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Cork oak physiological responses to manipulated water availability in a Mediterranean woodland

Cathy Kurz Besson[a,*], Raquel Lobo-do-Vale[b], Maria Lucília Rodrigues[b], Pedro Almeida[b], Alastair Herd[b], Olga Mary Grant[c], Teresa Soares David[d], Markus Schmidt[e], Denis Otieno[e], Trevor F. Keenan[f], Célia Gouveia[a], Catherine Mériaux[a], Maria Manuela Chaves[b,g], João S. Pereira[b]

[a] Centro de Geofísica da Universidade de Lisboa, Instituto Dom Luiz, Lisboa, Portugal
[b] Instituto Superior de Agronomia, Universidade técnica de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal
[c] University College Dublin, Belfield, Dublin 4, Ireland
[d] Instituto Nacional de Recursos Biológicos, Quinta do Marquês, Av. da República, 2784-505 Oeiras, Portugal
[e] Universität Bayreuth, 95440 Bayreuth, Germany
[f] Harvard University, 22 Divinity Avenue, Cambridge, MA 02138, USA
[g] Instituto de Technologia Química e Biológica, Av. da República, 2780-157 Oeiras, Portugal

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ABSTRACT

This study details the physiological responses of cork oak (*Quercus suber* L.) to manipulated water inputs. Treatments named as dry, ambient and wet, which received 80, 100 and 120% of the annual precipitation, respectively, were applied to a Mediterranean woodland in southern Portugal. Tree ecophysiology and growth were monitored from 2003 to 2005.

The impacts of the water manipulation were primarily observed in tree transpiration, especially during summer drought. Rainfall exclusion reduced the annual stand canopy transpiration by 10% over the 2-year study period, while irrigation increased it by 11%. The accumulated tree transpiration matched precipitation in spring 2004 and 2005 at the stand level, suggesting that cork oak trees rely on precipitation water sources during the peak of the growing season. However, during the summer droughts, groundwater was the main water source for trees.

Despite the significant differences in soil water content and tree transpiration, no treatment effects could be detected in leaf water potential and leaf gas exchange, except for a single event after spring irrigations in the very dry year 2005. These irrigations were intentionally delayed to reduce dry spell duration during the peak of tree growing season. They resulted in an acute positive physiological response of trees from the wet treatment one week after the last irrigation event leading to a 32% raise of stem diameter increment the following months. Our results suggest that in a semi-arid environment precipitation changes in spring (amount and timing) have a stronger impact on cork oak physiology and growth than an overall change in the total annual precipitation.

The extreme drought of 2005 had a negative impact on tree growth. The annual increment of tree trunk diameter in the ambient and dry treatments was reduced, while it increased for trees from the wet treatment. Water shortage also significantly reduced leaf area. The latter dropped by 10.4% in response to the extreme drought of 2005 in trees from the ambient treatment. The reduction was less pronounced in trees of the wet treatment (−7.6%), and more pronounced in trees of the dry treatment (−14.7%).

Cork oak showed high resiliency to inter-annual precipitation variability. The annual accumulated tree transpiration, the minimum midday leaf water potential and the absolute amount of groundwater used

Abbreviations: (A), carbon assimilation; (A_{max}), maximum carbon assimilation; (CV), crown volume; (DBH), diameter at breast height; (DBH_{inc}), trunk diameter increment; (E), sap flux, tree transpiration; (E/DBH), normalized tree transpiration; (ET), potential evapotranspiration; (g_s), stomatal conductance; (g_{smax}), maximum stomatal conductance; (G_t), whole tree specific hydraulic conductance; (LAD), leaf area density; (LAI), leaf area index; (PAR), photosynthetically active radiation; (PCA), projected crown area; (SLA), specific leaf area; (SWC), soil water content; (T), air temperature; (VPD), vapour pressure deficit; (Ψ), leaf water potential; (Ψ_{md}), midday leaf water potential; (Ψ_{pd}), predawn leaf water potential; ($\Delta\Psi$), sap flow driving force; (Ψ_{π}), osmotic potential; (Ψ_p), leaf turgor; (π_s), leaf solute content; (RSC), regression slope comparison; (SEM), standard error of the mean.

* Corresponding author at: Instituto Dom Luiz, Centro de Geofísica da Universidade de Lisboa, Faculdade de Ciências, Campo Grande, Ed. C8, piso 3, Sala 26, 1749-016 Lisboa, Portugal. Tel.: +351 21 750 08 84; fax: +351 217 500 807.

E-mail addresses: cbbesson@fc.ul.pt, cathybesson@gmail.com (C.K. Besson), raquelvale@isa.utl.pt (R. Lobo-do-Vale), mlrodrigues@isa.utl.pt (M.L. Rodrigues), pedroccta@yahoo.com (P. Almeida), a.herd@tft-forests.org (A. Herd), olgamgrant@yahoo.com (O.M. Grant), teresasdavid@gmail.com (T.S. David), mwtschmidt@gmx.com (M. Schmidt), dennis.otieno@uni-bayreuth.de (D. Otieno), tkeenan@oeb.harvard.edu (T.F. Keenan), cmgouveia@fc.ul.pt (C. Gouveia), cameriaux@fc.ul.pt (C. Mériaux), mchaves@isa.utl.pt (M.M. Chaves), jspereira@isa.utl.pt (J.S. Pereira).

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by trees appeared unaffected by the extreme drought of 2005. Our study shows that cork oak rapidly and completely recovered from the extreme dry year of 2005 or from rainfall exclusion. Our results support the eco-hydrological equilibrium theory by which plant acquire complementary protective mechanisms to buffer the large variability in water availability experienced in semi-arid ecosystems. In optimizing their structural biomass increase in response to increasing drought stress, cork oak trees succeeded in restricting water losses to maintain the minimum leaf water potential above the critical threshold of xylem embolism, though with narrower hydraulic safety margins in 2005.

Our findings highlight cork oak's sensitivity to the amount and timing of late spring precipitation. This could be critical as future climate scenarios predict a reduction of spring precipitation as well as enhanced severity of droughts in the Iberian Peninsula by the end of the 21st century. In inducing water stress before the onset of summer droughts, the predicted spring precipitation decline could drive the species closer to the threshold of catastrophic xylem embolism at the peak of the drought period.

1. Introduction

Mediterranean savanna-type evergreen oak woodlands are man-made ecosystems. They are characterized by a sparse native tree cover, which mostly consists of *Quercus* species (mainly evergreen cork oak, *Quercus suber* L., and/or holm oak, *Quercus ilex* ssp. *rotundifolia* Lam.) and understory vegetation ranging from shrub formations to grasslands. In Portugal, cork oak savanna-type ecosystems-montados-cover about 0.74 Mha and represent 23% of the national forested area (ICNF, 2013). The species has a significant economic value. It provides 0.7% of the gross domestic product, about 15,000 jobs, and supplies 54% of the worldwide cork production (Evangelista, 2010). Montados are also ecosystems with a high conservation value, supporting high levels of biodiversity (Bugalho et al., 2011), and are considered national heritage.

According to the most recent Portuguese forest inventories, montados show signs of an increasing vulnerability. In only 12 years, cork oak mortality rate and fire indices rose sharply (by 450% and 200%, respectively) and tree density declined by 30% on average (AFN, 2001, 2010). All recent climate projections for the Mediterranean basin agree in forecasting future longer summer droughts, with more frequent extreme events, such as heat waves or severe droughts (Barriopedro et al., 2011; Coumou and Rahmstorf, 2012; Giorgi and Lionello, 2008; IPCC, 2007; Miranda et al., 2006). Projections also predict that spring and summer precipitation will decrease, by a magnitude ranging from −20 to −40%, depending on the climate change scenarios (Philandras et al., 2011; Giorgi and Lionello, 2008). Montados are mostly concentrated in the southern region of the country, which has scarce water resources and a long dry summer season usually coupled with high temperatures and high radiation (Faria et al., 1996). Under frequently limited water availability, Mediterranean plants evolved physiological and morphological adaptions to optimize water use (see review by Sardans and Peñuelas, 2013). Cork oak have acquired many features to cope with water stress and, ultimately, avoid xylem cavitation and embolism (Pereira et al., 2009). At the leaf level, stomatal closure induced by drought stress (Grant et al., 2010; Otieno et al., 2007; Pinto et al., 2012; Vaz et al., 2010) restricts water loss while limiting the rate of CO_2 assimilation (Chaves, 1991; Farquhar and Sharkey, 1982). Biochemical constraints in the maximum Rubisco CO_2 fixation capacity and the maximum rate of electron transport may also take place under prolonged drought conditions (Lawlor and Cornic, 2002; Lawlor and Tezara, 2009; Tezara et al., 1999) and be even more relevant under severe drought (Bota et al., 2004; Chaves et al., 2003, 2009; Grassi and Magnani, 2005; Vaz et al., 2010). Leaf osmotic adjustment improves water uptake capacity (Otieno et al., 2007). At the plant level, a deep rooting system enhances water uptake capacity via groundwater access (David et al., 2007) and hydraulic lift (Kurz-Besson et al., 2006; Otieno et al., 2006). The reduction of vessel diameter provides further resistance against xylem cavitation while the decrease of leaf area surface (Aranda et al., 2005; Chaves and Oliveira, 2004) avoids an excessive water loss.

These drought avoidance adaptations confer *Q. suber* with a high degree of resilience (Grant et al., 2010; Vaz et al., 2010). However, it remains uncertain whether these adaptations will allow plant survival under more extreme conditions as forecasted for the future. Therefore, there is a need for further rainfall manipulation studies to better predict the vulnerability of Mediterranean ecosystems under climate change (Beier et al., 2012; Wu et al., 2011).

Although cork oaks seem to be able to adapt to water scarcity in semi-arid ambients, the species has never been tested under the predicted future climatic conditions. This study aimed at evaluating *Q. suber*'s physiological responses to rainfall manipulation so as to assess the vulnerability of Mediterranean Savannah-like ecosystems to future precipitation changes. Soil water availability was experimentally manipulated in a montado area in southern Portugal, by means of rainfall exclusion and addition. Treatments were designed according to the predicted range of precipitation changes in the Mediterranean basin (Giorgi and Lionello, 2008; Miranda et al., 2006). With increasing aridity, trees were expected to show progressively higher stomatal resistance, resulting in lower carbon assimilation rate, especially during the drought periods. These lower carbon assimilation rates would affect the carbon balance at the whole plant level leading to changed morphological and growth traits. Some uncertainties still remain on how higher stomatal resistance under increasing water shortage would affect the ecosystem water balance, which would experience lower transpiration rates but higher groundwater discharges.

Following the evolution of tree water status, sap flux, gas exchange, growth and morphological traits over two years of rainfall manipulation, our results show that not all the expectations were fulfilled. Finally, we discuss the relevance of spring precipitation quantity and distribution to cork oak's physiological performance in a particularly dry year.

2. Material and methods

2.1. Experimental conditions

The study was conducted in Herdade da Mitra (N 38° 31.664′, W 8° 01.380′, 221 m altitude) in southern Portugal from 2003 to 2005. The climate is Mediterranean mesothermic humid. The experimental site lies on an acid Litholic non-Humic soil derived from Gneiss with a pH of 4–6, on a 5% slope. From the surface to 1 m depth the soil consists of 88.9% sand, 4.9% silt, and 6.3% clay, with a low (5%) water holding capacity. The experimental site (46 m × 60 m) is covered with *Q. suber* L. trees planted in 1988, with an understory mainly composed of *Cistus salviifolius* L. *and C. crispus* L. and herbaceous winter–spring C_3 annual plants. Twenty-seven representative *Q. suber* trees were selected for monitoring. The average tree density on the experimental site was 1997 ± 134 trees ha^{-1}.