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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 (± 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 (±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.

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^2 and 8.5 to 9.5 m in *Q. suber* and from 0.33 to 0.43 m, 47.71 to 89.99 m^2 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^2 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, Rhyl, 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^{-2} day^{-1}), D (Pa) and rainfall (P, mm day^{-1}) 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