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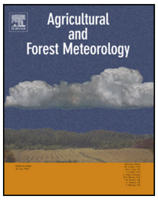

Effects of an extremely dry winter on net ecosystem carbon exchange and tree phenology at a cork oak woodland

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ABSTRACT

In seasonally dry climates, such as the Mediterranean, lack of rainfall in the usually wet winter may originate severe droughts which are a main cause of inter-annual variation in carbon sequestration. Leaf phenology variability may alter the seasonal pattern of photosynthetic uptake, which in turn is determined by leaf gas exchange limitations. The current study is based on the monitoring of an extremely dry winter in an evergreen cork oak woodland under the Mediterranean climate of central Portugal. Results are focused on net ecosystem CO_2 exchange (NEE), phenology and tree growth measurements during two contrasting years: 2011, a wet year with a typical summer drought pattern and 2012, with an extremely unusual dry winter (only 10 mm of total rainfall) that exacerbated the following summer drought effects. Main aims of this study were to assess the effects of an extreme dry winter in (1) annual and seasonal net ecosystem CO_2 exchange, and in (2) cork oak phenology. The dry year 2012 was marked by a 45% lower carbon sequestration (-214 vs. $-388\,\mathrm{g\,C\,m^{-2}\,year^{-1}}$) and a 63% lower annual tree diameter growth but only a 9% lower leaf area index compared to the wet year 2011. A significant reduction of 15% in yearly carbon sequestration was associated with leaf phenological events of canopy renewal in the early spring. In contrast to male flower production, fruit setting was severely depressed by water stress with a 54% decrease during the dry year. Our results suggest that leaf growth and leaf area maintenance are resilient ecophysiological processes under winter drought and are a priority carbon sink for photoassimilates in contrast to tree diameter growth. Thus, carbon sequestration reductions under low water availabilities in cork oak woodland should be ascribed to stomatal regulation or photosynthetic limitations and to a lesser extent to leaf area reductions.

1. Introduction

Cork oak (*Quercus suber* L.) open woodlands cover an area of about 2–2.5 million ha in the western Mediterranean (Aronson et al., 2009). These are man-made ecosystems exploited with low-impact agro-forestry, with high biodiversity and conservation value (Bugalho et al., 2011). In Portugal these woodlands cover 0.74 million ha and represent 23% of all forested area. Cork oak has a significant economic value. It provides 0.7% of Portugal gross domestic product and supplies 54% of the worldwide cork production (Evangelista, 2010). Cork is a natural product consisting of continuous annual layers of suberized tissue produced by phellogen, a secondary meristem wrapping the inner bark. Cork wine bottle stoppers is the main product and to obtain commercial grade cork stripping is done traditionally every 9 years. Cork removal can only be safely done when the phellogen cells are actively dividing, in late-spring and early-summer, to prevent injuries to the tree (Costa et al., 2003).

Cork oak is well adapted to the adverse semiarid Mediterranean climate and its ecophysiology has been well studied in the last decades (e.g., Otieno et al., 2007; Pereira et al., 2009; Vaz

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Abbreviations: (C/N), carbon-to-nitrogen ratio; (DBH), diameter at breast height; (DOY), day of year; (ET), ecosystem evapotranspiration; (GPP), gross primary productivity; (LAI), leaf area index; (LAI_{max}), maximum leaf area index; (LAI_{min}), minimum leaf area index; (LUE), light use efficiency; (NEE), net ecosystem exchange; (PAR), photosynthetically active radiation; (PLC), percentage loss in hydraulic conductivity; (Ψ_{md}), midday leaf water potential; (Ψ_{pd}), predawn leaf water potential; (R_{eco}), ecosystem respiration; (se), standard error of the mean; (SLA), specific leaf area; (SWC), soil water content; (u^*), friction velocity; (VPD_{max}), maximum vapor pressure deficit.

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et al., 2010). Adverse conditions result mainly from scarce water resources during a long dry summer season, usually coupled with high temperatures and high radiation. In a seasonal climate such as the Mediterranean, a drought is said to occur when precipitation shortages, often coupled to high evaporative demand, reduce moisture availability for an extended period during the normally wet season (Pereira et al., 2006). Successful adaptations to cope with water stress range from an efficient root and water transport system (David et al., 2007; Kurz-Besson et al., 2006) to a tight stomatal regulation at the leaf level, restricting water loss while limiting the rate of CO_2 assimilation (Otieno et al., 2007; Pinto et al., 2012; Vaz et al., 2010). Nevertheless, and despite being considered drought resilient, a succession of dry years or severe stress events may lead the trees to surpass their tolerance thresholds and result in episodes of tree mortality (Pereira et al., 2009). In addition, the Mediterranean region is among the most sensitive regions to climate change, with all recent climate projections forecasting more frequent extreme events (Reichstein et al., 2013), such as heat waves and severe droughts (e.g., Giorgi and Lionello, 2008).

In Mediterranean regions phenological patterns are strongly influenced by a marked climatic seasonality and species evolved to synchronize maximum vegetative activity to the most favorable periods of the year (Misson et al., 2011; Pinto et al., 2011; Richardson et al., 2010). Timing of budburst and growing season length can directly impact net ecosystem carbon uptake (Baldocchi, 2008; Richardson et al., 2010) and leaf age effects on canopy carbon uptake (Niinemets et al., 2005). However, an earlier spring onset can be associated with either enhanced or decreased productivity later in the growing season (e.g., depending on interactions with water availability), and thus, early-season gains can be offset by sustained late-season reductions in physiological activity (Richardson et al., 2010). Therefore, the evaluation of interactions between climate change effects, phenological events and net ecosystem exchange requires specific ecosystem scale analysis.

In the case of Mediterranean forests, droughts are a main source of interanual variation in carbon sequestration as they strongly reduce gross primary productivity as well as net ecosystem exchange (NEE) (Pereira et al., 2007). Under drought conditions, leaf phenology may play an important role in controlling the temporal dynamics of tree crown productivity and NEE, not only in deciduous forests but also in evergreen species with a short leaf life-span. In the latter (as it is the case of cork oak), senescence and development of a new canopy in spring may control, to a large extent, the patterns of photosynthetic uptake in the following growing season. We hypothesized that a winter drought is liable to impose limitations on leaf phenophase progression (e.g., budburst and leaf expansion) which might exacerbate summer drought effects.

Table 1
General soil, climate, and vegetation characteristics in 2011 and 2012. Values are means ± se.

Characteristic	2011	2012	Units
Soil			
Organic matter	3.2 ± 0.2		(%)
C/N	19.3 ± 1.4		
Carbon stock (up to 60 cm)	62.2		($t\,C\,ha^{-1}$)
Climate			
Mean temperature	16.1	15.2	(°C)
PAR	13033	13606	($mol\,m^{-2}$)
Reference evapotranspiration	1461	1469	(mm)
Total precipitation	800	469	(mm)
Total evapotranspiration (ET)[a]	454	340	(mm)
winter	75 (293)	103 (10)	(mm)
spring	161 (217)	106 (113)	(mm)
summer	148 (26)	84 (33)	(mm)
autumn	69 (264)	47 (313)	(mm)
Vegetation			
Tree density	177		($trees\,ha^{-1}$)
Tree crown cover	50		(%)
Tree height	7.9 ± 0.26		(m)
Tree DBH[b]	24.7 ± 1.2		(cm)
Maximum LAI[c]	1.15	1.05	($m^2\,m^{-2}$)
Total tree C stock	33.7		($t\,C\,ha^{-1}$)
Shrubs above-ground C stock	0.34 ± 0.10	0.51 ± 0.18	($t\,C\,ha^{-1}$)
Grasses above-ground C stock	0.32 ± 0.05	0.10 ± 0.02	($t\,C\,ha^{-1}$)

[a] Numbers in brackets are seasonal precipitation.
[b] DBH, diameter at breast height.
[c] LAI, leaf area index.

The current study is based on the monitoring of an extremely dry winter (only 10 mm of total rainfall) in a certified evergreen cork oak woodland under the Mediterranean climate of central Portugal. Results are centered on ecosystem CO_2 fluxes (micrometeorological method, eddy-covariance technique), phenology and tree growth measurements during two contrasting years: 2011, a wet year with a typical summer drought pattern and 2012, with an extreme dry winter that exacerbated the following summer drought effects. Main aims of this study were to assess the effects of an extreme dry winter in (1) annual and seasonal net ecosystem CO_2 exchange (NEE), and in (2) cork oak phenological events (e.g., budburst, tree growth, and fruit setting).

2. Material and methods

2.1. Site description

In 2009 an experimental site was established at Herdade da Machoqueira located in Central Portugal (39°08′18.29″N, 8°19′57.68″W). Vegetation consists of a ca. 50-yr-old cork oak (*Q. suber*) open woodland with an understory of semi-deciduous shrub species (e.g., *Cistus* sp. and *Ulex* sp.) and native grassland. This understory vegetation is highly seasonal with growth beginning after the autumn rains and lasting until June when grassland dies-out and shrubs enter a quiescent period. Maximum leaf area index measured in 2011 in the understory vegetation was 0.38 and 0.45 for shrubs and grassland, respectively (Correia et al., 2014). The climate is Mediterranean, with wet and mild winters and dry and hot summers. Average annual precipitation is 680 ± 210 mm and mean annual temperature is 15.9 °C (period 1955–2007, Inst. de Meteorologia, Lisbon). The soil is a cambisol (FAO), with 81% sand, 5% clay, and 14% silt, with roots mainly in the upper horizons (ca. 0–40-cm depth) and some sinker roots taking water from deeper soil horizons and subsoil. From observations from an underground tank the water table is estimated to vary between 3 and 5 m depth. Other general site characteristics are described in Table 1 for the studied period.

2.2. Environmental parameters

Meteorological data on rainfall (ARG100; Environmental Measurements Ltd., Gateshead, UK), photosynthetically active radiation (BF2; Delta-T Devices Ltd., Cambridge, UK), air humidity and temperature (CS215; Campbell Scientific, Inc., Logan, UT, US) were collected continuously in 30-min time intervals (CR10X; Campbell Scientific, Inc., Logan, UT, US). Soil volumetric water content was measured up to 40-cm depth (2, 10, 20, 30, and 40 cm) with dielectric soil moisture sensors in four different places (EC5; Decagon Devices, Inc., Pullman, WA, US). These measurements were automatically collected in a datalogger (Em50; Decagon Devices, Inc., Pullman, WA, US) as 30-min averages. Reference evapotranspiration was determined according to the FAO Penman–Monteith method (Allen et al., 1998).