Drought reduces tree growing season length but increases nitrogen resorption efficiency in a Mediterranean ecosystem

Raquel Lobo-do-Vale[1], Cathy K. Besson[2], Maria C. Caldeira[1], Maria M. Chaves[3], João S. Pereira[1]

[1]Centro de Estudos Florestais, Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal

[2]Instituto Dom Luiz, Centro de Geofísica da Universidade de Lisboa, Faculdade de Ciências, Campo Grande, 1749-016 Lisboa, Portugal

[3]Laboratório de Ecologia Molecular, ITQBNOVA, Universidade Nova de Lisboa, Av. da República, 2780-157 Oeiras, Portugal

Correspondence to: Raquel Lobo-do-Vale (raquelvale@isa.ulisboa.pt)

Abstract. Mediterranean ecosystems are hotspots for climate change, as the highest impacts are forecasted for the Mediterranean region, mainly by more frequent and intense severe droughts. Plant phenology is a good indicator of species' responses to climate change. In this study, we compared the spring phenology of cork oak trees (*Quercus suber*), an evergreen species, over two contrasting years, a mild year (2004) and a dry year (2005), which was the most severe drought since records exist. We evaluated the timing of occurrence, duration, and intensity of bud development, budburst, shoot elongation, trunk growth, and leaf senescence (phenophases) and assessed the nitrogen resorption efficiency from senescent to green leaves. The temperature was the main driver for budburst. Nevertheless, water had a main role constraining all the other phenophases, by strongly reducing the growing season length (-48 %) and consequently tree growth. Basal area increment was the most affected growth variable (-36 %), although occurring at a similar rate in the two years. Shoot elongation was also reduced (-21 %), yet elongation occurred at a higher rate in the dry as compared to the mild year. Leaf senescence during the bulk period was higher in the dry year, in which leaves were shed at the same rate over a longer period. Nitrogen concentrations in green and senescent leaves were affected by drought and nitrogen resorption efficiency increased remarkably (+22%). Our results highlight the importance of studying different phenological metrics to improve our understanding of the ecosystems responses to climate change. The faster dynamics observed in shoot elongation, while all other phenophases developed at the same rate, indicate that leaf area development is privileged in cork oak. Water availability was the main driver of spring growth in this Mediterranean ecosystem, however, growth may be affected by complex interplays between precipitation and temperature, such as higher temperatures during dry winters or heat waves during spring, that are likely to anticipate water stress. Longer studies are needed to disentangle those interplays. Finally, a higher nitrogen resorption efficiency in response to drought appears to be an adaptive trait that mitigates the limitation in nitrogen uptake by the roots during drought and contributes to improve tree fitness in the short-term, but will probably exert a negative feedback on the nitrogen cycle in the long-term which might affect the ecosystem functioning under the forecasted droughts.

1 Introduction

Plant phenology is an important indicator of the ecosystems responses to climate change (Jeong et al., 2011; Polgar and Primack, 2011; Richardson et al., 2013; Han et al., 2018). Shifts in plant phenology have broad consequences for ecosystems, not only directly through changes in the cycling of carbon, water and nutrients, but also indirectly through feedbacks on the climate system (Diez et al., 2012; Richardson et al., 2013; Tang et al., 2016; Han et al., 2018), which in turn may strongly influence ecosystem productivity (Tang et al., 2016). However, the response of species phenology to climate change is complex and highly variable, depending on species, spatiotemporal scales (seasonal or annual), or main climate driver (precipitation, temperature or both) (Penuelas et al., 2004; Polgar and Primack, 2011; Diez et al., 2012; Tang et al., 2016; Gerst et al., 2017). It is critical to have a better understanding of the patterns and climate drivers of the different phenophases in a broader range of tree species (Richardson et al., 2013; Tang et al., 2016; Lempereur et al., 2017). In particular, there is a dearth of information on Mediterranean schlerophyllous species (Misson et al., 2011; Bussotti et al., 2014; Costa et al., 2016) that grow in regions where the impacts of climate change will be amplified, mainly by more severe and longer droughts (Giorgi and Lionello, 2008; Jacob et al., 2014; Perkins-Kirkpatrick and Gibson, 2017).

Temperature is one of the most important drivers of plant phenology (e.g. Pinto et al., 2011; Flynn and Wolkovich, 2018). An earlier budburst and a lengthening of the growing season due to increased temperatures, have been reported by many studies (e.g. Peñuelas et al., 2002; Menzel et al., 2006; Gordo and Sanz, 2009; García-Mozo et al., 2010; Jeong et al., 2011). However, it was hypothesized that precipitation may be more important than temperature for the phenology of Mediterranean plant species (Penuelas et al., 2004). Still, available information of the effects of precipitation on phenology is scarce. Few studies indicated that precipitation had an impact on the onset of some phenophases, such as flowering and fruiting (Penuelas et al., 2004; García-Mozo et al., 2010; Swidrak et al., 2013). For tree growth and overall ecosystem productivity, summer drought is the most limiting period (Niinemets, 2010; Lempereur et al., 2017) while precipitation over the growing season determines growth and productivity (e.g. Pereira et al., 2007; Oliveira et al., 2016). Mediterranean trees are plastic and adjust their vegetative activity to the periods when water is available and temperatures are favourable, mainly during spring (Gordo and Sanz, 2010; Misson et al., 2011; Pinto et al., 2011). Both total and seasonal precipitation are important for tree growth (Besson et al., 2014; Oliveira et al., 2016). Costa et al. (2002) suggested that winter precipitation enhanced early spring growth while Costa-e-Silva et al. (2015) reported reductions in stem growth due to a dry winter. Furthermore, Costa et al. (2016), studying cork oak growth on different sites, identified different sensitivities to climate, showing that cork oak strategies to cope with drought ranged from drought tolerance to drought avoidance. The effect of temperature on tree growth seems to be tightly linked to the precipitation (Sardans and Peñuelas, 2013; Oliveira et al., 2016), stimulating growth if warmer temperatures occur in wetter years and having no effect or decreasing growth in dry years. However, it is not clear how these two climatic drivers affect the timing and length of other tree phenophases such as shoot elongation or leaf senescence. For most deciduous and evergreen species, the length of the growing season depends on the timing of budburst in spring but also on leaf senescence in autumn. For example, Jeong et al. (2011), reporting changes in phenology on the northern hemisphere suggested that the

lengthening of the growing season was due to extended leaf senescence in autumn rather than an earlier budburst. But, Han et al. (2018), reported both an earlier spring growth and an extended leaf senescence, in European forests. In the Mediterranean region, Gordo and Sanz (2009), in a study with 29 perennial species, reported that an extended growing season was due to an earlier budburst in spring.

5   Shifts in plant phenology can affect the cycling of nutrients that in turn might affect the nutrient availability for plant growth (Richardson et al., 2013). In addition, drought can condition nutrient availability for plant growth, either by decreased litterfall decomposition due to limited microbial activity and/or by limited nutrient uptake by roots due to lower mass flow and diffusion. Retranslocation of nutrients from senescent to new leaves is a key process that contributes for the nutrient conservation in plants, reducing the dependence of plants on soil nutrient availability (Aerts, 1996; Fioretto et al., 2003; Xu et al., 2017; Wang
10 et al., 2018). Nutrient retranslocation typically increases in the Mediterranean tree species before leaf senescence (Sardans and Peñuelas, 2013). Climate is a primary driver of nitrogen resorption efficiency (i.e. percentage of nitrogen that is retranslocated or resorbed, from senescent to green leaves, NRE) (Aerts, 1996), which is known to globally decrease with mean annual precipitation and temperature (Vergutz et al., 2012; Wang et al., 2018). However, it is not clear if NRE depends directly on annual precipitation or if the reduced water availability elicits a response in NRE (Brant and Chen, 2015). The reported impacts
15 of drought on NRE are not consistent. Studies with herbaceous species reported drought to either increase (Zhao et al., 2017) or decrease NRE (Drenovsky et al., 2012; Khasanova et al., 2013). Also, no changes in NRE were observed in Australian sclerophyll species between two distinct rainfall zones (Wright and Westoby, 2003). More importantly, in Mediterranean ecosystems, that usually have nutrient-poor soils (Sardans and Peñuelas, 2013), it is not known how increasing drought severity will affect NRE (Sardans and Peñuelas, 2013).

20   Due to a plethora of adaptation strategies to withstand long periods of water shortage (see a review by Sardans and Peñuelas (2013)), among other particularities, Mediterranean ecosystems are considered exceptional models to study the effects of climate change (Niinemets and Keenan, 2014; Doblas-Miranda et al., 2015). One important Mediterranean tree species is cork oak (*Quercus suber*). It is an evergreen tree with short-lived leaves that usually are shed within one year (Natividade, 1950; Pereira et al., 1987; Escudero et al., 1992; Aronson et al., 2009), concurrently with spring growth. Like other Mediterranean
25 oaks, cork oak is adapted to the Mediterranean climate, being able to survive summer drought. However, this tree species is showing signs of increasing vulnerability, mostly due to increased drought occurrence and poor management practices (Costa et al., 2011; Camilo-Alves et al., 2013). Cork oak phenological responses to the forecasted increase of severe droughts are still largely unknown. In addition, available studies on cork oak rarely compared nutrient dynamics in green and senescent leaves (Delarco et al., 1991; Andivia et al., 2009).

30   In this study, we discuss the phenophases characterizing the vegetative growing season of cork oak in spring (bud development, budburst, shoot elongation, leaf senescence and trunk growth) in two contrasting years, a mild year and an extremely dry year. Each phenophase is characterized by timing, duration and growth. Also, the nitrogen resorption efficiency is determined and compared between the mild and extremely dry years. We aimed to assess the effect of the extremely dry year on the cork oak

spring phenology and growth. More specifically, we hypothesised that drought would: 1) affect the timing of the different phenophases; 2) decrease the length of the spring growing season, negatively affecting growth and; 3) increase the nitrogen resorption efficiency from senescent to new leaves.

2 Materials and methods

2.1 Study site

The study was conducted at Herdade da Mitra (N 38º31.664', W 8º01.380', 221 m altitude) in southern Portugal. The climate is typically Mediterranean, with hot and dry summers. The soil is sandy (88.9 % sand, 4.9 % silt, and 6.3 % clay), with a low water holding capacity (~5 %) and slightly acid (pH 4-6), on a 5 % slope. The experimental area was 0.3 ha. Cork oak (*Q. suber*) trees were 16 years old. Tree density was 1997 ± trees ha^{-1}. The understory was mostly composed by *Cistus salviifolius* and *C. crispus* shrubs, and C3 annual herbaceous species, ending their cycle typically at the beginning of the summer period (June). Spring phenology and growth was monitored over two years (2004 and 2005) in 15 trees under natural conditions. Mean tree height at the beginning of the study was 5.0 ± 0.2 m.

We used the experimental set-up of a water manipulation study, as described in Besson et al. (2014), in which 3 treatments were applied. Dry, Ambient and Wet treatments received, respectively 80, 100 and 120% of current precipitation. Since rainfall exclusion had hardly any impact on cork oak physiology, we pooled the data from Dry and Ambient treatments. We excluded the Wet treatment because a significant treatment effect was only observed after a single pulse irrigation in late spring, applied as a punctual experiment. For this study, we used only Dry and Ambient trees that were sampled for both phenological and physiological measurements (n = 15). For every variable presented in this study, a previous statistical check (ANOVA) for treatment effects was performed, to confirm that the pooling was correctly applied, i.e., no treatment effect was observed.

2.2 Environmental monitoring

Precipitation (ARG100 rain gauge, EM Ltd., Sunderland, UK), air temperature (*T*) at 2 m height (Thermistor M841, Siemens, Munich, Germany), photosynthetically active radiation (PAR, LI-190 quantum sensor, Licor Inc., Lincoln, NB, USA) and air humidity (Fischer 431402 sensor, K. Fischer GmbH, Drebach, Germany) were measured in 5 min intervals and 30-min averages recorded with a datalogger (DL2e, Delta-T Devices Ltd., Cambridge, UK). Daily mean temperatures were used to calculate the thermal time needed for budburst, or degrees-day sum (DDS), *i. e.*, the accumulated temperature above a certain base temperature during a certain period of time (Cannell and Smith, 1983). We considered DDS from the 1st of January, assuming bud dormancy break (Sampaio et al., 2016), until budburst date, for each year. Base temperature was set to 6.2 ºC, in agreement with the threshold estimated for cork oak in a previous study in the same region (Pinto et al., 2011). To better characterize interannual variations in climatic conditions, our field meteorological data were compared to a reference period

(1971-2000, (IPMA, 2018)). We also retrieved the Standard Precipitation Evapotranspiration Index (SPEI) from the Global SPEI database (http://sac.csic.es/spei/database.html), with a 0.5º spatial resolution for the study site, to complement climatic conditions, as SPEI is currently the most widespread index for drought analyses in the Mediterranean (Vicente Serrano et al., 2010).

5 Results are presented as hydrological years, as they better represent the seasonality of water availability for tree functioning and growth. The hydrological year of 2004 is comprised between October of 2003 and September 2004 and the hydrological year of 2005 between October 2004 to September 2005.

2.3 Tree phenology and growth measurements

10 Phenological observations were performed in one randomly marked apical branch, sun-exposed (south-facing), from a total of 15 trees, at least once a week. We registered the days of bud activation (when bud was visible) and budburst (when shoot emerged). We also registered shoot elongation (when first leaves unfolded and could be count) and trunk growth onset and cessation, and leaf senescence. Then, we determined bud development duration (as the number of days since bud activation to budburst), shoot elongation and trunk growth duration (as the number of days since the onset to the cessation of shoot 15 elongation and trunk growth). The spring growing season length was defined as the number of days since bud activation until trunk growth cessation.

Shoot elongation was measured since budburst with a ruler and leaves counted. Trunk diameter at breast height (dbh) was measured from October 2003 with tree dendrometers (I-802-D1, UMS GmbH, Munich, Germany), at the same time of the day and at least once a month during spring, and basal area increment (BAI) determined. Since trunk growth in cork oak can be an 20 almost continuous process, depending on climatic conditions (Costa et al., 2002), the onset and cessation of the spring growth period were defined when dbh increments were lower than 0.05 ‰ day^{-1}.(relative to the total tree dbh). BAI was expressed as the percentage of increment relative to the basal area at the onset of spring growth, of each tree in each year. Autumn BAI was used to confirm the end of the growing season of the dry year because the measurement performed at the end of July was inadvertently lost (Fig. S2a). Spring and autumn BAI were regressed against the day of year (DOY).

25 Leaf area index (LAI) was measured at the end of the summer, as described in Besson et al. (2014). Specific leaf area (SLA), calculated as the ratio of leaf area to dry weight, was determined from 6 discs (with 0.7 cm diameter), collected from three leaves, at least, in each tree, at the onset and at the end of the growing season.

For litterfall determination, six sets of three litter traps (0.15 m^2 each) were randomly placed in areas including at least two of the studied trees (n = 6). Litterfall was collected at least once per month, and more frequently during spring, from 13 January 30 2004 until the end of the study period. Litterfall was separated in leaves and branches, oven dried at 80 ºC for 48 h and the dry weight of litter leaves obtained. As litterfall was collected in short time intervals, litter leaves were actually senescent leaves.

Here, only this litterfall fraction was reported and named as senescent leaves (in g leaves dry weight per m^{-2} ground). The bulk period of leaf senescence was considered when fall rate was consistently higher than 0.5 % day^{-1}. Senescent leaves were then used for nitrogen (N) content determination at the onset and at the end of the bulk leaf senescence period, indicating, respectively, minimum and maximum N content in senescent leaves for each year. N determination is described below.

5   To evaluate the intensity of occurrence of the different phenophases, the rate of shoot elongation (cm day^{-1}), trunk growth (cm^2 day^{-1}) and leaf senescence ((g m^{-2}) day^{-1}) were calculated at the end of the growing period.

2.4 Physiological measurements

To monitor tree water status, leaf water potential was measured at predawn (Ψ_{pd}) in three south-exposed mature leaves in each

10   of the 15 trees. Measurements were performed periodically over the study period, with a Scholander-type pressure chamber (PMS Instrument Co., Corvallis, Oregon, USA). To monitor carbon assimilates potentially allocated to growth, daily courses of photosynthesis were measured at 10:00, 13:00 and 16:00 in south-exposed leaves of the selected 15 trees, in same days than Ψ_{pd}, and maximal rate of photosynthesis (A_{max}) obtained. Measurements were performed with two cross-calibrated portable photosynthesis systems (Li-6400, Licor Inc., Lincoln, Nebraska, USA).

2.5 Nitrogen resorption efficiency

Green leaves were sampled periodically, 10 from each of the 15 trees and frozen in liquid nitrogen before being freeze-dried. Green and senescent leaves were ground in a laboratory mill for later analysis of N content. N content was determined in green ($[N_{gr}]$) and senescent ($[N_{se}]$) leaves by near-infrared reflectance spectral analysis (NIR). All samples were scanned with a

20   near-infrared reflectance spectrophotometer (NIRSystems 5000, FOSS, Denmark). One-fourth of the scanned samples (~80 samples) were representatively selected to perform chemical analyses of N (elemental CHN analyser, Carlo Erba EA1108, Isomass Scientific Inc., Calgary, Canada). This calibration set was chosen using the SELECT procedure of the ISI software by performing a principal component analysis on spectral information excluding samples with redundant spectral information. Calibrations equations were developed using the modified partial least-squares regression (PLS) estimate the optimal number

25   of terms in the calibration according to Joffre et al. (1992). Calibration equations that gave the lowest standard error of cross-validation (SECV) were selected. R^2 values were all above 0.89. Since six samples of $[N_{se}]$ were obtained, $[N_{gr}]$ data from the 15 trees were polled according to the distribution of litter traps (n=6). Nitrogen resorption efficiency (NRE) was determined according to Finzi et al. (2001), Eq. (1), at the onset and at the end of the bulk litter fall period:

NRE (%) = ($[N_{gr}]$ – $[N_{se}]$)/$[N_{gr}]$ x 100,   (1)

30   where $[N_{gr}]$ was N content in green leaves and $[N_{se}]$ was N content of senescent leaves.

2.5 Statistical analysis

We used paired t-test or the non-parametric Mann-Whitney test, when test assumptions were not verified, to compare the timing and duration of the different phenophases and growth variables between years. To evaluate the effects of drought on [N_{gr}], [N_{se}], and NRE, a two-way repeated measures ANOVA was performed, as the same trees and litter traps were repeatedly sampled over the study period, with years (mild and dry year) and phenological stage (onset and cessation of leaf senescence, thus maximum and minimum [N_{se}]) as factors. The post-hoc Student-Newman-Keuls test was performed when significant factor effects were found. To evaluate the physiological status over the growing season, an F-test for slopes and intercepts comparison between years was performed. The Spearman correlation coefficient was used to evaluate the relationships between variables and, when adequate, linear regressions were obtained. All statistical analyses were carried out with IBM SPSS Statistics 24 and considered significant when p-value <0.05. Results are presented as mean ± SEM.

3 Results

3.1 Environmental conditions

Total precipitation and distribution patterns were distinct between the two hydrological years of the study (Fig. 1a, Table S1). In the first year of the study (2004), a wet autumn and winter were followed by a dry spring (-49% of the long-term average precipitation). In contrast, in the second year (2005), a typically wet autumn preceded an extremely dry winter (-73% of the long-term average precipitation) and a moderately dry spring (-21 % of the long-term average precipitation). Total precipitation was 607 mm in 2004 and 410 mm in 2005. Indeed, 2005 was the driest year in the last 140 years in the southwestern Mediterranean (García-Herrera et al., 2007; Caldeira et al., 2015). The SPEI computed on a 6-month period prior to the growing season (March) was, respectively for 2004 and 2005, -0.4 (mild drought) and -1.7 (severe drought) (Banimahd and Khalili, 2013; Mendes et al., 2016). For these reasons, the studied years will be named henceforth as mild and dry years, for 2004 and 2005, respectively. Regarding temperature (Fig. 1b), the mild year was slightly warmer than the dry year (mean annual temperature was 16.3 and 15.3 ℃, respectively; Table S1), mostly due to the occurrence of an unusually cold winter during the dry year. Compared to the long-term average, both years presented cooler autumns and winters and warmer springs and summers. From March to May, mean air temperatures were higher in the dry year, as compared to the mild year. In June, mean air temperatures were 25.4 and 22.8 ℃, respectively for the mild and dry year.

The degrees-day sum (DDS) until budburst were not significantly different between years (p>0.05, 461 ± 13 and 431 ± 19 ℃ for the mild and dry year, respectively, Fig. S1b).
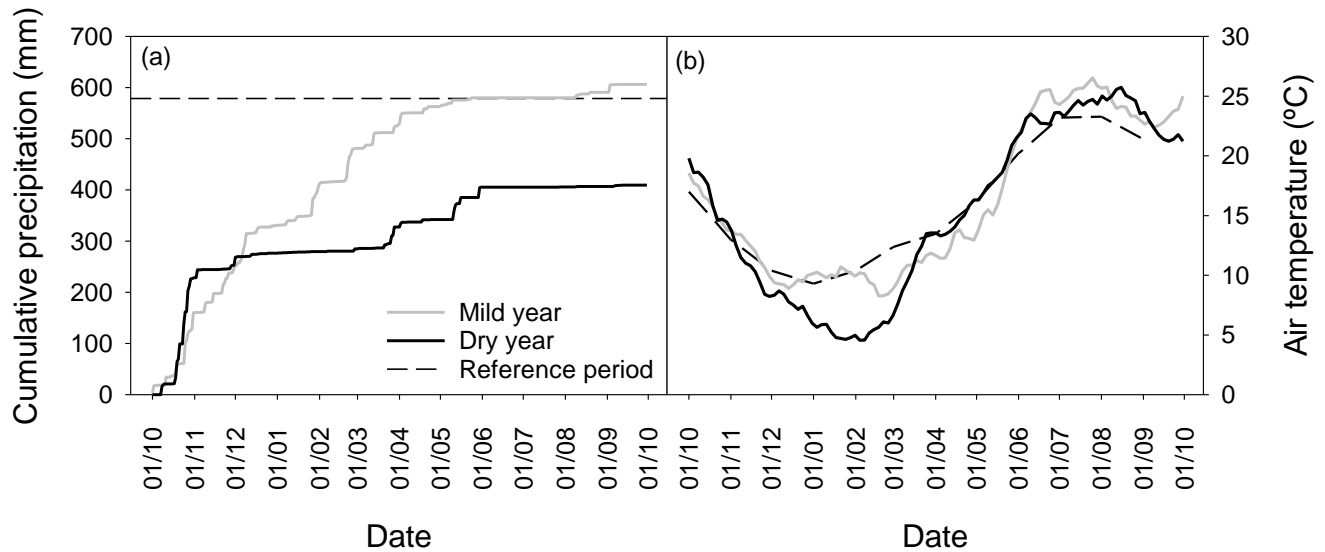
Figure 1. (a) Cumulative precipitation (mm) and **(b)** smoothed (7 days running average) daily mean temperature (ºC) for the study period. The long-term precipitation and monthly mean temperatures are included as a reference.

3.2 Phenological responses to drought

3.2.1 Phenophases timing and duration

The onset of the bud development and budburst were significantly delayed in the dry year (p<0.001) in comparison to the mild year, with no significant reduction of the bud development duration (p>0.05, 18 ± 2 and 16 ± 2 days for mild and dry years, respectively, Fig. 2). Shoot elongation, consequently, started later in the dry year (p<0.001) but ended earlier than in the mild year (p<0.001), leading to an important shortening of the shoot elongation period in ca. of 42 days (p<0.001, 66 ± 2 and 24 ± 2 days for mild and dry years, respectively; Fig. 2).

Significant differences were also observed in the timing and duration of trunk growth between years. Trunk growth started slightly later (p>0.05) and ended significantly earlier (p<0.001) in the dry year than in the mild year, thus showing a significantly shorter trunk growing period (p<0.001, 88 ± 3 and 57 ± 2 days for mild and dry years, respectively; Fig. 2). As a consequence, the spring growing season length was dramatically shortened (p<0.001, -48 %). It is noteworthy that all trees ceased trunk growth within the same week in both years (Table S2). The bulk of leaf senescence period was significantly delayed (p<0.05) and was longer in the dry year (p<0.05, 53.0 ± 1.3 versus 78.0 ± 0.0 days in the mild and dry years, respectively, corresponding to 50.9 ± 2.3 % and 76.1 ± 2.6 % of the total leaf senescence; Fig. 2 and Fig. 3).
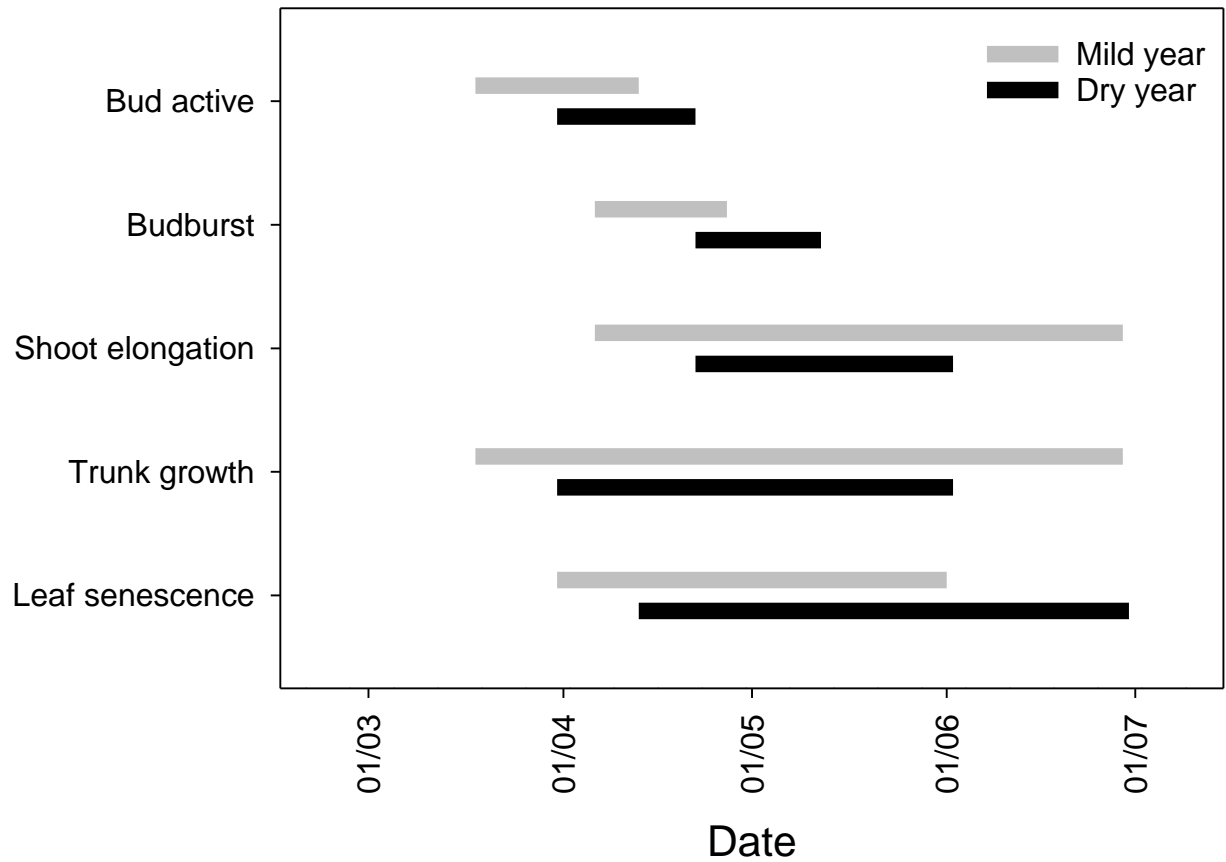
Figure 2. Timing of the onset and cessation of bud development (bud active), budburst, shoot elongation, trunk growth and leaf senescence in the two contrasting years. The bars represent the duration of each phenophases since the first until the last observation, in spring (n=15).
5 Significant differences between years in the timing and duration of the different phenophases are shown in Table S2.

Along with the delay in the studied phenophases of the cork oak trees in the dry year, changes in their dynamics were also observed (Fig. 3). Budburst, despite the significant starting delay in the dry year, had a similar development dynamics in both years (Fig. 3a). Shoot elongation, which started after budburst (Fig. 3b), had a faster development in a shorter period in the dry
10 year, with a fast buildup of new leaves (Fig. 3c). Spring trunk growth (BAI) exhibited a similar pattern in both years, ceasing growth earlier in the dry year (Fig. 3d). Leaf senescence was the most decoupled phenophase between years, with a later start in the dry year, but then progressing almost in parallel with the mild year (Fig. 3e). In the mild year, the bulk of leaf senescence finished before shoot elongation and trunk growth cessation. In contrast, in the dry year, the bulk senescence period was

extended beyond the growing season (Fig. 2 and Fig. 3). In the dry year, the shoot elongation rate was significantly higher than in the mild year ($p<0.001$, 0.39 ± 0.07 and 0.85 ± 0.16 cm day^{-1} for mild and dry years, respectively). In turn, no changes were observed in the rate of BAI ($p>0.05$, 0.049 ± 0.005 and 0.050 ± 0.006 % day^{-1} for mild and dry years, respectively) nor in leaf senescence rate ($p>0.05$, 1.62 ± 0.16 and 1.69 ± 0.12 g m^{-2} day^{-1} for mild and dry years, respectively).
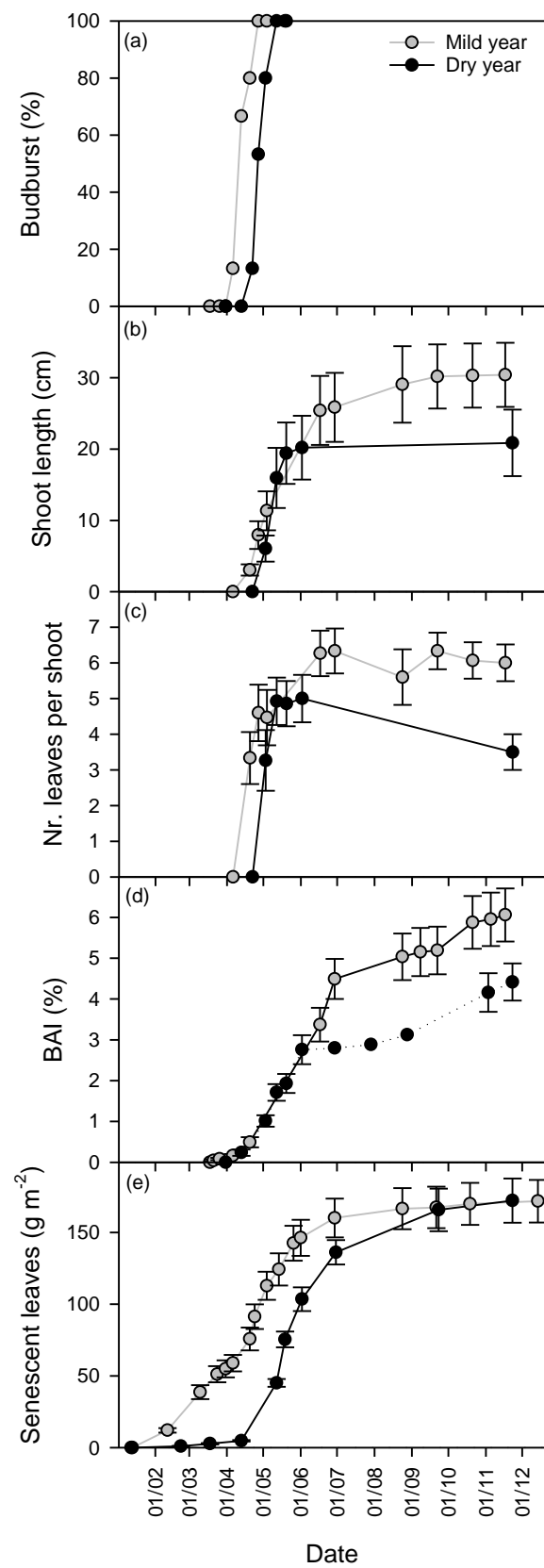
Figure 3. Growth dynamics in the mild and dry year, from January to December. **(a)** Budburst (%). **(b)** Shoot elongation (cm). **(c)** Number of leaves per shoot. **(d)** Basal area increment (BAI, %). **(e)** Senescent leaves (g m^{-2}). Values are mean ± SEM (n = 15).

3.2.2 Tree growth

Overall tree growth was extremely hindered by drought (Fig. 3 and Fig. 4). Shoot elongation was significantly reduced in the dry year with new shoots being shorter (-22 %, $p<0.05$; Fig. 4a) and producing proportionally less leaves (-21 %, $p<0.05$; Fig. 4b) which was also corroborated by the absence of a significant difference in the internode length between years ($p>0.05$; Fig. S3). BAI was also significantly lower in the dry year, showing the highest reduction among the evaluated growth variables (-36 %, $p<0.01$; Fig. 4c). Leaf senescence was higher in the dry year ($p<0.001$; Fig. 4d), yet LAI was not affected ($p>0.05$, Fig. 4e). SLA was strongly reduced in the dry year (-23 %, $p<0.001$; Fig. 4f).
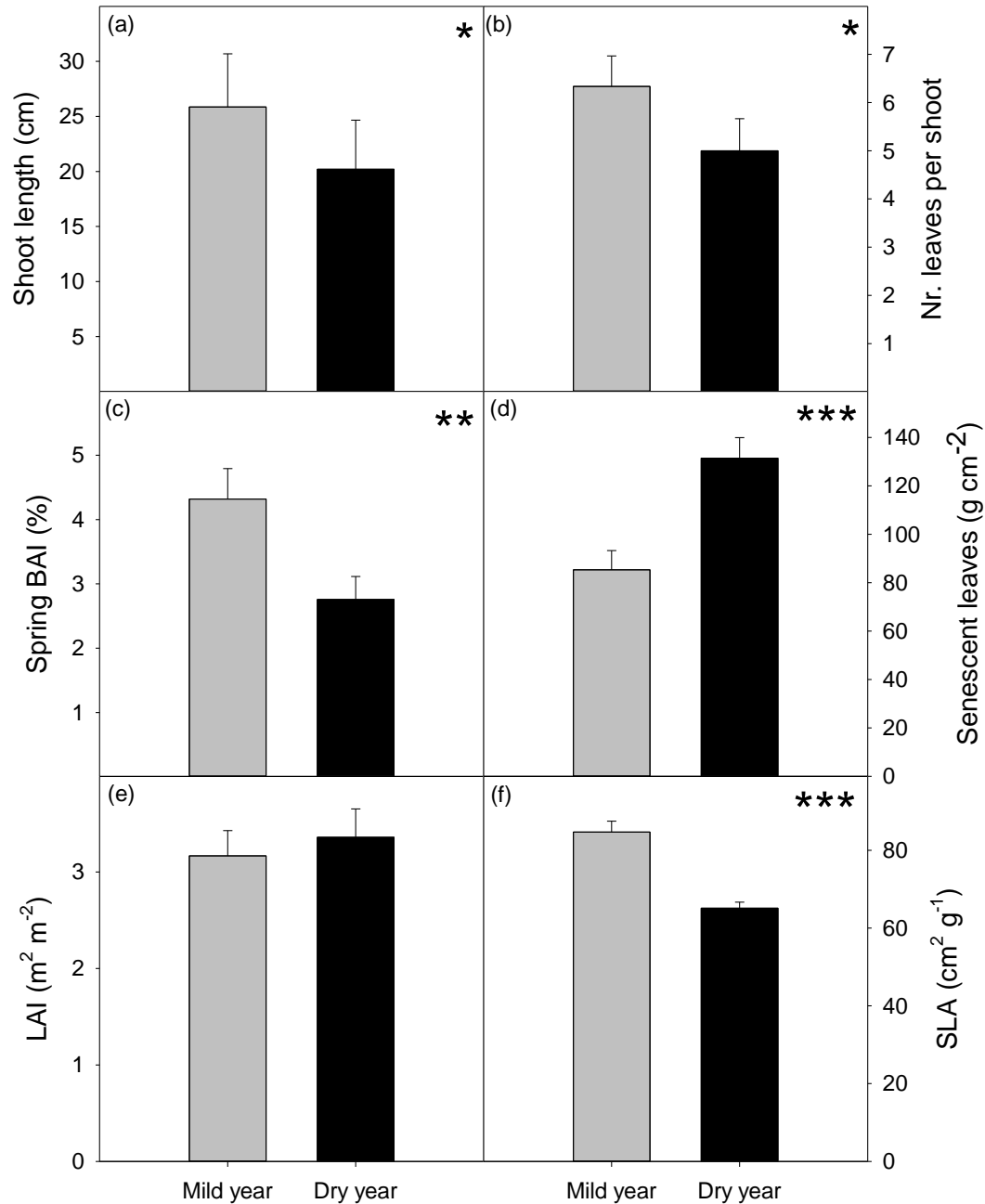
Figure 4. Growth variables evaluated at the end of the growing season, in the mild and dry year. **(a)** Shoot length (cm). **(b)** Number of leaves per shoot. **(c)** Basal area increment (BAI, %) expressed as percentage of basal area at the beginning of each year. **(d)** Senescent leaves (g m^{-2}). **(e)** Leaf area index (LAI, leaves m^2 per ground m^2). **(f)** Specific leaf area (SLA, g cm^{-2}). Values are mean ± SEM (n = 15). Significant
5   differences between years are indicated when * p<0.05, **p < 0.01, ***p < 0.001.

Shoot elongation period was positively correlated with trunk growth period (r = 0.83, p<0.001, Fig. S4a). Significant correlations were also found between BAI and shoot length, either when BAI was considered as a percentage of initial basal area (r = 0.43, p<0.05, Fig. S4b) or as absolute growth, in cm^2, (r = 0.57, p<0.001, Fig. S4c). Trunk growth duration was positively correlated with spring BAI (%, r = 57, p<0.01). Shoot length was positively correlated with SLA (r = 0.48, p<0.01, Fig. S4d).

3.3 Physiological status

Drought significantly decreased leaf water status (p<0.0001; Fig. 5a). Predawn leaf water potential (Ψ_{pd}) over the growing season was lower in the dry year than in the mild year, starting to decrease earlier. Then, Ψ_{pd} decreased in parallel, as indicated by the absence of significant differences between regression slopes (p>0.05). Leaf carbon assimilation was also affected by drought (p<0.01; Fig. 5b). Maximal photosynthetic rate (A_{max}) was higher at the beginning of the growing season in both years, decreasing similarly as drought stress progressed (similar regression slope, p>0.05). Growth cessation, as indicated by the red asterisks in Fig. 5a, occurred at lower Ψ_{pd} in the dry year than in the mild year. Indeed, interpolated Ψ_{pd} values were -0.84 and -1.33 MPa, for mild and dry year, respectively. Interestingly, the interpolated A_{max} at growth cessation was similar in the studied years, as indicated by the red asterisks in Fig. 5b.

BAI was weakly but positively related with A_{max} at the onset of the growing period (BAI (%) = -0.777 + 0.357 March A_{max}, r^2 = 0.18, p<0.05, Fig. S5).
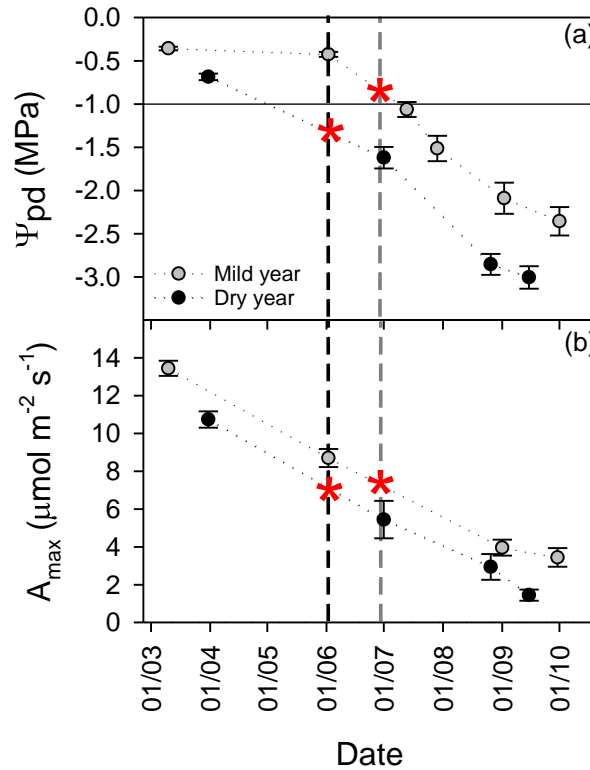
Figure 5. Tree physiological status over the growing season in the mild and in the dry year. **(a)** Predawn leaf water potential (Ψ_{pd}, MPa). **(b)** Maximal photosynthetic rate (A_{max}, μmol m^{-2} s^{-1}). Vertical dashed lines represent the mean day of growth cessation for mild (grey) and dry (black) years, red asterisks are indicative of the interpolated Ψ_{pd} and A_{max} at growth cessation. The horizontal black line is a reference
5 for the reported threshold of Ψ_{pd} (-1.0 MPa) for growth cessation in cork oak (Pereira et al., 1987). Values are mean ± SEM (n = 15).

3.4 Nitrogen resorption efficiency

Nitrogen concentration in green leaves was significantly different between years (p<0.01; Fig. 6a), mostly due to a significant reduction of [Ngr] at the onset of bulk leaf senescence period in the dry year. Mean [Ngr] was 16.1 ± 0.3 and 15.0±0.2 mg g^{-1}
10 in mild and dry year, respectively. The [Nse] decreased significantly in the dry year (p<0.01; Fig. 6b) and notably over the senescence period (p<0.001, see also Fig. S6 in which is noticeable the onset of leaf senescence with a steep decrease of [Nse] over time). The observed changes in [Nse] led to a significant increase of NRE, from the onset to the end of leaf senescence period (p<0.001) and, more importantly, in response to drought (+22 %, p<0.01; Fig. 6c). Furthermore, NRE was closely explained by [Nse] (NRE = 97.19 - 6.13 [Nse], r^2 = 0.97, p<0.0001; Fig. S7).
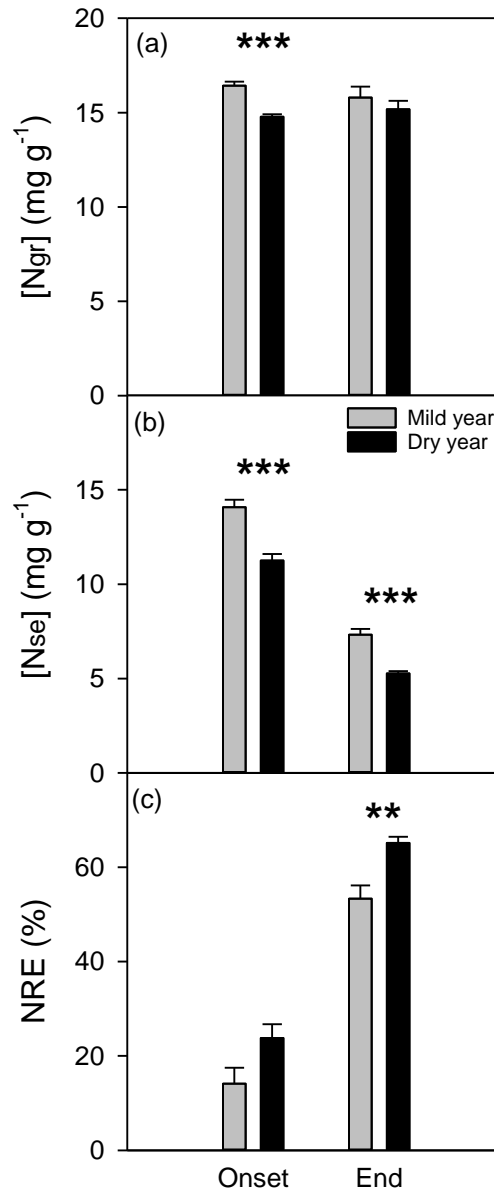
Figure 6. Nitrogen dynamics evaluated at the onset and end of bulk leaf senescence period in the mild and dry year. **(a)** Nitrogen concentration in green leaves ([Ngr], mg g^{-1}). **(b)** Nitrogen concentration in senescent leaves ([Nse], mg g^{-1}). **(c)** Nitrogen resorption efficiency (NRE, %). Values are mean $\pm$ SEM (n = 6). Significant differences between years are indicated when * $p<0.05$, **$p<0.01$, ***$p<0.001$.

4 Discussion

4.1 Drivers of the onset, cessation and length of the spring growing season

The timing of budburst of cork oak trees (Fig. 2) was determined by DDS as previously shown in other studies (e.g. Pinto et al., 2011; Sampaio et al., 2016). The DDS until budburst were not significantly different between years (Fig. S1b).

5   Nevertheless, budburst was delayed in the dry year, due to the colder temperatures observed during the winter and the accumulated thermal time was only reached after the increase in temperature in the early spring. The importance of temperature on budburst, either cumulative (DDS) and/or early spring temperature, has been highlighted in several studies (e.g. Menzel et al., 2006; Richardson et al., 2006; Vitasse et al., 2009; García-Mozo et al., 2010; Körner and Basler, 2010; Pinto et al., 2011). Pinto et al. (2011) reported that the only variable related to budburst date of adult cork oaks was air temperature, in particular

10   the average daily temperature 1.5 months prior to budburst. In a study across Europe, the timing of budburst was found to be highly correlated with the temperature of the preceding month (Menzel et al., 2006) and in a hardwood forest in the northern USA, DDS accounted for more than 90% of the variation in spring canopy development (Richardson et al., 2006). In a cork oak provenances study (Sampaio et al., 2016), apart from a strong effect of the provenance origin, DDS was the strongest environmental determinant of the timing of budburst between different years. Interestingly, the budburst dates found in our

15   study and in the Sampaio et al. (2016) study were similar for the same mild (DOY 107 and 105, respectively) and dry years (DOY 120 and 113, respectively).

The impact of concurrent drought on tree phenology is scarcely mentioned in the literature and it seems to indicate only a minor and not significant effect on budburst timing of Mediterranean trees (Ogaya and Penuelas, 2004; García-Mozo et al., 2010). Our results are in agreement with these studies, showing the major effect of temperature on the onset of phenological

20   development, as well as the importance of spring temperatures to fulfill the temperature requirements for budburst (Fig. S1).

Climate has been shown to account for more than 80% of the variability of budburst day and growing season length in Mediterranean plants, mostly due to temperature, while precipitation only accounted for less than 10% in that variability (Gordo and Sanz, 2010). In our study, water availability determined the growing season length. Cumulative precipitation was significantly lower in the dry year (Fig. 1a), actually the driest year in the last 140 years in the southwestern Mediterranean

25   (García-Herrera et al., 2007; Caldeira et al., 2015). The growing season length in the dry year, compared with the mild year, was more constrained by an earlier cessation of growth (-30 days), determined by water availability, than by a delayed budburst (+ 15 days), determined by temperature. The major influence of water availability is partly explained by the phenology of cork oak. In cork oak, leaf renewal (budburst and leaf senescence) occurs concurrently and in a short period during spring/early summer, which diverge from the more common pattern of spring budburst to autumn leaf senescence (Gordo and Sanz, 2010).

30   Late spring/early summer corresponds to the onset of the drought season that was anticipated in the severe drought year critically affecting the functioning of trees.

Trunk growth started concomitantly with bud activity (Fig. 2 and Fig. 3), when temperatures increased, as already shown for cork oak trees (Oliveira et al., 1994), and for other Mediterranean trees (Lempereur et al., 2015). Shoot elongation and trunk growth ceased earlier in the dry year and, interestingly, in a very synchronously way between trees in both years, as also reported by Oliveira et al. (1994). This observed synchrony suggests a trigger for growth cessation. A threshold of -1.0 MPa of leaf water potential, which was considered to be the onset of severe plant water stress, has been suggested to trigger growth cessation in cork oak (Pereira et al., 1987). A threshold of -1.1 MPa was recently suggested for growth cessation of *Q. ilex* (Lempereur et al., 2015). In our study, growth ceased at interpolated Ψ_{pd} values of -0.84 and -1.33 MPa, for mild and dry year, respectively, which suggests some acclimation to the precipitation conditions of the year. As Ψ_{pd} reflects soil water availability for trees, it integrates the cumulated precipitation and appears to be a suitable trigger of growth cessation in water-limited ecosystems, as already suggested by Pinto et al. (2011). In our study, growth ceased at significantly lower Ψ_{pd} in the dry year compared with the mild year (Fig 5a), but at a similar carbon assimilation rate (Fig. 5b). This points to a possible carbon limitation for growth driven by stomatal closure, which occurred earlier in the dry year induced by drought (Besson et al., 2014). Nevertheless, the divergent values of Ψ_{pd} call attention to a different trigger, other than Ψ_{pd}, of growth cessation in the mild year. The high vapour pressure deficit (VPD) observed at the end of the growing season in the mild year (Fig.S8), by triggering stomatal closure, was probably the trigger of growth cessation. It was recently demonstrated that elevated VPD limits tree growth (Sanginés de Cárcer et al., 2018). The authors proposed a VPD threshold of 15 hPa and concluded that the sensitivity to VPD is species-specific, due to different tolerance thresholds. The time frame of this study is narrow and longer studies are needed to fully understand the interactive effects of precipitation and temperature on triggering growth cessation.

The leaf senescence period was reported to be smaller than the shoot growth period (Pereira et al., 1987), as observed in the mild year in our study (Fig. 2), besides some leaf senescence registered before the bulk period (Fig. 3), probably due to strong rain events. In the dry year, the bulk of leaf senescence was the longer phenophase (Fig. 2), ceasing later than shoot or trunk growth. Losing more leaves for a longer period may be a response to drought, as by shedding older leaves, trees prevent water loss (Pereira et al., 2009) and/or as a nitrogen conservation strategy. The lower [Nse], observed at the end of the bulk period in the dry year, suggests that trees were able to recycle N likely by shedding leaves for a longer period. By increasing NRE, hence increasing N concentration in current year leaves, trees may have mitigated the negative effects of drought on N acquisition (Fig. S4), as discussed below.

4.2 Impact of drought on spring tree growth

Mediterranean evergreen trees take advantage of every favourable environmental condition for carbon assimilation and growth (Larcher, 2000). Our data clearly show this, as trees had higher carbon assimilation rates (Fig. 5) while water was still not limiting, as indicated by predawn leaf water potential. Drought, by first decreasing cell turgor, affects primarily growth (Taiz and Zeiger, 1998). Stomatal closure occurs next, limiting carbon assimilation while preventing water loss (Chaves, 1991;

Chaves et al., 2016). A strong stomatal control is an important feature of cork oak to withstand long periods of water shortage which is closely linked to carbon assimilation (Otieno et al., 2007; Grant et al., 2010; Vaz et al., 2010; Pinto et al., 2012; Besson et al., 2014), corresponding to a drought avoidance, or isohydric, behavior. A_{max} at the onset of growth that responds to short-term weather conditions was significantly related to spring BAI. However, A_{max} only explained 18% of the variability observed in BAI. The weakness of the relationship may reflect the allocation of carbon not only for trunk growth but also to roots and canopy. In fact, a deep rooting system is of major importance for cork oak during summer (David et al., 2013) and constitutes a considerable sink of carbon reserves (Mendes et al., 2016).

Growth was intrinsically linked to phenology dynamics, in which the duration of the phenophases exerted a major control (Fig. 3). This was particularly true regarding trunk growth, given the same growth rate over a shorter period in the dry year (Fig. 3d). In a drought manipulation study with *Q. ilex*, growth duration was the best predictor of BAI (Lempereur et al., 2015). In our study, spring BAI was also positively correlated with trunk growth duration, while reduced roughly in the same proportion than precipitation, when comparing the dry year with the mild year (-36% and -30 %, for BAI and precipitation, respectively). In turn, trunk growth duration and shoot elongation duration were positively correlated, as well as BAI with shoot length. Nevertheless, shoot elongation was less inhibited by drought (-22 %) than BAI. Despite the severe drought observed, the shoot length in our study was considerably higher than that reported in another study with juvenile cork oak trees (Oliveira et al., 1994), in which values ranged between 1.8 and 6.2 cm yr^{-1}. This has probably to do with the fact that the sampled branches in that study were not clearly defined as apical, as we measured, thus showing lower growth. The lower reduction in shoot elongation, in comparison to trunk growth, combined with an absence of significant changes in LAI suggests that leaf carbon assimilation is privileged in cork oak, by maintaining leaf area, as suggested elsewhere (Costa-e-Silva et al., 2015).

Although reported LAI or litterfall responses to drought are conflicting (Reichstein et al., 2002; Ogaya and Penuelas, 2004; Limousin et al., 2009; Martin-StPaul et al., 2013; Costa-e-Silva et al., 2015), we would expect a reduction in LAI as a consequence of lower shoot elongation and lower number of leaves, without a corresponding decrease in total litterfall. Despite the higher leaf senescence observed during the bulk period, in the dry year, total litterfall (from January to September) was similar between years (Fig 3e). This could be explained by trees retaining a portion of leaves in the canopy longer than a year or simply because litterfall reflects the growth of the previous year, that was not affected by drought. Similarly, in a study realized in the Mediterranean region, no changes were observed in *Q. ilex* litterfall between the same years (Limousin et al., 2009).

The observed reduction of SLA is another characteristic response of Mediterranean trees to drought (Chaves and Oliveira, 2004). By limiting the transpiring area, trees will be able to keep photosynthetic activity for a longer period, as suggested by Ramírez-Valiente et al. (2010). More schlerophyllous leaves were also associated with low soil nutrient availability (Salleo and Nardini, 2000), due to their higher ratio of carbon to nitrogen.

Short-term interactions between precipitation and temperature are complex (Gerst et al., 2017; Lempereur et al., 2017). The higher rate of shoot elongation observed in the dry year and the longer duration of shoot elongation in the mild year suggest, respectively, a positive effect temperature early in the growing season but a negative or null effect during the elongation period in the mild year, supported by the cessation of shoot elongation at a higher Ψ_{pd}. A longer study period would be required to get reliable conclusions.

Cork oak trees "used water sparingly" (Pereira et al., 2009) and spring precipitation was of utmost importance for growth in the dry year, which is in agreement with other studies (Besson et al., 2014; Costa et al., 2016; Oliveira et al., 2016). In contrast, for the mild year, the cumulated precipitation allowed for a longer growing period and consequently for higher tree growth, irrespective of a warmer and drier spring. (Fig. 1 and Fig. S1)

4.3 Nitrogen contents and resorption efficiency

A decrease in soil N availability is an expected consequence of drought (Sardans et al., 2008), which might be aggravated by the forecasted changes in precipitation regimes (Rodríguez et al., 2019), leading to decreased [N_{gr}] (Fig. 6a) (Delarco et al., 1991). The variation of [N_{gr}] in the mild year, was within the same range of values than those observed in other studies (Delarco et al., 1991; Escudero et al., 1992; Oliveira et al., 1996; Kattge et al., 2011). Nonetheless, Andivia et al. (2009) reported a higher variation in [N_{gr}] over the growing season.

Nitrogen concentration in senescent leaves [N_{se}], known as resorption proficiency (Killingbeck, 1996) decreased steeply from the onset to the end of the bulk period of leaf senescence (Fig 6b, Fig. S4). Silla and Escudero (2003), studying the internal N cycling of *Q. ilex*, observed that after budburst, plants firstly relied on soil uptake and later on N resorption to supply growth requirements, which might explain our results. A simpler explanation lies on the fact that the first leaves shed by the tree were not senescent yet, thus N was incompletely resorbed from them.

More importantly, [N_{se}] decreased significantly in the dry year, reaching minimum values around 5.27 ± 0.12 mg g^{-1}. Minimum reported resorption proficiency for oaks was 4.5 mg g^{-1} and trees with [N_{se}] lower than 7 mg g^{-1} were considered highly proficient (Killingbeck, 1996). According to the exposed, the resorption observed in cork oak was highly proficient and the lowest values of [N_{se}] observed at the end of the senescence period, in the dry year, suggest the maximum resorption for cork oak trees.

An increase in nitrogen resorption from senescent leaves is a recognized feature of Mediterranean plants (Andivia et al., 2009; Sardans and Peñuelas, 2013) and is a key feature of nutrient conservation strategies (Vergutz et al., 2012; Brant and Chen, 2015; Xu et al., 2017). Cork oak has been reported to

resorb more N than the average of Mediterranean woody species (Delarco et al., 1991). The NRE in the dry year (63 %) was higher than the values reported for evergreen trees (47 % or 56 %) (Aerts, 1996; Vergutz et al., 2012) or for cork oak (48 % or 52 %) (Delarco et al., 1991; Escudero et al., 1992), the latter being similar to NRE in the mild year (54 %) in our study.

Cork oak significantly increased NRE (+22 %) with drought (Fig. 6c) and, by doing this, mitigated the effects of drought on N uptake from soils, as [N_{gr}] at the end of the growing period was similar between years (Fig. 6a). We found no general correlation between [N_{gr}] and [N_{se}] nor between NRE and [N_{gr}] during leaf senescence. NRE was only highly significantly and negatively correlated with [N_{se}]. These findings underline the lack of nutritional control on NRE (Aerts and Chapin, 1999), as previously reported (Delarco et al., 1991; Aerts, 1996; Kazakou et al., 2007), despite recent studies have identified leaf nutrient status as the major control of NRE (Kobe et al., 2005; Vergutz et al., 2012; Zhao et al., 2017). Rather, the major control on NRE was exerted by nutrient proficiency, as observed elsewhere (Kazakou et al., 2007). Although nutrient resorption can vary significantly from year to year (Killingbeck, 2004), it has been considered a possible adaptive trait (Vergutz et al., 2012). Our data confirm this last statement.

5 Conclusions

This study reports changes in tree phenology in response to a naturally occurring extreme drought. As far as we are aware, this study was the first to integrate the timing and duration of several phenophases with growth, while using green and leaf senescent to assess leaf nitrogen dynamics during the growing period. Our results confirmed temperature as a major driver of budburst, yet drought severely constrained tree growth mainly by strongly reducing the growing season length. The different dynamics observed in shoot elongation, in contrast with the other phenophases, are indicative that cork oak privileges leaf area development, while all other phases develop at the same rate. Notably, the nitrogen resorption efficiency from senescent to green leaves increased as a response to drought. A higher nitrogen resorption efficiency in response to drought may clearly improve tree fitness in the short-term but is likely to exert a negative feedback on the nitrogen cycle which might affect ecosystem functioning in the long-term under the forecasted increasing occurrence of droughts.

We are aware that the time frame of this study is narrow and longer studies are needed to confirm our results and to understand the interactive effects of warming and heat waves with drought on the phenology and growth of Mediterranean trees. Nevertheless, our study shows the dynamics of the different vegetative phenophases, which is not possible to assess by ring-width analysis, while contributing for a deeper understanding of Mediterranean trees responses to drought. Finally, the sensitivity of phenology to climate change has implications for land management, including adaptation measures (Richardson et al., 2013; Han et al., 2018) to mitigate the deleterious effects of climate change.

Author contributions. RLV performed fieldwork, data analysis, and wrote the manuscript. CKB planned the experiment, performed fieldwork and contributed to manuscript writing. MCC assisted in the interpretation of the data and contributed to manuscript writing. All authors critically discussed and reviewed the manuscript.

Competing interests. The authors declare that they have no conflict of interest.

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