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Does the geography of cork oak origin influence budburst and leaf pest damage?

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A B S T R A C T

Spring shoot phenology is an adaptive trait highly responsive to climatic conditions that influences plant growth and development, as well as plant–herbivore interactions. We investigated if the geographic origin of cork oak influenced spring shoot phenology (timing of budburst) and if the variation among provenances (advances and/or delays) had consequences for leaf pest damage. The study was conducted in two provenance trials (planted in 1998) located in central and southern Portugal; each trial was surveyed during a two-year period. The variation in budburst timing was compared for 35 cork oak (*Quercus suber* L.) provenances sampled from the entire natural distribution of the species. Budburst exhibited high broad-sense heritability (0.79–0.94). Two East/West groups effectively separated *Q. suber* genetic structure and the timing of budburst. Provenances from the western part of the natural range tended to burst later than provenances from the eastern part. Budburst provenance ranking was similar between sites and years. Climate strongly influenced budburst date: in the year with warmer winter months (2004), all provenances in both sites exhibited earlier budburst in comparison with 2003 and 2005. Leaf pest damage was assessed at the southern provenance trial. Differences in the timing of budburst had a significant effect on insect activity (herbivory), which was more concentrated in time and thus more important in the year with later budburst. However, North African provenances with earlier budburst were more exposed to insect herbivory within each year. This study demonstrated a significant provenance effect on budburst timing of *Q. suber* that is partly genetically determined and has consequences for exposure to herbivory. Knowledge of cork oak locally adapted provenances is important for sustainable forest management in Mediterranean climate conditions, particularly for (re)forestation actions, because it favors higher survival and growth.

1. Introduction

Sustainable forest management in the Mediterranean climate requires an understanding of the adaptation potential of woody species to cope with different environmental stress events linked with climate that affect plant performance either directly (e.g., drought and frost) or indirectly (e.g., pests and diseases). Phenology, which determines the timing of life cycle events, such as budburst, flowering, fruiting and autumn leaf-fall (Lieth, 1974), is a key adaptive trait of temperate tree species that are sensitive to climate change (Bertin, 2008). Indeed, climate change-induced warming has led to an advancing spring phenology in many plant species (Menzel et al., 2006; Root et al., 2003). Shifts in phenology may have important ecological consequences, including the length of the growing season and the amount of net assimilation, that affect a tree's growth potential (Vitasse et al., 2009a) and the potential to modify patterns of defoliation with significant disturbance in tree fitness (Foster et al., 2013). The advance or delay in budburst affects the phenological window, i.e., the period when foliage quality and quantity is favorable for successful colonization and persistence of the emerging individuals (Hunter and Lechowicz, 1992). This phenological window also determines phenological (mis)matches between trophic levels such as herbivore

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insects and their host trees (Schwartzberg et al., 2014; van Asch and Visser, 2007; Visser and Holleman, 2001). Therefore, changes in plant phenology may create insect–plant asynchronies, which has been proposed as a plant defense mechanism against leaf herbivores (Tikkanen and Julkunen-Tiitto, 2003; Tuomi et al., 1989). Moreover, a wide phenological variation will tend to reduce the overlap period of high quality foliage among neighbor trees, thereby limiting colonization by insect herbivores (Tikkanen and Julkunen-Tiitto, 2003). A key issue is to understand how insect herbivores will cope with rising uncertainty in the timing and duration of phenological events caused by climate change and tree genetic variability.

Cork oak (*Quercus suber* L.) is a key tree species in Portuguese forest ecosystems, representing 23% of the national forested area, 54% of the global industrial cork, and 34% of the total Portuguese forest exports (AFN, 2010). It is widely distributed in the Western Mediterranean region where it occurs across a wide range of climatic conditions (Natividade, 1950). Compared with other Mediterranean trees, *Q. suber* is a late blooming species, with leaf unfolding and shoot growth occurring during mid-spring, usually from April onwards (Pausas et al., 2009; Pinto et al., 2011). Leaf life span is approximately 12 months, with the main leaf shedding event contemporary with budburst (Pausas et al., 2009). In addition to the spring periodic growth based on the expansion of buds formed in the previous year, several growth flushes of proleptic shoots may occur (Pinto et al., 2011) in frequent but rather unpredictable events in time or by tree, leading to sub-continuous growth (C. Varela, pers. obs.).

Studies on the phenology of *Q. suber* have primarily addressed the effects of environmental variables such as temperature, photoperiod and rainfall on periodic shoot growth (Oliveira et al., 1994; Pinto et al., 2011) and the ecology of floral phenology (Díaz-Fernández et al., 2004; Elena-Rossello et al., 1993; Varela et al., 2008). However, because the natural distribution of *Q. suber* encompasses significant environmental and geographic gradients, it can be expected that long-term natural selection and genetic drift have resulted in a high level of genetic variation among populations in adaptive traits such as budburst. For other oak species, large clinal variations in phenological traits are well documented (Alberto et al., 2011; Deans and Harvey, 1995; Ducousso et al., 1996; Jensen, 1993) and a moderate to high degree of heritability was generally reported for these traits (reviewed in Howe et al., 2003). The relationship between genetic variation of *Q. suber* phenology, particularly the timing of budburst and insect herbivory, has received little attention despite previous studies of *Q. suber* populations that revealed distinct geographical patterns for growth and for specific physiological and morphological traits (Aranda et al., 2005; Gandour et al., 2007; Ramírez-Valiente et al., 2010, 2011), as well as for phenological traits (Ramírez-Valiente et al., 2014).

The main aim of our study was to evaluate the variability in the *Q. suber* timing of budburst as a function of seed geographical origin and its consequences for leaf pest damage. Additionally, we analyzed the inter-annual variation and stability in the provenances of budburst and the effect of geographical variables and environmental conditions on the timing of budburst. The study was conducted in two provenance trials that are part of a multi-locality provenance test belonging to a Euforgen Network established through a Concerted Action "European network for the evaluation of genetic resources of cork oak for appropriate use in breeding and gene conservation strategies", where 35 cork oak provenances covering all the natural distribution range are represented. These trials assess the effect of geographic origin on adaptive traits, which provides a powerful tool to estimate adaptation of *Q. suber* provenances to different environmental conditions through genetic adaptation or phenotypic plasticity. Additionally, these trials are well-suited to study the long-term responses of trees to climate change and to develop general seed transfer guidelines for reforestation, thereby improving forest productivity.

2. Materials and methods

2.1. Study sites and plant materials

The study was conducted in two cork oak provenance trials, Mata das Virtudes (39°05′N, 8°59′W), Azambuja, in central Portugal and Herdade do Monte Fava (38°00′N, 8°70′W), Santiago do Cacém in southern Portugal, hereafter referred to as the Central and South trials, respectively. Both sites are characterized by a Mediterranean climate with hot dry summers, cold and mild wet winters, and precipitation mainly concentrated in the October–May period. Long-term (1951–1980) mean annual temperature is 15.8 °C and 16.2 °C and mean annual precipitation is 557 mm and 587 mm in the South and Central trials, respectively (Instituto de Meteorologia, Lisbon). The Central trial is at an altitude of 25 m whereas the South trial is at an altitude of 79 m. Soil texture is sandy in both trials.

The provenance trials were established in March 1998 as part of a European cork oak network, FAIR 1 CT 95-0202 (Varela, 2000). Plant material included in both field trials resulted from a seed collection conducted in 35 cork oak provenances that cover the entire natural distribution range of cork oak. Each seed lot was collected from at least 20 trees located 50–100 m apart; mother trees were selected according to acorn production, sanitary status and age (greater than 50 years to minimize human impact on gene flow due to afforestation). Detailed information describing all provenances, including climate data for seed sources, is given in Table 1. Hereafter, provenances will only be mentioned by their respective code for simplicity. The experimental design in each trial was a randomized complete block design with 30 blocks and four plants per provenance and block (two-tree plot), planted at 6×6 m spacing.

Meteorological data (Instituto de Meteorologia, Lisbon) from the nearest meteorological station, i.e., Fonte Boa (39°20′N, 8°74′W) and Alvalade (37°95′N, 8°39′W), were used to represent the meteorological conditions at the Central and South trials, respectively.

2.2. Budburst observations

The phenological variable considered was budburst day. Monitoring was performed in 2003 and 2004 at the Central trial, and in 2004 and 2005 at the South trial. Phenological observations were made at weekly intervals from February to May in 11 trees per provenance for the 35 cork oak provenances. For the common monitored year (2004), observations were always made for consecutive days at the two sites. Budburst observation refers to the monitoring of the first spring flush. Because the sampled cork oak trees were still in a juvenile stage, we recorded the vegetative phenology, known to be highly correlated with the reproductive stage (Díaz-Fernández, 2000). On each observation date, the vegetative terminal bud was observed in four shoots per tree, selected according to the cardinal directions (N, S, W and E). A categorical four-level scale was developed to describe bud-bursting phases: (1) Dormant bud (no activity, bud is not visible), (2) Swollen bud (bud is visible and starts to swell; colored brown), (3) Red bud (bud turns reddish), and (4) Open bud (bud bursts, very young green leaves observed). At the South trial, bud consumption when observed was registered. Budburst day was defined as the day of the year when at least two of the observed buds of each tree reached the fourth phenological class.