



## Phenology and growth dynamics in Mediterranean evergreen oaks: Effects of environmental conditions and water relations

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### ABSTRACT

Budburst date and shoot elongation were measured in two mature Mediterranean evergreen oaks (*Quercus suber* and *Quercus ilex*) and their relationships with meteorological and tree water status (predawn leaf water potential) data were analysed. Experimental work took place at two sites: Mitra 2 – Southern Portugal (2002–2003) and Lezirias – Central Portugal (2007–2010). *Quercus suber* phenology was studied at both sites whereas *Q. ilex* was only studied at Mitra 2. *Quercus suber* budburst date occurred at a photoperiod around 13.8 h ( $\pm 0.26$ ) – late April/early May – and was highly related to the average daily temperature in the period 25 March – budburst date (ca. 1.5 months prior to budburst), irrespective of site location. In that period, budburst date was much more dependent on average maximum than average minimum daily temperature. Base temperature and thermal time for *Q. suber* were estimated as 6.2 °C (within the reported literature values) and 323 degree-days, respectively. *Q. ilex* budburst occurred about 6 weeks earlier than in *Q. suber* (photoperiod: 12.3 h ( $\pm 0.3$ )). Relationships of *Q. ilex* budburst date and temperature were not studied since only 2 years of data were available for this species. *Q. suber* shoot elongation underlying mechanisms were quite different in the two sites. At Mitra 2 (*Q. suber* and *Q. ilex*), there was a considerable tree water stress during the dry season which restricted shoot elongation. Shoot growth was resumed later in the wet autumn when tree water status recovered again. At the Lezirias site *Q. suber* water status was not restrictive. Therefore, shoot elongation was mainly dependent on nutrient availability in top soil, as suggested by the strong and positive relationships between annual shoot growth and long-term cumulative rainfall (2–4 months) and short-term average temperature (1 month) prior to budburst. Annual shoot elongation at this well-watered site was higher than in Mitra 2, and variability of growth between trees was enhanced after warm, wet springs when shoot elongation was higher. Results obtained are relevant to the carbon balance, productivity and management of evergreen Mediterranean oak woodlands, particularly under the foreseen climate change scenarios.

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### 1. Introduction

Phenology plays an important role in the carbon balance, productivity, fitness of individuals and management of terrestrial ecosystems (Loustau et al., 2005; Rathcke and Lacey, 1985). Furthermore, the timing of tree phenological events is crucial for the survival of trees in most environments and a trait highly responsive to environmental changes, particularly in the Mediterranean (Gordo and Sanz, 2009; Kikuzawa, 1995). Phenological

patterns in Mediterranean regions are strongly influenced by a marked climatic seasonality and species evolved to synchronise maximum vegetative activity to the most favourable periods of the year (Baker et al., 1982; de Lillis and Fontanella, 1992; Gill and Mahall, 1986; Mahall et al., 2010).

In seasonal climates, the timing of budburst and the subsequent leaf and twig growth dynamics are critical to characterise tree phenology. In boreal and temperate species budburst is known to be mainly driven by temperature, though also correlated with photoperiod (Cannell and Smith, 1983; Chmielewski and Rötzer, 2001; Chuine and Cour, 1999; Hänninen, 1990; Kramer, 1994; Vitasse et al., 2009; Wielgolaski, 1999). In Mediterranean tree species, the timing of budburst has been often considered determined by temperature, photoperiod and also water availability (Jato et al., 2007; Ogaya and Peñuelas, 2004; Sanz-Pérez and Castro-Díez, 2010; Sanz-Pérez et al., 2009; Spano et al., 1999). Leaf and twig

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expansion dynamics is known to depend on physiological and environmental variables (Hsiao, 1973; Shurr et al., 2000; Tardieu et al., 2000; Way and Oren, 2010). In Mediterranean regions, temperature, nutrient and water availability are often regarded as the main constraints to plant growth (Körner, 2006; Milla et al., 2005).

In Central-Southern Portugal, Mediterranean evergreen oaks (*Quercus suber* and *Quercus ilex* spp. *rotundifolia* Lam.) are the dominant species, covering about 1.3 million hectares (AFN, 2010). Although sympatric, they usually occur in slightly different geographical areas (*Q. suber* dominates in wetter, coastal and montane areas whereas *Q. ilex* prevails in inland, drier regions) and differ in tolerance to the seasonal summer drought (David et al., 2007). Most of these woodlands are anthropogenic ecosystems of high socio-economic and conservation value, and display high biodiversity (Bugalho et al., 2009). In this study we have monitored the triggering date of budburst and the amount of shoot elongation in *Q. suber* (cork oak) and *Q. ilex* (holm oak).

*Quercus suber* budburst timing was followed at two sites: Lezirias – Central Portugal and Mitra 2 – Southern Portugal. At the latter site, *Q. ilex* budburst date was also monitored. Apical shoot elongation was regularly measured at both sites from leaf unfolding to the end of the most active growing period. Relationships of budburst timing, mean apical shoot elongation, and mean number of leaves per shoot with environmental (temperature, photoperiod, rainfall, solar radiation and vapour pressure deficit) and physiological (predawn leaf water potential) variables were analysed. Overall, this study aims to give some insight into the processes underlying budburst and growth dynamics in Mediterranean evergreen oak species, which are located in a global warming hot spot and subject to recurrent environmental stresses.

## 2. Materials and methods

### 2.1. Experimental sites

The study was conducted in two different evergreen oak woodlands located in Central-Southern Portugal, approximately 80 km apart, hereafter referred to as Mitra 2 and Lezirias. Mitra 2 (38° 32' N, 8° 00' W) is located at Herdade da Alfarrobeira – Évora (ca. 150 km South-East of Lisbon), in a sparse mixed evergreen oak stand (*Quercus ilex* being the dominant species and *Q. suber* occurring in scattered patches). The site has a slightly undulating topography (220–250 m a.s.l.). The soil is a Dystric Cambisol (FAO, 1988), with a depth of around 1 m and a low water retention capacity, overlying a granite bedrock. Lezirias site (38° 50' N, 8° 49' W) is located at the estate of Companhia das Lezirias – Samora Correia, approximately 50 km East of Lisbon, in a typical *Q. suber* stand. Site topography is flat (20 m a.s.l.). The soil is a deep Arenosol (FAO, 1988), with high permeability and a low water retention capacity, overlying a thick clay layer at approximately 9 m depth.

The climate in both sites is of the Mediterranean type, with hot dry summers and wet mild winters. Long-term (1951–1980) mean annual rainfall is 665 and 644 mm for Mitra 2 and Lezirias, respectively (INMG, 1991a, 1991b). Rainfall occurs predominantly from autumn to early-spring (October–April). Mean annual temperature is 15.0 and 15.6 °C for Mitra 2 and Lezirias, respectively (INMG, 1991a, 1991b). Field measurements were carried out during two consecutive years (2002–2003) at Mitra 2 and during 4 consecutive years (2007–2010) at Lezirias.

### 2.2. Plant material

At Mitra 2, phenological measurements were carried out, in five mature cork oak (*Q. suber* L.) trees and six mature holm oak (*Quercus ilex* spp. *rotundifolia* Lam.) trees, randomly selected from

adjacent plots (150 m apart). In Lezirias, three adult cork oak trees were studied.

At Mitra 2, trunk diameter at breast height, crown projected area and height of the sampled trees ranged from 0.45 to 0.53 m, 91.13 to 150.19 m<sup>2</sup> and 8.5 to 9.5 m in *Q. suber* and from 0.33 to 0.43 m, 47.71 to 89.99 m<sup>2</sup> and 7.0 to 8.0 m in *Q. ilex*, respectively. At Lezirias, the corresponding values for the sampled *Q. suber* trees ranged from 0.64 to 0.98 m, 198.69 to 247.97 m<sup>2</sup> and 12.1 to 14.5 m, respectively.

### 2.3. Meteorological data

Meteorological variables were continuously monitored at both sites. Automated weather stations were installed at each site on the top of scaffold towers (25 and 16 m height in Mitra 2 and Lezirias, respectively) to perform solar radiation (CM6B, Kipp and Zonen, Delft, The Netherlands) and dry and wet bulb temperature (psychrometer H301, Vector Instruments, Rhyll, UK) measurements. Rainfall (tipping-bucket rain gauge recorder ARG100, Environmental Measurements, Gateshead, UK) measurements were carried out at ground level in both sites. Meteorological data were recorded every 10 seconds and stored as 10-min means or totals by CR10X data loggers (Campbell Scientific, Shepshed, U.K.). Air vapour pressure deficit ( $D$ ) was calculated from dry and wet bulb temperatures.

For all years and at both sites, daily values of temperature (mean, maximum and minimum) ( $T$ , °C), solar radiation ( $R_s$ , MJ m<sup>-2</sup> day<sup>-1</sup>),  $D$  (Pa) and rainfall ( $P$ , mm day<sup>-1</sup>) were averaged ( $T$ ,  $R_s$ ,  $D$ ) or summed ( $P$ ) for several time intervals prior (starting on fixed calendar dates: 1 January, 1 February, 1 March, 15 March, 25 March and 1 April) and after budburst, up to the end of the vegetative growth period (elongation).

### 2.4. Leaf water potential

Seasonal variation of tree water status was assessed by measuring predawn leaf water potential ( $\Psi_{l,pd}$ ) approximately every month from January 2002 to November 2003 in Mitra 2 and from February 2007 to November 2008 in Lezirias. To avoid artificial variability in  $\Psi_{l,pd}$ , leaves were collected at similar heights from the South-facing part of the crowns of all studied trees. In each measuring date, three to four leaves were sampled from each tree just before sunrise, severed at petioles with razor blades, placed in plastic bags and immediately measured with a Scholander pressure chamber (PMS 1000, PMS Instruments, Corvallis, Oregon, USA) (Scholander et al., 1965).  $\Psi_{l,pd}$  is a surrogate of soil water potential near the roots.

### 2.5. Phenological measurements

Two phenological phases were considered: budburst date and vegetative growth (shoot elongation). Measurements were carried out in twelve apical shoots per tree in Lezirias and in three apical shoots per tree in Mitra 2. Phenological observations were carried out in apical vegetative buds of previous-year sun exposed shoots, on the South-facing part of the crowns. Access to crowns was provided by fixed scaffold towers and/or portable ladders. The date of budburst was defined as the first sampling day when new leaves or leaf tips emerging from the bud were visible. Subsequently, shoot growth was measured as the increase in length (cm).

In the beginning of each year (January), twigs of different accessible branches of the upper two-thirds of the crowns were randomly selected and labelled. In the periods with more intense phenological activity (bud development and shoot elongation), measurements were carried out weekly (therefore, budburst was assessed with an error of less than a week). During the rest of

the year, when there was little change in phenology, observations were done every 2–4 weeks. Elongation was assessed using a steel tape (error range  $\pm 1$  mm). At the Lezirias site, after leafing, we also monitored the number of leaves per shoot in every observation day.

The budburst date of each species for a specific year was estimated as the average of the budburst dates of all the sampled buds, since the variance of budburst date within a specific tree was frequently higher than between trees of the same species. Annual shoot elongation was also averaged from all the sampled twigs, considering averages per tree and species. The relationships between budburst date or total annual shoot elongation and the sums or means of meteorological data were studied through linear regression analyses, to test for causal effects. Similarly to what has been done by Nizinski and Saugier (1988), this procedure was used for each meteorological variable for several time intervals prior (with different starting dates: see Section 2.3) and after budburst.

### 2.6. Day length estimation

Day length or photoperiod (day-light hours) for a specific day was estimated as recommended by Allen et al. (1998). The average day length of budburst for each species was estimated as the average for all the buds selected in the trees of that species, for all years.

### 2.7. Base temperature and thermal time

Budburst date is known to be related with previously accumulated temperature above a threshold temperature during a time interval ( $t$ , days) (Cannell and Smith, 1983; Kramer, 1994; Monteith, 1977). At temperatures below this threshold or base

temperature ( $T_{\text{base}}$ , °C) bud development is so slow that the rate of bud development is taken as zero. Assuming a linear relationship between bud development rate and air temperature above  $T_{\text{base}}$ , up to an optimum temperature where the rate is highest, it is possible to determine the thermal time ( $\theta$ , accumulated temperature in day-degrees) for budburst and its  $T_{\text{base}}$  (Cannell and Smith, 1983; Kramer, 1994; Monteith, 1977) by regressing the effective rate of development ( $1/t$ ) against  $T_{\text{mean}}$  (average daily mean temperature over the time period  $t$ ). The time-interval with the best fit from the regression analyses (higher  $R^2$ ) was selected as the one that better meets the theoretical requirements. From the selected regression equation,  $T_{\text{base}}$  was found as the intercept with the temperature axis and thermal time obtained from the slope ( $\theta = 1/\text{slope}$ ).

## 3. Results

### 3.1. *Quercus suber*: budburst

Fig. 1 shows the daily mean temperature and cumulative rainfall for all the years of observation: 2002–2003 for the Mitra 2 site and 2007–2010 for the Lezirias site. Mean daily air temperature of the first 4 months of the year were 11.8 and 11.2 °C in Mitra 2 (for 2002 and 2003, respectively) and 12.2, 12.7, 11.9 and 12.4 °C in Lezirias (from 2007 to 2010, respectively). Cumulative rainfall, for the same periods, was 291.2 and 344.8 mm in Mitra 2, and 147.2, 322.0, 222.5 and 445.5 mm in Lezirias. Average budburst day in *Q. suber* fall between late-April and mid-May (varying from DOY 119 (2010) to 130 (2003)). For each single tree, vegetative budburst between twigs varied within a short period: 2–3 weeks.

For all tested climate data (solar radiation, vapour pressure deficit, rainfall and temperature), air temperature was the only variable found to be related to budburst date, both in Mitra 2 and

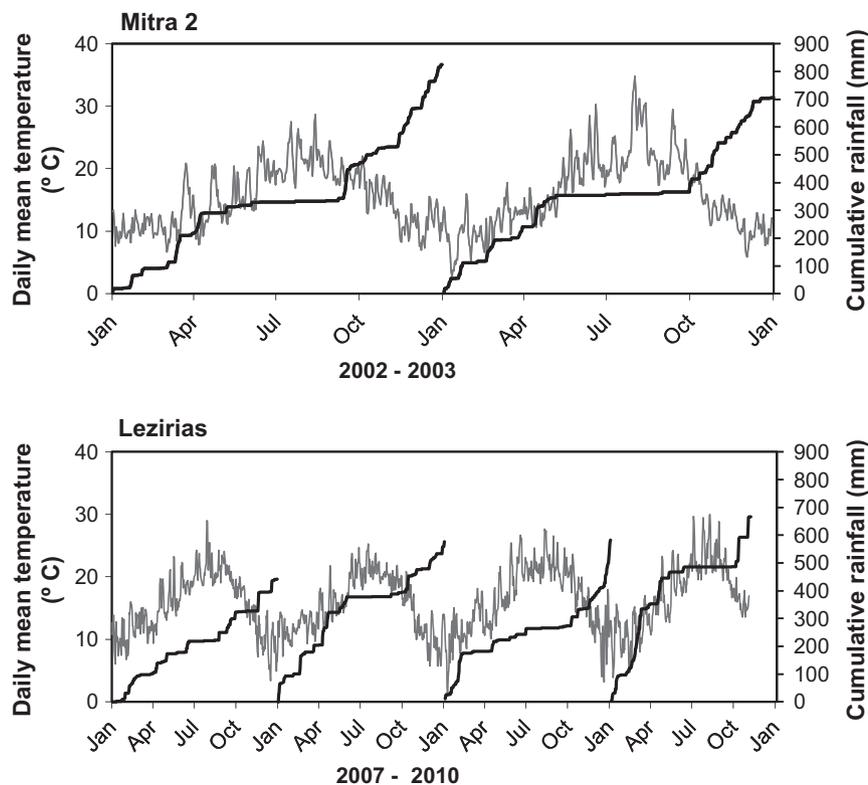


Fig. 1. Daily mean temperature and cumulative rainfall for all the years of observation: 2002–2003 for the Mitra 2 site (upper panel) and 2007–2010 for the Lezirias site (lower panel).

**Table 1**

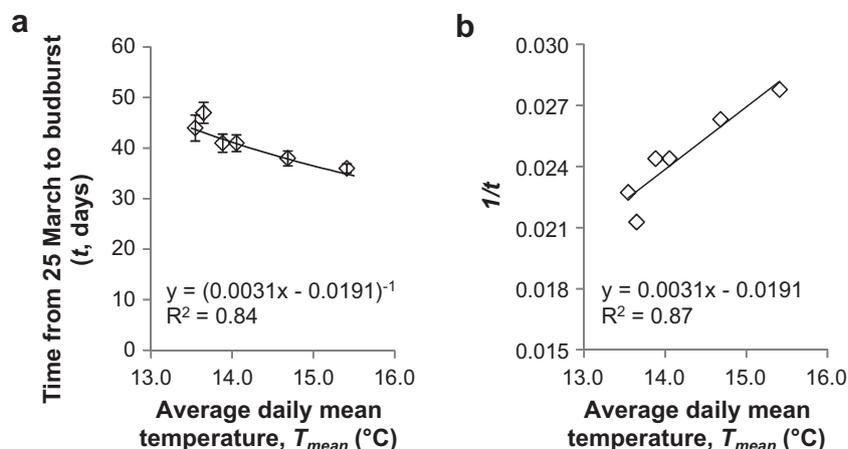
Linear regression analysis between mean annual budburst date in *Quercus suber* and meteorological variables, for different periods prior to budburst. Meteorological variables are: cumulative rainfall,  $P_{cum}$ ; mean daily temperature,  $T_{mean}$ ; mean daily solar radiation,  $R_{s,mean}$ ; and mean daily vapour pressure deficit,  $D_{mean}$ . The budburst dataset was of 6 years: 2002–2003 from the Mitra site and 2007–2010 from the Lezirias site. The best fit is highlighted in grey.

	$R^2$ ; sign of slope			
	$P_{cum}$	$T_{mean}$	$R_{s,mean}$	$D_{mean}$
1 Jan – Budburst day	0.05; –	0.76; –	0.33; +	0.00; +
1 Feb – Budburst day	0.08; –	0.72; –	0.13; +	0.00; –
1 Mar – Budburst day	0.00; +	0.56; –	0.01; +	0.04; +
15 Mar – Budburst day	0.12; +	0.72; –	0.00; –	0.00; +
25 Mar – Budburst day	0.15; +	<b>0.81; –</b>	0.00; +	0.06; –
1 Apr – Budburst day	0.02; +	0.75; –	0.06; +	0.05; –

Lezirias. The highest correlation for the relationship between budburst date and the average mean daily air temperature ( $T_{mean}$ ), was found for the time-interval between 25 March and budburst ( $R^2 = 0.81$ ) (Table 1). Furthermore, the linear fits between the rate of bud development ( $1/t$ , being  $t$  the time from the starting date to budburst day) and  $T_{mean}$  were better close to budburst ( $R^2$  of 0.87 and 0.82 after 25 March and 1 April, respectively) than in earlier starting periods ( $R^2$  from 0.74 to 0.53). For the best fit (Fig. 2) the relationship is unique, irrespective of the site. In the years with higher average daily mean air temperature ( $T_{mean}$ ) after 25 March, bud development was faster and new growth occurred earlier (Fig. 2a). From the regression equation of Fig. 2b ( $1/t$  vs.  $T_{mean}$ ),  $T_{base}$  and thermal time ( $\theta$ ) for *Q. suber* were estimated as 6.2 °C and 323 degree-days, from 25 March, respectively.

The relationships shown in Fig. 2 were obtained with the average mean daily air temperatures for the selected time interval. However, the mean temperatures include both the maximum and minimum daily values and, therefore, the relationships do not discriminate between the causal effects of these two temperature extremes on budburst date. Therefore, and to improve the analysis, we have re-done the relationship of Fig. 2a with the average of daily maximum (Fig. 3a) and daily minimum (Fig. 3b) temperatures. Data of Fig. 3 show that budburst timing is highly related to the average daily maximum temperature ( $R^2 = 0.895$ ), but not related with the average daily minimum temperature ( $R^2 = 0.002$ ). Therefore, the relationship of Fig. 2a (with the average mean daily temperature) seems predominantly determined by the effect of the maximum daily temperature values.

The overall average day length (photoperiod) at budburst was 13.8 h ( $\pm 0.26$ ) and never shorter than 13 h (considering both experimental sites).



**Fig. 2.** *Quercus suber*: relationship between time from 25 March to average budburst day ( $t$ , days (a) or  $1/t$  (b)) and average daily mean temperature (°C) in the same period. Each point corresponds to a year of observations. Data include measurements for Mitra 2 (2002–2003) and Lezirias (2007–2010). Error bars in Fig. 2a are standard errors.

### 3.2. *Quercus suber*: shoot elongation

In *Q. suber*, shoot elongation patterns were different in the two sites (Fig. 4). At Mitra 2 (closed symbols), the annual shoot elongation was similar in both studied years (3.9 and 3.3 cm in 2002 and 2003, respectively) but shorter and smaller than in Lezirias (open symbols), where it varied between years (from a minimum of 7.1 cm in 2009 to a maximum of 19.6 cm in 2010).

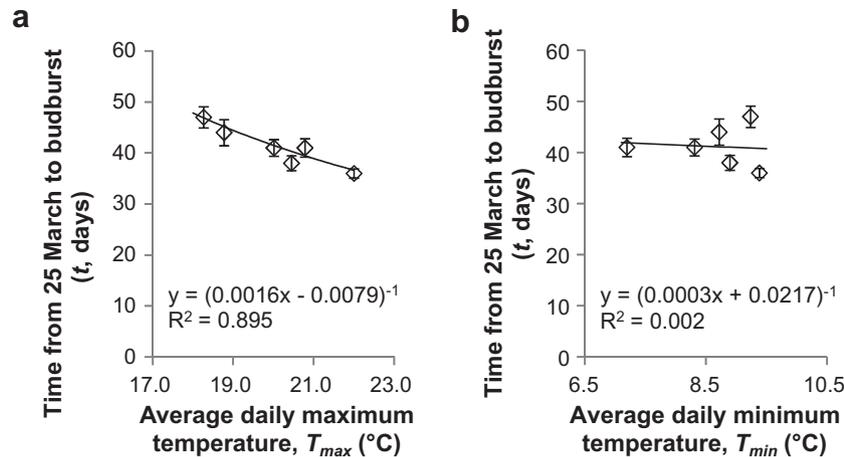
Considering both sites together, no causal relationships were found between mean annual elongation and any meteorological variable, prior or after budburst. However, some relationships were found when testing Lezirias data alone. Given the very different patterns of shoot elongation between the two sites, data from each of them will be analysed separately.

#### 3.2.1. *Quercus suber* shoot elongation – Lezirias site

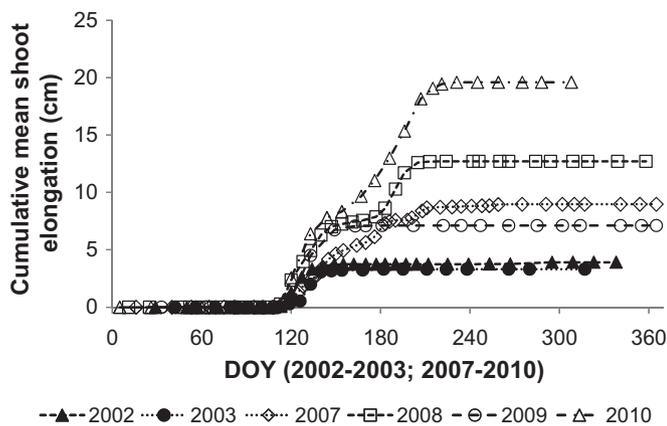
Tree water status was monitored at Lezirias during 2007 and 2008. *Q. suber* predawn leaf water potential,  $\Psi_{l,pd}$ , remained always high (above  $-0.5$  MPa) and approximately constant throughout the year (Fig. 5). Yearly minimum  $\Psi_{l,pd}$  values were  $-0.45$  MPa and  $-0.33$  MPa in November 2007 and August 2008, respectively. During the observation period,  $\Psi_{l,pd}$  was not influenced by the amount or distribution of rainfall (Fig. 1).

Mean annual shoot elongation at Lezirias was found to be positively correlated to rainfall sums and average temperatures prior to budburst. Elongation was found to be strongly correlated to cumulative rainfall over the 2–4 months prior to budburst (starting dates: 1 January, 1 February and 1 March) ( $R^2 \geq 0.90$ ) (Table 2). The strength of the relationship decreases for shorter periods, i.e., starting dates approaching budburst. A similarly strong relationship was found between annual shoot elongation and the average of daily mean air temperature for the periods closer to budburst ( $R^2 \geq 0.97$ , starting dates: 25 March and 1 April) (Table 2). In the periods when shoot elongation was strongly correlated to cumulative rainfall, a concomitant good fit was also found with solar radiation (Table 2). However, solar radiation is negatively correlated to shoot elongation (Table 2), which suggests that radiation is not an explanatory variable. The simultaneous occurrences of high correlations between shoot elongation and both cumulative rainfall and radiation is due to the high dependence between these two meteorological variables ( $R^2 > 0.9$ ): higher rainfall means more cloudiness and, therefore, less radiation. No causal relationships were found between meteorological conditions during the period of vegetative growth and total shoot elongation.

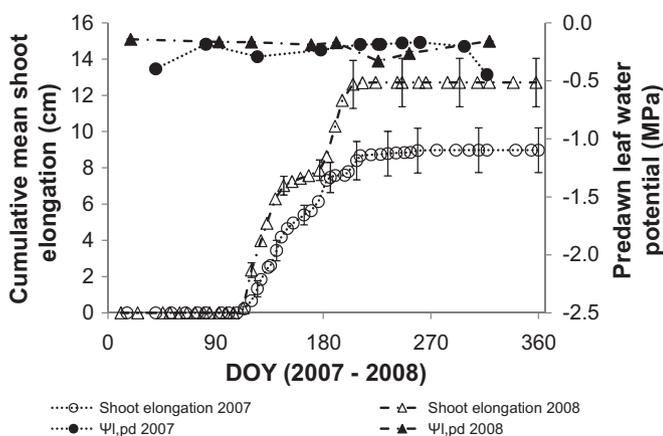
Mean number of leaves per shoot followed closely stem elongation patterns (data not shown). Therefore, annual leaf production



**Fig. 3.** *Quercus suber*: relationships between time from 25 March to average budburst day ( $t$ , days) and average daily maximum temperature ( $^{\circ}\text{C}$ ) (a), and average daily minimum temperature ( $^{\circ}\text{C}$ ) (b), in the same period. Each point corresponds to a year of observations. Data include measurements for Mitra 2 (2002–2003) and Lezírias (2007–2010). Error bars are standard errors.



**Fig. 4.** *Quercus suber* cumulative mean apical shoot elongation (cm) at Mitra 2 – closed symbols (2002 and 2003) and at Lezírias – open symbols (2007–2010).



**Fig. 5.** *Quercus suber* at Lezírias: cumulative mean apical shoot elongation (cm) – open symbols and seasonal variation of predawn leaf water potential (MPa) – closed symbols, for 2007 and 2008. Error bars are standard errors. Error bars in predawn leaf water potential are contained within the size of the symbols.

was also highly correlated to cumulative rainfall and air temperature prior to budburst.

In three of the studied years (2007, 2008 and 2010), two consecutive and distinctive spring shoot growth periods were observed.

**Table 2**

Linear regression analysis between mean annual total shoot elongation in *Q. suber* and meteorological variables, for different periods prior to and after budburst. Meteorological variables are: cumulative rainfall,  $P_{\text{cum}}$ ; mean daily temperature,  $T_{\text{mean}}$ ; mean daily solar radiation,  $R_{\text{S,mean}}$ ; and mean daily vapour pressure deficit,  $D_{\text{mean}}$ . The shoot elongation dataset was of 4 years (2007–2010), from the Lezírias site. The better fits are highlighted in grey.

	$R^2$ ; sign of slope			
	$P_{\text{cum}}$	$T_{\text{mean}}$	$R_{\text{S,mean}}$	$D_{\text{mean}}$
1 Jan – Budburst day	<b>0.90</b> ; +	0.17; +	<b>0.99</b> ; –	0.55; +
1 Feb – Budburst day	<b>0.99</b> ; +	0.00; +	<b>0.97</b> ; –	0.22; +
1 Mar – Budburst day	<b>0.96</b> ; +	0.22; +	<b>0.96</b> ; –	0.17; +
15 Mar – Budburst day	0.43; +	0.71; +	0.81; –	0.58; +
25 Mar – Budburst day	0.47; +	<b>0.99</b> ; +	0.69; –	0.57; +
1 Apr – Budburst day	0.40; +	<b>0.97</b> ; +	0.75; –	0.60; +
Budburst day – End of elongation	0.02; –	0.04; +	0.11; +	0.20; +

In 2009, with drier and cooler early spring conditions, the second period of growth did not occur (Fig. 4).

In the first spring growth flush, current-year shoots developed through proleptic (delayed) branching (Barthélémy and Caraglio, 2007) from previous-year vegetative apical buds. The second growth period occurred in late-spring after a small rest phase. In this case, newly produced buds (just apical or apical and axillary) originated a new set of stems and a new leaf cohort (through immediate branching). Sometimes, the twigs that emerged from the spring bud continued elongation until mid-summer. In these cases, after an initial period of high elongation rate, growth slowed down and new axillary buds were produced. When apical shoot elongation resumed initial rate, buds developed into new lateral shoots and leaves. By the end of the summer, a new set of vegetative buds was produced and fully developed but a generalised separate autumn flush was never observed at Lezírias.

*Quercus suber* trees in Lezírias exhibited a high degree of phenophase synchrony between years, with budburst onset overlapping with flowering, in the same period during spring. Although generally new leaves start expanding a few weeks before abscission of the majority of old ones, leaf shedding may also occur before budburst, as observed more pronouncedly in 2008 and 2010.

### 3.2.2. *Quercus suber* shoot elongation – Mitra 2 site

Tree water status was monitored during 2002 and 2003 and its seasonal pattern was similar in both years. Predawn leaf water potential was high during the wet season, and dropped during the

summer. The decline started in early June, and became more pronounced as the summer drought progressed. A recovery of tree water status was observed in autumn, with  $\Psi_{l,pd}$  returning to wet season values, around  $-0.2$  MPa (Fig. 6). Therefore, and contrary to what was observed in Lezirias, *Q. suber* trees at the Mitra 2 site suffered from dry season water stress. During 2002, shoot elongation occurred from early May to early June, when  $\Psi_{l,pd}$  was still high (above  $-0.3$  MPa). Elongation ceased when  $\Psi_{l,pd}$  began to decrease. Growth was resumed in October, when tree water status ( $\Psi_{l,pd}$ ) recovered upon the onset of autumn rains. A small increase of about 4.4% of the total year elongation was then observed. In 2003, the pattern of current-year shoot growth was similar but no autumn growth was observed. In spring, only one flush of shoot growth was observed in both years. In Mitra 2, the mean annual apical shoot length was considerably smaller than in Lezirias (Fig. 4).

No relationship was found between *Q. suber* annual shoot elongation and rainfall at Mitra 2. Mean shoot elongation was similar in both years, though annual rainfall was 14.4% higher in 2002 than in 2003.

### 3.3. *Quercus suber* shoot elongation: Variability between trees in Lezirias site

A great variability in cork oak current-year shoot elongation was observed at Lezirias, between years and trees (Fig. 7). The annual vegetative growth of the 3 sampled trees varied between 6.1 and 22.2 cm from 2007 to 2010, respectively (Fig. 7). The years with smaller cumulative mean elongation (2009 and 2007, see Fig. 4) also showed a smaller difference between trees (Fig. 7).

### 3.4. *Quercus suber* and *Q. ilex* budburst and shoot elongation: comparison between species in Mitra 2 site

For *Q. ilex*, average budburst day was DOY 87 (end of March), during the two studied years. For this species, estimated average day length (photoperiod) for budburst was 12.3 h ( $\pm 0.3$ ), although some sampled buds burst at day lengths as short as 11.5 h. Budburst in *Q. suber* occurred about 6 weeks later than in *Q. ilex* (Fig. 8) (40 and 43 days of difference in 2002 and 2003, respectively).

Seasonal tree water status ( $\Psi_{l,pd}$ ) was also monitored in *Q. ilex* at Mitra 2 (see David et al., 2007). Seasonal patterns of predawn leaf water potential were similar to those of *Q. suber*, but dry season water stress was less pronounced (David et al., 2007).

Both species also exhibited a similar seasonal shoot elongation pattern, with most of the current-year shoot growth taking place during spring, when tree water status was still high. In autumn,

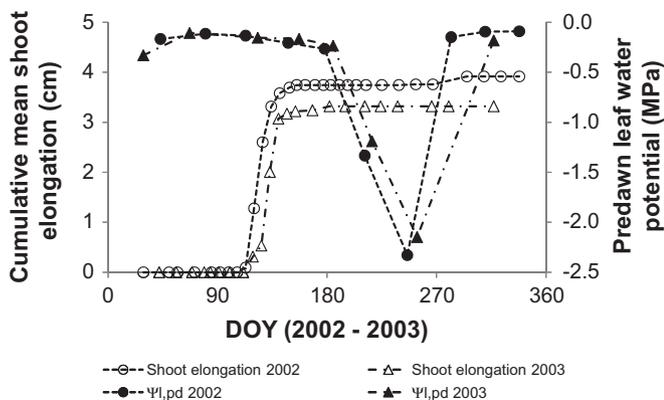


Fig. 6. *Quercus suber* at Mitra 2: cumulative mean apical shoot elongation (cm) – open symbols and seasonal variation of predawn leaf water potential (MPa) – closed symbols, in 2002 and 2003.

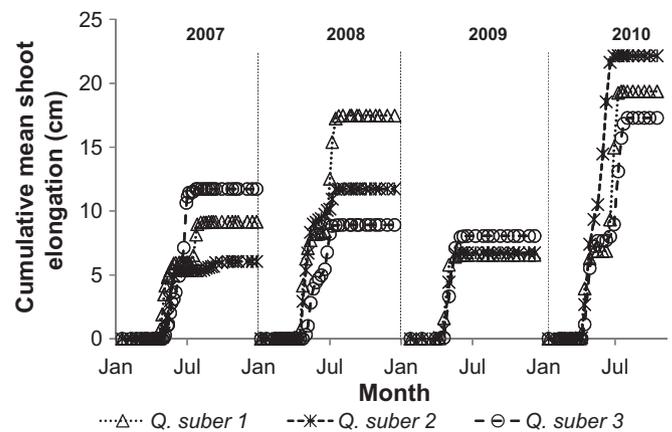


Fig. 7. Cumulative mean apical shoot elongation (cm) in the 3 sampled *Q. suber* trees at the Lezirias site, from 2007 to 2010.

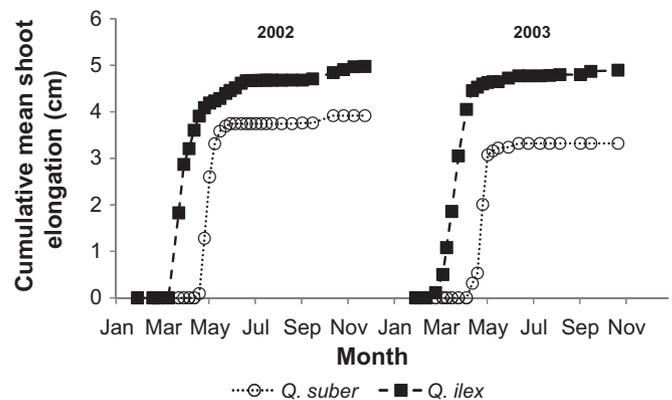


Fig. 8. Cumulative mean apical shoot elongation (cm) at Mitra 2, in *Q. suber* (open circles) and *Q. ilex* (closed squares), for 2002 and 2003.

when  $\Psi_{l,pd}$  recovered from the summer drought, a second smaller elongation period was observed (Fig. 8). In 2002, autumn growth was responsible for a 5.9% and 4.4% increase in the total current-year shoot elongation in *Q. ilex* and *Q. suber*, respectively. In 2003, autumn growth was only observed in *Q. ilex*, though smaller than in 2002 (2.5% of total annual growth).

## 4. Discussion

### 4.1. *Quercus suber*: budburst

Air temperature was found to be the main environmental driver of *Q. suber* budburst timing. This has also been reported for other Mediterranean oak species of the Iberian Peninsula (Morin et al., 2010; Peñuelas et al., 2002; Sanz-Pérez et al., 2009). Our results showed that high mean and maximum daily temperatures in periods close to budburst (late-March and April) accelerate more effectively bud development than those of earlier periods (January and February) (Table 1 and Figs. 2 and 3). This is in agreement with the evidence reported by Menzel and Sparks (2006) and Wielgolaski (2001) who state that high temperatures in the preceding 1–3 months may promote earlier leafing and flowering in some tree species. García-Mozo et al. (2006) reported that weather conditions (air temperature and rainfall) 1 month prior to flowering were the most influential on oak phase timing.

In the period with the best fit between budburst date and temperature (late-March to budburst) minimum daily temperature had no influence on budburst (Fig. 3b). However, in many other

places and species, chilling temperatures have been reported to be determinant for the break of bud dormancy (Cannell and Smith, 1983; Hänninen, 1990; Kramer, 1994). Even considering longer periods of temperature averaging, our dataset failed to show any evidence on the chilling effect (results not shown). Similar findings have been reported for other Mediterranean species (Chuine, 2000; Chuine and Cour, 1999; García-Mozo et al., 2008). However, other authors acknowledge the possible importance of chilling even under Mediterranean conditions (Jato et al., 2007; Morin et al., 2010).

We estimated  $T_{\text{base}}$  for cork oak budburst as 6.2 °C. This value is close to that reported for *Q. ilex* budburst (Sanz-Pérez et al., 2009) and for Iberian *Quercus* flowering phase (Jato et al., 2002): 7 °C. Thermal time for cork oak budburst was found to be 323 degree-days, cumulated after 25 March. Some authors report different thermal requirements for other Mediterranean oaks. This may be due to differences in climatic conditions or in the assumed starting dates and threshold temperatures (García-Mozo et al., 2002; Jato et al., 2007; Spano et al., 1999).

*Quercus suber* budburst never occurred at day lengths shorter than 13 h, either at Mitra 2 or Lezirias, even when the temperatures in the previous month were high. This suggests that photoperiod may play an additional role in the triggering mechanisms of budburst on cork oak by constraining the influence of temperature to a safer period (Menzel and Sparks, 2006). This dependency on photoperiod was also observed for holm oak (Sanz-Pérez et al., 2009).

We did not find any relationship between rainfall and budburst date in *Q. suber* at our sites. Spano et al. (1999), although verifying a correlation between flowering dates of some non-native species and rainfall sums of the previous month, found little effect of rainfall on budburst of Mediterranean species. However, Peñuelas et al. (2004) found an overall relationship between October to February rainfall and budburst date for a range of Mediterranean species.

An important feature of the relationships that we found between budburst date in *Q. suber* and average mean and maximum daily temperatures, as well as with photoperiod, is that they are valid irrespective of site location (Mitra 2 and Lezirias). Therefore, our findings on budburst triggering mechanisms in *Q. suber* seem species-specific, regardless of local soil and water conditions.

#### 4.2. *Quercus suber* shoot elongation – Lezirias site

All studied *Q. suber* trees, at the Lezirias site, experienced a favourable and spatially homogeneous water status throughout the experimental period, irrespective of the amount and distribution of rainfall (Figs. 1 and 5). This suggests that the tree deep roots were freely tapping water from the shallow water table, whose level never dropped below 4.7 m (unpublished data). Therefore, at this site water supply never constrained tree growth and, hence,  $\Psi_{\text{lpd}}$  did not explain the between-year difference in annual apical twig elongation.

Mean annual shoot elongation and mean number of leaves per shoot were found to be highly correlated to cumulative rainfall and temperature, over the 2–4 months and 1 month prior to budburst, respectively (Table 2). Average annual apical twig elongation and annual leaf production were mainly dependent on the conditions preceding the time of major growth activity.

A distinct second period of twig expansion and leaf flushing in late-spring, after an intermediate growth rest, as observed in 3 of the 4 studied years at Lezirias (see Fig. 4), has been also reported by other authors (Oliveira et al., 1994). This pattern does not seem to be a general feature of mature cork oak populations (see Fialho et al., 2001), but it has been observed in oak saplings (Mediavilla and Escudero, 2009) and young trees (Oliveira et al., 1994). The triggering mechanisms of this second growth flush are still unknown.

Since *Q. suber* trees kept a favourable water status even throughout the summer, it was surprising to find a relationship with rainfall (Table 2). To explain this, it is important to consider that plant growth depends not only on water but also on nutrient availability (Ryel et al., 2010). High water potentials are a baseline requirement for plant growth since they allow the maintenance of high cell turgor pressure (Hsiao, 1973) and therefore of stomatal aperture. Under non-limited water conditions (such as in Lezirias), nutrient availability may be considered as the main factor explaining differential growth. Deep soil and groundwater pools can maintain a favourable plant water status but are poor in nutrient content (Davis and Mooney, 1986; Ryel et al., 2010). Nutrients are mainly concentrated in the top soil layers (Cui and Caldwell, 1997; Ryel et al., 2010). Antecedent cumulative rainfall and surface soil moisture promote nutrient absorption by shallow roots (Nord and Lynch, 2009), and warmer temperatures contribute to a higher mineralisation rate of litter and soil organic matter (Körner, 2006; Jobbágy and Jackson, 2001). Our data suggest that optimal nutrient availability requires long-term rainfall accumulation (2–4 months) and a short-term high temperature effect (1 month) prior to budburst. Rainfall needs time and amount to accumulate in the soil profile whereas temperature may have an immediate effect on nutrient release. Rainfall decreases and becomes less relevant as spring progresses. In Lezirias, the years with better environmental conditions for nutrient uptake in the period prior to budburst showed higher shoot elongation and leaf production (Table 2, see also Fig. 1).

Previous observations reported that cork oak generally keeps most of previous-year leaves until the new ones are fully expanded (Fialho et al., 2001; Mediavilla and Escudero, 2003; Pereira et al., 1987). At Lezirias, we observed that an important part of the crown leaves were discarded in the weeks prior to budburst, particularly in years of earlier budburst and higher shoot elongation. This may be a consequence of increases both in growth demands (Milla et al., 2004) and in the translocation/remobilization of the nutrient/carbon reserves (Bussotti et al., 2003; Milla et al., 2005; Sanz-Pérez et al., 2009).

#### 4.3. *Quercus suber* shoot elongation – Mitra 2 site

In Mitra 2, *Q. suber* shoot elongation was restricted to periods of favourable water status and maximum growth rates were observed in mid-spring. This growing pattern has been also observed in other oaks and shrubs in Mediterranean climate regions (e.g., Arianooutso and Mardiris, 1987; de Lillis and Fontanella, 1992; Fialho et al., 2001; Gill and Mahall, 1986; Mediavilla and Escudero, 2009). In Spain, Molinas et al. (1992) observed in mature *Q. suber* trees mean elongation values of 4.2 cm, similar to our results (3.3–3.9 cm).

In a previous study at the same site, the groundwater table level was found to be shallow and never deeper than 4–5 m in the summer (David et al., 2007). However, the tree deep root access to groundwater was not as efficient as in Lezirias, due to the hard nature of the bedrock (granite). Therefore, a progressive drop in pre-dawn leaf water potential was observed after early-June, restraining twig elongation in *Q. suber* (Fig. 6), since shoot and leaf expansion are known to be highly sensitive to even mild levels of water stress (Hsiao and Xu, 2000; Munns et al., 2000). The recovery of tree water status, upon the onset of autumn rains, allowed the start of a new growth period in 2002. Vegetative growth in autumn has been reported as a frequent feature of Mediterranean evergreen oaks in the Iberian Peninsula (Castro-Díez and Montserrat-Martí, 1998; Molinas et al., 1989; Pereira et al., 1987). Other authors did not report this feature at all (Fialho et al., 2001; Oliveira et al., 1994). In some Mediterranean sites, such as Mitra 2, when soil/geology somehow restrains deep rooting and trees suffer

from spring–summer water stress, oak phenological development and growth is mainly dependent on water availability (Baker et al., 1982; Mahall et al., 2010; Peñuelas et al., 2004).

Although rainfall was higher than the long-term average in both studied years, it did not influence mean annual elongation similarly to what has been reported by Oliveira et al. (1994) for other cork oak trees in Southern Portugal.

#### 4.4. *Quercus suber* shoot elongation: variability between trees in Lezirias site

The average growth observed in the first spring period in *Q. suber* at Lezirias was similar between trees and years (5–9 cm, Fig. 7). However, considerable differences were found on total current-year mean apical twig elongation (Figs. 4 and 7). This suggests that, in this fully watered site, “maximum elongation” and “maximum leaf production” require not only a comfortable water status but also optimum nutrient conditions. Therefore, years with wetter and warmer conditions prior to the growing season always showed higher shoot elongation and greater variability both within and between trees. Genetic variability between trees seems to emerge when environmental conditions (water and nutrients) are less restrictive.

#### 4.5. *Quercus suber* and *Q. ilex* budburst and shoot elongation: comparison between species in Mitra 2 site

The timing of budburst was observed in the two oak species with a high degree of synchronicity. Budburst of *Q. suber* occurred about 6 weeks later than in *Q. ilex* (Fig. 8). Other studies also reported a similar pattern for *Q. suber* budburst timing (late-April to mid-May) (Oliveira et al., 1994), later than in other Iberian *Quercus* species (Jato et al., 2002; Mediavilla and Escudero, 2003). Conversely, in NE Spain, budburst date in *Q. ilex* may vary up to 4 weeks between years (from mid-March to mid-April), showing some degree of phenophase overlapping with other Mediterranean oaks (*Quercus pyrenaica*, *Quercus faginea*, *Quercus robur*) (Milla et al., 2010). The possible dependence on photoperiod observed in cork oak (see Section 4.1) has also been reported for holm oak (Sanz-Pérez et al., 2009) and may explain differences in the timing of budburst between the two species: holm oak begins growing at a much lower photoperiod than cork oak. This delay is also observed in flowering (Jato et al., 2002), creating a phenological barrier to hybridisation between cork and holm oaks even when they share the same habitat (Varela et al., 2008).

Similarly to *Q. suber* at Mitra 2, most of *Q. ilex* vegetative growth occurred during spring. In Mediterranean climate sites, it is only at this time of the year that temperature, water and nutrients are all favourable to growth (Davis and Mooney, 1986). *Q. ilex* trees also suffered from late-spring/summer water stress, although to a smaller degree (see David et al., 2007). That may explain the difference on annual elongation values (higher in *Q. ilex*).

*Quercus ilex* trees at Mitra 2 displayed an additional small growth flush in autumn in response to water status recovery. This phenological pattern, previously reported for *Q. ilex* trees (Crescente et al., 2002; de Lillis and Fontanella, 1992; Ogaya and Peñuelas, 2004) allows the extension of the growing season through autumn using more effectively all periods with favourable environmental conditions.

## 5. Final remarks

Climate change predictions for the Mediterranean region foresee warmer and drier springs and an increase in the length and severity of seasonal summer drought (Miranda et al., 2002).

According to our results on temperature/budburst date, budburst in Mediterranean evergreen oaks will tend to anticipate in time (similarly to what has been reported for many other species and regions), although probably within a range of species-specific photoperiod limits.

In respect to shoot elongation, two main situations may arise:

- In water-limited areas, the drier springs and summers will lengthen the tree water stress period, restricting shoot elongation;
- In fully watered places, shoot growth will be then limited by nutrient availability prior to budburst. Predicted warmer, but drier springs may have contradictory effects on nutrient recycling. On one hand, the expected decrease in spring rainfall will tend to slow down nutrient recycling whereas the foreseen increase in spring temperature will tend to have the opposite effect. Our data do not allow distinguishing between the relative importances of these two counteractions.

Most commonly, future trends on the phenology of Mediterranean evergreen oaks will be characterised by an anticipation of budburst and a reduction of shoot elongation.

The work reported here may have some limitations inherent to sample size and length of the measuring period (4 years at the Lezirias site and 2 years at the Mitra 2 site). However, during the experiment a significant number of meteorological and physiological variables were intensively monitored, some of which are not frequently surveyed in phenological studies (such as predawn leaf water potential). This allowed an integrative and process-based approach to improve the understanding on the mechanisms underlying budburst and shoot elongation. To our knowledge, the results are innovative, particularly for mature *Q. suber* trees.

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