 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  
656 trend (Ying *et al.*, 2015), with an enhanced effect on winter temperature in Eurasia (Li *et al.*,  
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  
661 trends in targeted and concurrent climate variables such as temperature and drought should fully  
662 capture the complexity of climate change impacts (Mazdiyani & Aghakouchak 2015). Climate  
663 projections for the Mediterranean region forecast an increase in potential evapotranspiration  
664 and a decrease in summer precipitation by the end of the 21<sup>th</sup> century (Gao & Giorgi 2008;  
665 Ruffault *et al.*, 2014), which are likely to move the onset of drought forward more strongly than  
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.

669

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950

## 951 **SUPPORTING INFORMATION**

952 **Fig. S1** Relationships used to rescale the ring width series to the tree DBH at the time of the  
953 cut: tree tapering (base diameter minus DBH) against DBH, and bark thickness against DBH.

954 **Table S1** Summary of climate data for Puéchabon and St Martin-de-Londres meteorological  
955 stations.

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 ( $t_0$ ) and the January to March  
961 temperature ( $T_{JFM}$ ) for the meteorological station of St Martin-de-Londres.

962 **Fig. S5** Relationship between observed and predicted day of the year of growth cessation due  
963 to drought ( $t_1$ ) 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  
967 basal growth period ( $\Delta t_{0-1}$ ) showing the years 2002 and 2010 that are outliers for the series  
968  $BAI_{FS}$ .

969 **Table S3** Results of the Theil-Sen tests for the trends of temperature, precipitation,  
970 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.