Effects of cork oak stripping on tree carbon and water fluxes

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Abstract

Cork is a high value periodical forest product which ensures the economic, social and ecological sustainability of cork oak woodlands. Abiotic and biotic stresses lead to tree decline which is endangering the productivity and sustainability of these ecosystems. It is therefore critical to find and implement management practices that minimize the impact of these stresses. The current study was conducted in a certified evergreen cork oak woodland of central Portugal under Mediterranean climate. The main aims of the study were to assess the effects of cork stripping in tree water and carbon fluxes. Results are based on the monitoring of cork stripped and unstripped (control) trees. The experiment was repeated with different sets of trees during

two contrasting summers (2014 and 2015). 2014 was a wet year (924 mm) with a typical summer drought pattern and 2015 a dry year (440 mm) with a 31% reduction in annual average precipitation. In 2015 the experimental site was entirely cork harvested and effects on ecosystem CO_2 fluxes were evaluated. Results showed that the amount of carbon in harvested cork represents less than 1.5% of net primary production on a yearly basis. In addition, cork tissue is very low demanding in nutrients: primary macronutrients content in cork represents approximately 2% of the yearly nutrient needs of leaf canopy. Regardless of the climatic year, trunk water losses following cork stripping amounted to only 2% of canopy transpiration not affecting significantly summer tree water balance. However, cork stripping induced a 46% decrease on sap flow in the dry year suggesting that cork stripping triggered an increase in stomatal closure through an interaction between stripping traumatic effects and soil water scarcity. Although the effects of summer drought on carbon sequestration are more prominent than cork stripping effects, this superimposed stress led to a significant reduction of summer net carbon ecosystem exchange *(ca*. 32%). Our results suggest that cork stripping detrimental effects can be especially critical in more vulnerable trees growing near their vitality breakdown threshold. Therefore, and concerning cork oak woodland management, the cork stripping practice should be avoided in severe dry years and in the more stress-prone trees.

Key-words: *Quercus suber* L., cork harvesting, summer drought, water stress, sap flow, Mediterranean ecosystem

1. Introduction

Cork oak (*Quercus suber* L.) open woodlands cover an area of about 2-2.5 million ha in the western Mediterranean Basin. The largest areas are located in Portugal (0.74 million ha) and Spain (0.6 million ha), corresponding to more than 50% of its world distribution area (Aronson

51 *et al.*, 2009). Cork is a high value renewable forest product, which ensures the economic, social
52 and ecological sustainability of cork oak woodlands (Bugalho *et al.*, 2011). Portuguese cork
53 provides 0.7% of the gross domestic product, with cork wine bottle stoppers the most valuable
54 derived product, and amounts to 54% of the worldwide cork production (Evangelista, 2010).

55 Cork oak bark is produced by the phellogen (cork cambium), a secondary meristem that
56 maintains its activity throughout the tree life and forms successive annual cork layers. Cork
57 stripping is done traditionally every 9 years to obtain commercial grade cork. It is removed for
58 the first time when the tree is 18–25 years old and thereafter successively every 9 years during
59 the tree lifespan (150 – 200 years). After cork stripping the phellogen dies and a new one is
60 formed almost immediately (25 – 35 days). Cork stripping is a delicate manual process,
61 requiring skilled workers to remove cork with an axe without reaching and damaging the
62 vascular cambium below the phellogen (Pereira, 2007). Stem wounds constitute open windows
63 for infection and biological attack, liable to lead to a decline in cork production (Costa *et al.*,
64 2004) and ultimately to tree death. To prevent these injuries, cork can only be safely removed
65 when the phellogen cells are actively dividing – turgid cells with thin, fragile cell walls – from
66 late-spring to mid-summer. However, in the Mediterranean region this is a period of potential
67 water deficit, with high air evaporative demand and low soil water availability. Under these
68 conditions, cork stripping may be viewed as an additional stress factor due to immediate carbon
69 and water losses that entail changes in photosynthate allocation and in tree water balance.
70 Rough estimates of daily water loss from stripped surfaces suggested that they can equal
71 canopy transpiration (Correia *et al.*, 1992; Oliveira and Costa, 2012).

72 Tree strategies to compensate for this water loss should lead to a reduction in leaf
73 transpiration either through stomatal closure or leaf area reduction (e.g. leaf shedding).
74 However, in the short-term, the effects of stripping on stomatal conductance (*gs*) are discordant
75 in literature, ranging from small reductions on *gs* not limiting photosynthesis (Werner and

Correia, 1996) to different responses according to trees (Correia *et al*., 1992). Moreover, tree water status, reflected by leaf water potential, does not seem to change considerably in stripped cork oaks (Correia *et al*., 1992; Werner and Correia, 1996). On the other hand, effects of cork stripping on tree radial growth seem clear. After stripping, cork growth shows a notable increment in the first year which can reach 2 to 3 times the thickness of previous annual periods (Costa and Oliveira, 2001; Costa *et al.,* 2003). Conversely, radial wood growth exhibits a decrease in the years immediately after cork stripping, even under favourable water availability (Leal *et al.*, 2008). It is conceivable that during the intensive growth flush of cork oak (i.e. late spring) the allocation of recently assimilated carbon and of stored carbon to regenerate the cork layer (Aguado *et al.*, 2012) induces a general reduction in tree growth. Thus, even if it has been observed that cork stripping may induce stress in trees, the nature of this stress remains poorly understood (Oliveira and Costa, 2012).

Cork oak is a well-adapted tree to the adverse Mediterranean hot dry-summer climate, namely limited water availability, high temperatures and high light intensities during summers (Pereira *et al.*, 2009). Successful adaptations range from an efficient root-shoot architecture and water transport processes (David *et al.*, 2007, 2012; Kurz-Besson, 2006) to leaf morphology and physiology (David *et al.,* 2004; Vaz *et al.*, 2010) or phenology (Oliveira *et al.*, 1994; Pinto *et al.*, 2011). Nevertheless, and despite being considered drought resilient, a succession of dry years or severe stress episodes may lead water deficits that reach a breakdown threshold, resulting in tree decline or even mortality. Within the existing trend of tree decline, as a consequence of abiotic and biotic stresses endangering the productivity and sustainability of cork oak woodlands (*montados*), it is critical to understand how trees cope with cork stripping stress and how long they take to regain carbon and water balance, at tree and ecosystem level. This experimental knowledge is needed to support better management practices and decisions, based on solid predictions of ecosystem responses to abiotic risks.

The current study was conducted in a certified evergreen cork oak woodland under the Mediterranean climate of central Portugal. The main aims of the study were to assess the effects of cork stripping on: 1) tree water and carbon fluxes response; 2) net carbon ecosystem exchange (NEE). Results are based on the monitoring of two treatments: cork stripped and unstripped control trees. The experiment was repeated during two contrasting summers: 2014, a wet year, and 2015, a dry year. Main measurements comprised: tree water status, integrated branch carbon uptake and trunk gas exchanges. In 2015 the cork oak woodland was cork harvested and effects on ecosystem CO_2 fluxes were evaluated.

2. Material and methods

2.1 Site description, vegetation and climate

The experiment was conducted during summers of 2014 and 2015 in a cork oak open woodland located at Herdade da Machoqueira (39°08'18.29' N, 8°19'57.68' W) in Central Portugal. The property has 1017 ha of pure cork oak *montados*, being the average cork production per hectare of 1300 kg dry weight each 9 years. Vegetation consists of *ca.* 50-yr-old cork oak trees with an understory of semi-deciduous shrub species (e.g. *Cistus* sp., *Ulex* sp.) and native grassland (Costa-e-Silva *et al.*, 2015). The climate is Mediterranean, with wet, mild winters and dry, hot summers. Average annual rainfall is 638±66 mm and mean annual temperature is 15.7±0.1 ºC (2009–2018, site meteorological data). 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) with some sinker roots taking water from deeper soil horizons and subsoil. From observations at a nearby borehole the water table level is estimated to vary between 3 and 5 m depth. Other general site characteristics are described in Table 1 for the studied period. Total precipitation is based on

125 the hydrological year (October to September) beginning with the usual onset of autumn
126 precipitations.

127 Table 1. Climate in 2014 and 2015, tree and ecosystem characteristics. Values are means ± *se*.

Characteristic	2014	2015	Units
Climate			
Mean temperature	15.4	15.8	(ºC)
PAR	12694	13520	(mol m^{-2})
Total precipitation [a]	924	440	(mm)
Seasonal precipitation [b]			
Autumn (Oct-Dec)	333	285	(mm)
Winter (Jan-Mar)	288	86	(mm)
Spring (April-June)	147	54	(mm)
Summer (Jul-Sept)	156	15	(mm)
Vegetation			
Maximum leaf area index	2.1	1.8	
Density	177		(trees ha^{-1})
Crown cover	56.4		(%)
Height	9.5±0.5		(m)
Diameter at breast height	29.4±1.4		(cm)
Ecosystem			
Net ecosystem exchange	-381	-256	(g C m^{-2} $year^{-1}$)
Gross primary productivity	1527	949	(g C m^{-2} $year^{-1}$)
Total ecosystem respiration	1147	693	(g C m^{-2} $year^{-1}$)
Net primary productivity (trees)	887	558	(g C m^{-2} $year^{-1}$)

Cork harvesting [c]	8.2	(g C m^{-2} $year^{-1}$)

[a] hydrological year; [b] Considering 3-month sums; [c] Yearly carbon fraction removed in cork biomass (considering 1300 kg of cork in each 9-years harvesting and 57% of carbon content in cork according to Gil *et al.*, 2005)

2.2 Tree sampling

Following a survey of stand mean tree diameter, crown projected area and tree height, a sample of 12 trees per year was selected in 2014 and 2015, all in the same exploitation stage having reproduction cork (from the third harvesting onwards). All trees were selected within a representative plot of 40-m radius. In each year we separated the 12 selected trees in two similar pairwise sets of cork stripped and unstripped control trees to be monitored throughout the summer. Cork stripping of the 6 trees was done in July 7 (2014) and in June 30 (2015). In 2015, from June 11 to 13, all trees in the cork oak woodland were cork harvested (except the 12 treatment trees). Current legislation regulates maximum stripping height through the cork harvesting coefficient (HC): ratio between stripping height and trunk perimeter at 1.30 m above the ground (PBH). This index determines maximum values according to the tree exploitation stage, e.g. in the case of reproduction cork maximum stripping height can not exceed three times PBH (Oliveira and Costa, 2012). General tree morphological traits per treatment and year are presented in Table 2.

Table 2. General tree morphological traits per treatment (control and cork stripped trees) in 2014 and 2015. Values are means ± *se* (*n*=6).

	2014		2015	
	Control	Stripped	Control	Stripped
Height (m)	11.4±0.7	9.6±0.5	9.8±0.3	11.3±0.4

Diameter at breast height (cm) [a]	30.0±2.2	31.1±2.5	27.1±1.3	27.0±1.5
Crown projected area (m^2)	42.2±6.5	42.1±9.1	40.0±9.0	44.0±7.0
Harvesting coefficient – HC [b]	–	2.1±0.2	–	2.6±0.2
Cork stripping surface area (m^2)	–	2.6±0.5	–	2.2±0.2

147 [a] diameter measured under cork; [b] stripping height to PBH ratio

148

149 *2.3 Meteorological data*

150 The following meteorological data were collected at the experimental site: rainfall (ARG100;
151 Environmental Measurements Ltd., Gateshead, UK), photosynthetically active radiation (PAR)
152 (BF2; Delta-T Devices Ltd., Cambridge, UK), air humidity and temperature (CS215; Campbell
153 Scientific, Inc., Logan, UT, US). Values were recorded continuously in 30-min time intervals
154 (CR10X; Campbell Scientific, Inc., Logan, UT, US). Soil volumetric water content was
155 measured up to 40-cm depth (2, 10 and 40 cm) with dielectric soil moisture sensors in two
156 different places (EC5; Decagon Devices, Inc., Pullman, WA, US). These measurements were
157 automatically recorded in a datalogger (Em50; Decagon Devices, Inc., Pullman, WA, US) as
158 30-min averages.

159

160 *2.4 Litter fall and cork nutrient content*

161 Litter fall was collected in 16 litter traps of 0.5 m^2 placed in two transects across the
162 footprint area of eddy flux measurements and sampled every 15-30 days throughout 2011 to
163 2016. Separation of leaves, branches, male flowers (catkins) and acorns was performed on the
164 collected litter. Additionally, in six trees, budburst time and individual leaf dimension were
165 measured in a sampled branch per tree (selected in the south facing side of the canopy) to
166 determine the start and duration of the leaf growth period. Tree leaf area index (LAI) was

calculated using leaf biomass from litter fall and species-specific leaf area (SLA) following Costa-e-Silva *et al.*, (2015). Maximum LAI was assumed to be coincident with the end of new leaf growth in that year and was determined by the sum of the area of all leaves shed after that date and belonging to the leaf cohort of that year. Tree height, tree diameter, and crown cover were estimated by measuring the diameter, height and crown projected area of all trees in a representative plot of 40-m radius (December 2014).

Considering the average annual biomass production of leaves, acorns, catkins and cork at our site, and each tissue mineral composition, the amount of nutrients present per tissue was estimated and compared. The average annual (2011-2016) dry weight biomass production of leaves, acorns and catkins were, respectively, 2.78±0.2, 0.52±0.15 and 0.13±0.02 Mg ha^{-1}. For nutrient content determinations we used the mineral composition of each litter fall component (percentage dry weight) of a similar cork oak woodland (Oliveira et al., 1996). As well, we used the ash mineral composition of reproduction cork (P, K, Ca and Mg) as indicated in Pereira (2007) and N as determined by Domingues (2005).

2.5 Trunk gas exchanges

Trunk transpiration and respiration were measured using a differential CO_2/H_2O infrared gas analyzer (LCPro+; ADC BioScientific Ltd., Hoddesdon, UK) coupled with an adapted soil chamber. All 6 trees per treatment, were measured in the morning (0900 – 1100 h) and in the afternoon (1500 –1700 h) at the same north facing side trunk azimuth. In 2014, measurements were done in the cork stripping day (July 7) and then 1, 4, 8, 17, 28 and 59 days after cork removal. In 2015, measurements were done in the cork stripping day (June 30) and then 1, 3, 8, 14, 35 and 65 days after cork removal.

191 *2.6 Tree leaf water potentials*

192 Leaf water potential was measured at predawn (Ψ_{pd}, a surrogate of soil water potential near
193 roots) and midday (Ψ_{md}) with a Scholander-type pressure chamber (PMS Instruments,
194 Corvallis, OR, US) in the six trees per treatment. In each tree one fully developed sun-exposed
195 leaf was sampled at the same south facing side of the crown. Measurements were done before
196 the cork stripping day (June 19 and June 18 in 2014 and 2015, respectively) and in the same
197 days as indicated for trunk gas exchanges.

198

199 *2.7 Sap flow*

200 Sap flow was continuously measured in the 12 sampled *Q. suber* trees by the Granier method
201 (Granier, 1985) from early June to the end of September of both years. One sensor per tree (UP
202 GmbH, Landshut, Germany) was radially inserted in the south-facing xylem. Each sensor
203 consists of a pair of 2-cm-long probes inserted in the tree stem at breast height, 15 cm apart
204 vertically. The upper probe was heated by a constant current, whereas the lower probe was
205 unheated and remained at trunk temperature. In each tree sensors were insulated from radiation
206 through an aluminium foil covering. Sensors were connected to CR23X and CR1000 data
207 loggers (Campbell Scientific, Inc., Logan, UT, US), scanning temperature differences between
208 probes (ΔT) every 10 s and recording 30-min means. Power supply was provided by car
209 batteries and solar panel (SOP10, Solarex, Maryland, USA). Sap flux density (J_s) was
210 calculated from 30-min values and the absolute maximum temperature difference between
211 probes (ΔT_{max}) over variable periods, according to night time ΔT trends and vapor pressure
212 deficit (VPD).

213 From the end of July to the end of September of 2014 the radial profile of J_s at four
214 depths below the cambium (0.5, 1, 1.5 and 2 cm), was measured by the Compensation Heat

Pulse (CHP) method (Green *et al.*, 2003) in three trees per treatment. One set of heat-pulse probes (Tranzflo NZ Ltd., Palmerston North, NZ) was installed in the south-facing xylem of each tree at breast height. Two temperature probes were installed 10 mm downstream and 5 mm upstream of the heater probe, that released a heat pulse (60 J; 60 W over 1 s) once every 30 min. Data was recorded in two CR10X data loggers (Campbell Scientific, Inc., Logan, UT, US). Sapwood fractions of water and wood were measured on cores taken from four measured trees. Comparisons of sap flow data from the Granier and the CHP methods showed that although the radial distribution of sap flow density was non-uniform over the conductive area, the Granier method provided a good estimate for the average J_s over the entire conductive area (significant correlations with R^2 between 0.81-0.89, data not shown). Tree sap flow (F) was determined as the product of J_s (obtained by the Granier method) and the sapwood conductive area. The sapwood conductive thickness was estimated considering that only the outer 32% of the trunk radius of *Q. suber* is conductive (David *et al.*, 2007). Estimated hydroactive xylem thickness in the sampled trees ranged from 3.4 to 6.2 cm, which always exceeded the Granier probe length.

No relation was found between J_s and tree size (e.g. diameter, crown projected area) confirming that the sampling of J_s does not need to be done for particular size classes as was also shown by Schmidt *et al.* (2009) for *Q. suber*. Because only one sensor was installed per tree, errors may have arisen from neglecting circumferential sap flux variability. However, because an evenly distributed circumferential sap flux density is frequently assumed for diffuse-porous species (David *et al.*, 2007) and because the sampling and calculation procedures were the same in all trees, any errors will tend to have been systematic and should not affect our comparative analyses of the relative variation of tree sap flow in time or between treatments.

240 *2.8 Branch light use efficiency*

241 Closed-system portable chambers of 15 cm x 15 cm and 40 cm high connected to an Infrared
242 gas analyzer (LI-840A, LI-COR Inc., Lincoln, NE, USA) were used to measure CO_2 exchanges
243 on selected sun-exposed one-year-old branches from the south-side crown of the sampled trees.
244 A transparent chamber (light chamber) measured net branch CO_2 exchange (F_{nbe}) and an
245 opaque chamber (dark chamber) measured branch respiration (F_{br}). Branch carbon uptake (F_a)
246 was determined by the difference between F_{nbe} and F_{br}. Details on the closed-system portable
247 chambers construction and measurements are reported in Correia *et al.* (2014).

248 At the end of the experiment period all leaves from each selected branch (one branch
249 per tree) were collected and leaf area determined (WinRhizo; Regent Instruments Inc., Quebec,
250 Canada). Branch carbon uptake is expressed in μmol CO_2 m^{-2} s^{-1} normalized to branch leaf
251 area. Incident light levels on each branch were monitored using a *PAR* quantum light sensor
252 (QSO-S; Decagon Devices Inc., Pullman, WA, US) at the beginning and at the end of each
253 measurement. Because F_a is very sensitive to incident light levels variability and in order to
254 compare trees, we determined branch light use efficiency (LUE_b) as F_a / PAR expressed in
255 μmol CO_2 μmol^{-1}. Measurements were conducted in four trees per treatment throughout the
256 summer of both years, before and after cork stripping, in the same days as indicated for leaf
257 water potential.

258

259 *2.9 Ecosystem flux measurements*

260 The fluxes of CO_2, water vapor and sensible heat were continuously measured (23.5 m above
261 ground) by an eddy-covariance system installed at the top of a 22 m high tower. The system
262 consisted of a 3-D sonic anemometer (R3; Gill Instruments Ltd., Lymington, UK) and a closed-
263 path infrared gas analyzer (LI-7000; LI-COR Inc., Lincoln, NE, US), measuring temperature,

264 the three components of wind velocity, and the concentration of water vapor and CO_2. The inlet
265 tube of the gas analyzer (8 m long) was attached to one of the anemometer arms and operated
266 with an average flow rate of ca. 8 L min^{-1}. The reference cell is flushed with N_2, and CO_2 and
267 H_2O calibrations are done every 15 days. Data were continuously acquired on a field laptop
268 with EddyMeas (Meteotools, Jena, Germany; Kolle and Rebmann, 2007).

269 Eddy flux data was treated using the eddy-covariance data processing software package
270 EddyPro (v6.2.0; LI-COR Inc., Lincoln, NE, US). Fluxes were determined on a half-hourly
271 basis by block-averaging the 20 Hz data. Time lags compensation was performed by automatic
272 time lag optimization and for water vapor as a function of relative humidity (Ibrom *et al.*, 2007).
273 Compensation of density fluctuations was applied to raw concentration data according to Ibrom
274 *et al.*, (2007) although including the pressure-induced fluctuations terms. Spectral corrections
275 of low and high-pass filtering effects were done following Ibrom *et al.*, (2007) and Moncrieff
276 *et al.*, (2004), respectively. The sectorial planar fit method was used for the coordinate rotation
277 of wind vectors (Wilczak *et al.*, 2001).

278 For quality control, raw data despiking was done by the Vickers and Mahrt (1997)
279 method and on a half-hourly basis a friction velocity (u*) filtering was performed using a
280 moving point test (Papale *et al.*, 2006). All quality control tests were summed up in a simplified
281 flag system for every half-hourly flux value according to Mauder and Foken (2011). Gap filling
282 and flux-partitioning methods proposed by Reichstein *et al.* (2005) were used to fill data gaps
283 and to separate the net ecosystem exchange (NEE) into gross primary productivity (GPP) and
284 ecosystem respiration (R_{eco}). Determination of net primary productivity (NPP) was done
285 according to:

286 $$NPP=GPP-R_a \text{ and } R_{eco}=R_a+R_h,$$

287 where R_a is ecosystem autotrophic respiration and R_h is heterotrophic soil respiration. We
288 assumed that R_h is approximately 60% of R_{eco} based on reported values for a cork oak site in

similar Mediterranean edapho-climatic conditions (Unger *et al.*, 2009) and considering that soil respiration is relatively consistent among Mediterranean ecosystems (Correia *et al.*, 2012). The NPP of the cork oak trees in the ecosystem was determined through the reduction of the shrub layer productivity (17% of GPP) measured in closed chambers during 2011 and upscaled to the ecosystem level (Correia *et al.*, 2014). The herbaceous vegetation was considered to have a negligent effect on the annual carbon balance based on data from an undercanopy eddyflux tower established at the same site (Piayda *et al.*, 2014).

2.10 Data and statistical analysis

Summer drought stress and cork stripping effects on net carbon ecosystem exchange (NEE) were assessed by comparison of daily NEE throughout the experimental period in 2014 and 2015. To compare NEE between different periods we used only data from days without rain, with similar PAR conditions (60.7 ± 2.2 mol m^{-2} d^{-1}), using only original and high quality night-gapfilled data.

To examine differences between variables (e.g., leaf water potential, LUE_b, daily NEE) we used one-way ANOVA. When ANOVA assumptions where not met, namely normal distribution of the data and homogeneity of variances, non-parametric Kruskal–Wallis test was carried out. Analysis were performed using STATISTICA (Version 7, StatSoft, Inc., 2004).

3. Results

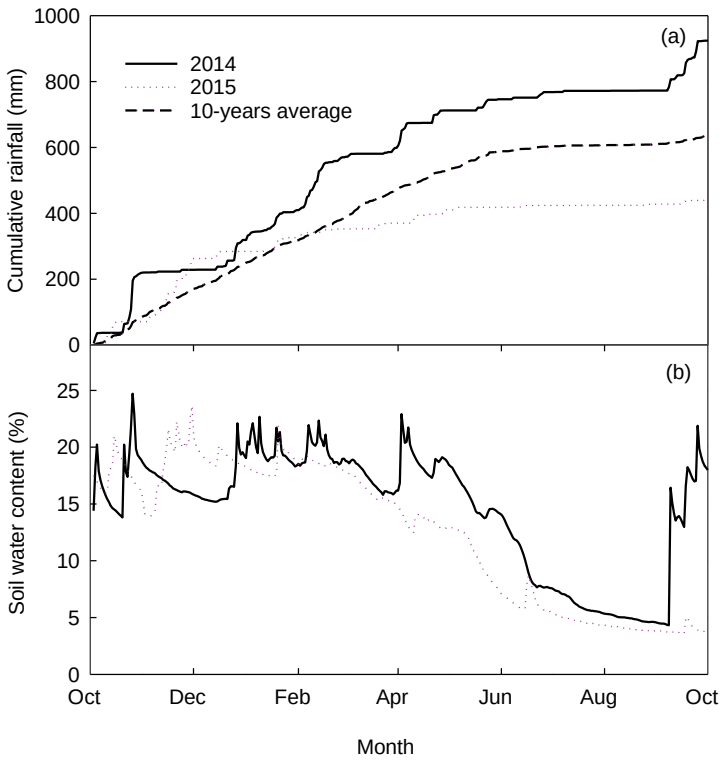
3.1 Climatic conditions

Rainfall during the study period was quite contrasting. The year 2014 was fairly wet with a hydrological annual rainfall of 924 mm, 45% higher than local average (638 mm). Conversely, 2015 was dry with an annual rainfall of 440 mm, 31% lower than average (Fig. 1a). In

312 particular, 2015 had a low winter rainfall (86 mm), and spring rainfall was 63% lower than in
313 2014 (54 vs. 147 mm, respectively, Table 1).

314 Volumetric soil water content (SWC) followed closely rainfall events. In both years
315 SWC shown high values until April. However, from April to June, SWC was lower in 2015
316 than in 2014 (Fig. 1b). In the months of July and August, SWC at 40-cm depth was low in both
317 years (6 to 4%). In September 2014 SWC increased noticeably upon soil rewetting with autumn
318 rains, contrasting to 2015.

319 Although 2015 was a dry year, its daily maximum vapor pressure deficit (VPDmax)
320 during the summer was lower than local average (Fig. 2). Thus, in 2015, with exception for
321 June, the low VPD somehow attenuated the drought effect of the summer period. Similarly, in
322 2014 the VPDmax during all summer was noticeably lower than local average, with the lowest
323 values recorded in the 10-years dataset.



324

Fig. 1. (a) Cumulative rainfall (mm) during the hydrological years of 2014 and 2015 and the 10-years local average. (b) Daily values of volumetric soil water content (%) at 40 cm depth during 2014 and 2015.

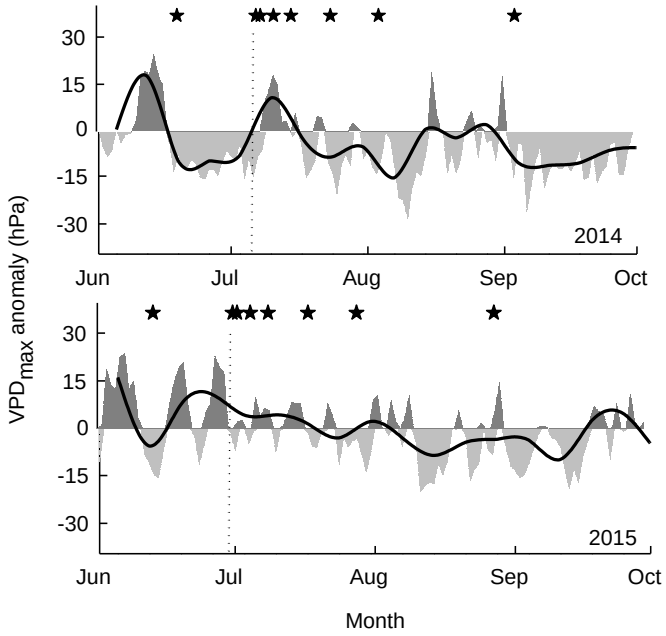


Fig. 2. Daily maximum vapor pressure deficit (VPD_{max}, hPa) anomalies in relation to local 10-years average, during 2014 and 2015. The black line stands for a 7-day running average. Asterisks (*) indicate measurement days (Ψ_w, LUE_b) and the dotted line the days of the cork stripping treatment in 2014 and 2015 (July 7 and June 30, respectively).

3.2 Cork nutrient content

Considering the average annual nutrient investment in canopy renewal it is noticeable that reproductive structures represent a significant nutrient investment (Table 3). Particularly, primary macronutrients content in acorns represent a high investment ranging from 15.9 to 44.5 % in N and K compared to nutrient content in leaves. In contrast, primary macronutrients content in cork removed by harvesting range from 1.4 to 2.9 % in P and K, respectively, which represents a low investment compared to reproductive structures or leaf canopy. Considering

341 the macronutrients Ca and Mg, they represent a low nutrient investment both in reproductive
342 structures or cork compared to leaf canopy.

343 Table 3. Annual nutrient content (kg ha^{-1} $year^{-1}$) of each litter fall component and of cork
344 removed in harvesting. Values are means ± *se* (*n* = 6).

	Leaves	Acorns [a]	Catkins [a]	Cork [a]
N	28.9±1.8	4.6±1.4 (15.9)	2.4±0.3 (8.4)	0.55 (1.9)
P	2.5±0.2	0.7±0.2 (29.1)	0.3±0.04 (12.8)	0.04 (1.4)
K	11.7±0.7	5.2±1.5 (44.5)	2.2±0.3 (18.6)	0.33 (2.9)
Ca	16.1±1.0	0.4±0.1 (2.3)	0.2±0.02 (1)	0.9 (5.6)
Mg	6.1±0.4	0.5±0.2 (8.5)	0.3±0.04 (5)	0.04 (0.6)

345 [a] numbers between brackets are percentage of tissue nutrients in relation to leaves nutrient content

346

347 *3.3 Trunk gas exchanges*

348 The pattern of trunk water loss and trunk respiration after cork stripping was similar in 2014
349 and 2015 (Fig. 3). Maximum trunk water loss occurred in the cork stripping day in 2015 and
350 four days after cork stripping in 2014 (Fig. 3a) coincident with a VPD peak (43.3 hPa, Fig. 2).
351 Trunk evaporation decreased linearly thereafter until a minimum was reached, 60 days after
352 cork stripping, similar to the values of control trees which were always close to zero in both
353 years (on average 1.6±0.9 μmol H2O m^{-2} s^{-1}). Considering the days of maximum trunk water
354 loss in 2014 and 2015 and the respective cork stripped area per tree (Table 2) the maximum
355 flux of water loss was on average 19.1±1.6 g H_2O h^{-1} $tree^{-1}$.

356 Trunk respiration presented a slightly different temporal variability, compared to stem
357 water loss, increasing sharply in the first 4 days after cork stripping and then decreasing to a

minimum in the next 10 days (Fig. 3b). One month after cork stripping trunk respiration slightly increased and maintained the same rates until the end of the experiment.

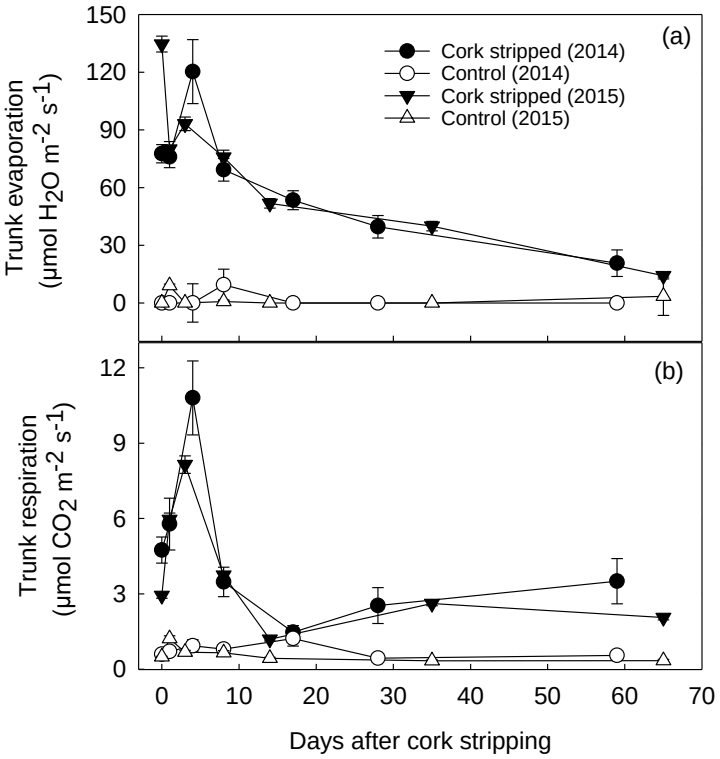
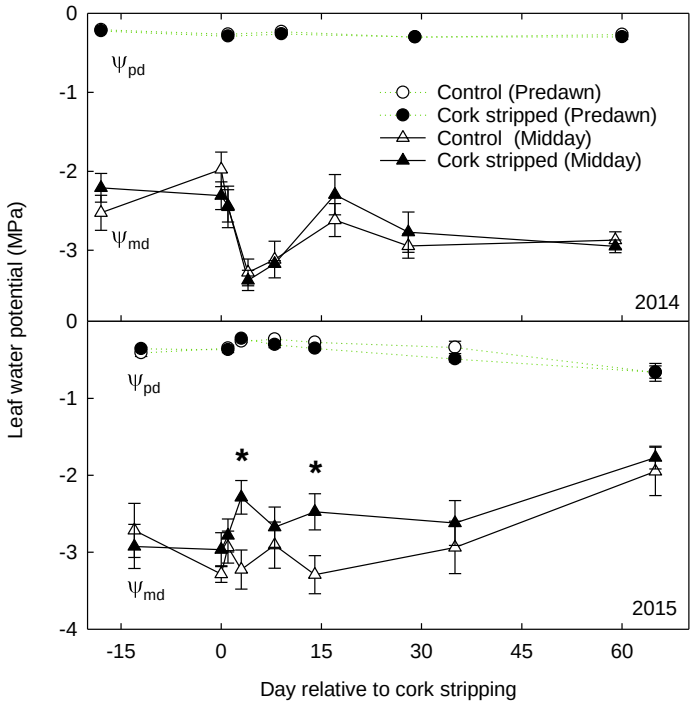


Fig. 3. Trunk gas exchanges measured in control and cork stripped trees during the study period. Cork stripping treatment was done on July 7 and June 30 in 2014 and 2015, respectively. (a) Trunk evaporation (µmol H_2O m^{-2} s^{-1}). (b) Trunk respiration (µmol CO_2 m^{-2} s^{-1}). Values are means ± se (n = 6).

3.4 Tree leaf water potential

Tree leaf water potential measured throughout the summer of 2014 indicated no signs of water deficits in both treatments: Ψ_{pd} remained always higher than -0.3 MPa (Fig. 4) confirming a high soil water availability. In this same year, Ψ_{md} values were low in both treatments with a decrease on days 4 and 8 after cork stripping in response to the high VPD. In 2015, there were

371 also no significant differences in Ψ_{pd} between both treatments along the summer although more
372 negative Ψ_{pd} were reached in the peak of summer stress (early September), 65 days after
373 treatment cork stripping (-0.7 MPa, on average). On the other hand, in 2015 there were
374 significant differences between treatments in Ψ_{md}. Cork stripped trees showed higher Ψ_{md} than
375 control trees, particularly from 3 to 14 days after cork stripping, suggesting higher stomatal
376 closure in this treatment. In late summer of 2015, 65 days after treatment cork stripping, the
377 smaller difference between Ψ_{pd} and Ψ_{md} shows that water stress had developed in both
378 treatments.



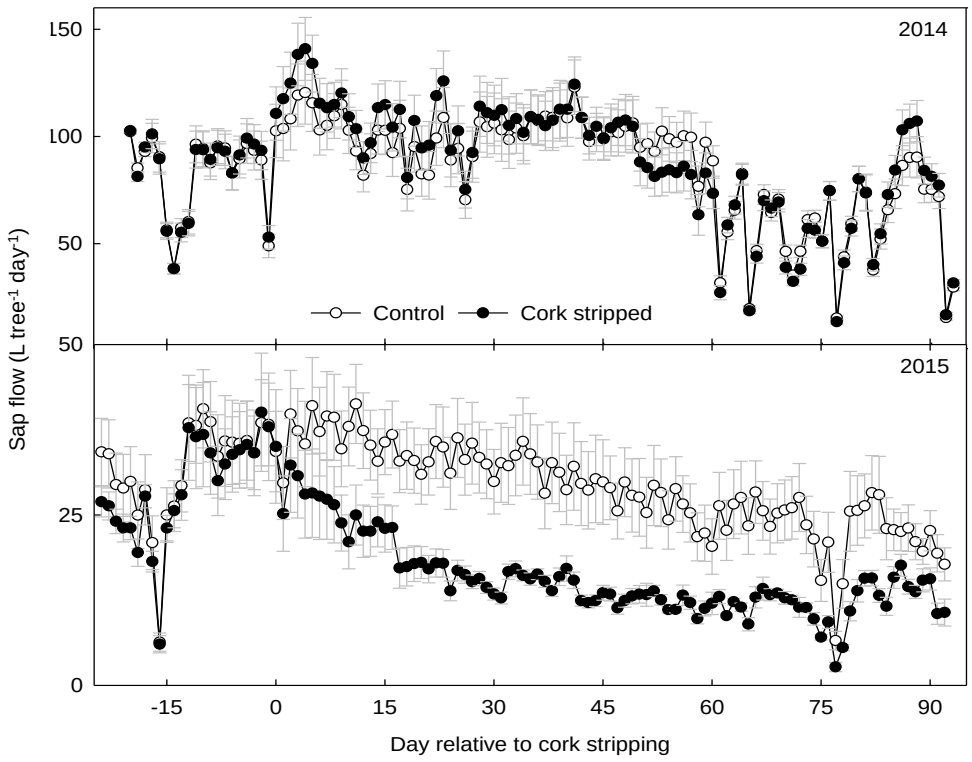
379

380 Fig. 4. Predawn (Ψ_{pd}) and midday (Ψ_{md}) tree leaf water potential (MPa) measured in control
381 and cork stripped trees during the study period. The cork stripping treatment was done on July
382 7 and June 30 in 2014 and 2015, respectively. Values are means ± se (n = 6). Asterisks (*)
383 represent statistical significant differences at $P < 0.05$.

384

385 *3.5 Sap flow*

386 During the study period of 2014 the patterns of tree sap flow (*F*) were similar for both
387 treatments (Fig. 5). High daily *F*, above 100 L tree^{-1} day^{-1}, were maintained until the end of
388 August (45 days after cork stripping) indicating that there were no restrictions on soil water
389 availability. At the end of the dry season, following the first autumn rains in early September
390 (60 days after cork stripping), maximum daily *F* decreased on average 20% in relation to the
391 maximum seasonal *F* showing that a lower evaporative demand (lower radiation and VPD (see
392 Fig. 2)) was limiting *F* rather than soil water availability. In 2015, during the first 30 days of
393 the study period, before the cork stripping treatment, maximum daily *F* showed a 2-fold
394 decrease in relation to the same period of 2014 as a result of the reduced water availability.
395 After cork stripping, trees showed an immediate 20% reduction in *F* compared to control trees,
396 and this difference increased progressively up to 55% after 30 days. On average cork stripped
397 trees showed a 46% decrease in *F* during the dry season of 2015 compared to control trees.
398 Furthermore, both treatments responded differently to drought along the dry season: control
399 trees maintained high *F* during July (0-30 days after treatment) and decreased maximum *F*, 13
400 and 31% in August (30-60 days after treatment) and September (60-90 days after treatment),
401 respectively, whereas cork stripped trees decreased 19, 57 and 56% maximum *F* in July, August
402 and September, respectively.



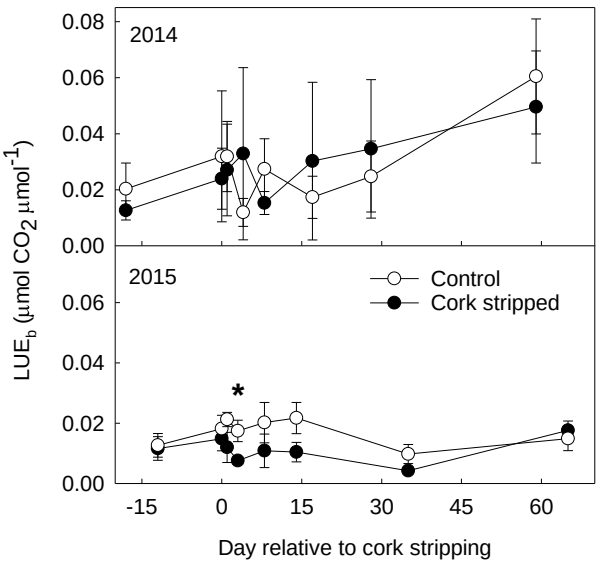
403

404 Fig. 5. Sap flow (L tree^{-1} day^{-1}) determined for control and cork stripped trees during the study
405 period. The cork stripping treatment was done on July 7 and June 30 in 2014 and 2015,
406 respectively. Values are means ± se (n = 6).

407

408 *3.6 Branch light use efficiency*

409 The main interannual differences and treatment variation in LUE_b can be perceived in Fig. 6.
410 During 2014, LUE_b showed no differences between treatments across the dry season with a
411 high variability between trees as a result of the high patchiness in incident PAR. In comparison
412 to 2014, LUE_b decreased on average 50% in 2015 (0.028 ± 0.015 *vs.* 0.014 ± 0.004 μmol CO2
413 μmol^{-1}, respectively). In the first 35 days after cork stripping in 2015, LUE_b showed an average
414 50% reduction in cork stripped trees compared to control trees. In addition, during the dry
415 season LUE_b of cork stripped trees showed a higher decrease than control trees in relation to
416 the maximum seasonal LUE_b (76 and 55%, respectively).



417

418 Fig. 6. Branch light use efficiency (LUE_b) measured in 1-year old branches of control and cork
419 stripped trees during the study period. The cork stripping treatment was done on July 7 and
420 June 30 in 2014 and 2015, respectively. Values are means ± se (n = 4). Asterisks (*) represent
421 statistical significant differences at $P < 0.05$.

422

423 *3.7 Ecosystem CO_2 uptake*

424 It is important to consider that in 2015, June 11 to 13, all trees in the cork oak woodland were
425 cork harvested with the exception of the 12 experimental trees (see section on Tree sampling,
426 Methods). Cumulative net ecosystem CO_2 exchange (NEE) clearly showed the effect of low
427 rainfall and cork stripping in 2015 by reducing carbon sequestration: after cork stripping till
428 the end of September absolute CO_2 uptake decreased 59%, from -246 in 2014 to -101 g C m^{-2}
429 in 2015 (Fig. 7a). However, before cork harvesting, from May to early June 2015, there was
430 already a 39% lower carbon uptake in relation to 2014 (-47 vs. -77 g C m^{-2}, respectively), which
431 can be ascribed to the lower water availability as also reflected by the concomitant lower sap
432 flow rates in the same period (Fig. 5). In addition, the maximum daily carbon uptake in early
433 June was also significantly higher in 2014 than in 2015 (-5.4 vs. -3.3 g C m^{-2} day^{-1}, Fig. 7b). In

the first 10 days after cork harvesting in 2015 NEE decreased 73% in relation to the June period before cork stripping. After the third week in June till the middle of July, NEE partially recovered being 38% lower than in early June (Fig. 7b and Fig. 8). While in 2014 high absolute values of carbon sequestration were maintained till the end of July to subsequently decrease steeply until the end of summer, in the dry 2015 the decrease in NEE occurs gradually after middle of July (Fig. 7b). In both years with the onset of autumn rains (6 and 15 September in 2014 and 2015, respectively), NEE decreases abruptly as a consequence of soil rehydration which induces a peak in soil respiration. In fact, NEE trend in September was similar in both years (Fig. 7a and b).

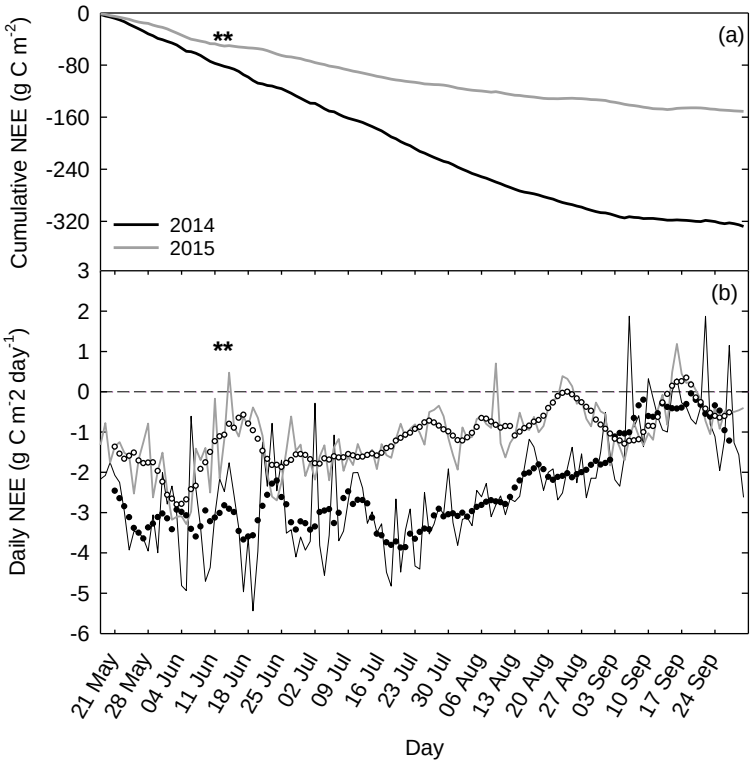


Fig. 7. Cumulative (a) and daily values (b) of net carbon ecosystem exchange (NEE) during 2014 and 2015. The black and open circles in panel (b) stands for a 7-day running average. Negative values represent carbon sequestration in the ecosystem while positive values

represent carbon emissions to the atmosphere. Asterisks (*) indicate the days of site cork harvesting in 2015 (11-13 June).

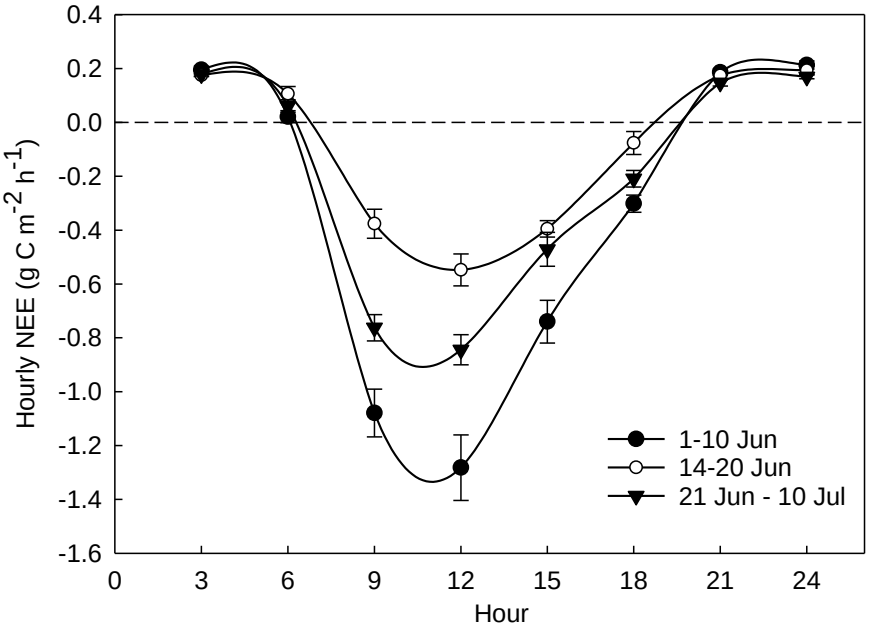


Fig. 8. Hourly mean values of net carbon ecosystem exchange (NEE) determined for three periods before and after site cork stripping in 2015 (11-13 June). Negative values represent carbon sequestration in the ecosystem while positive values represent carbon emissions to the atmosphere.

4. Discussion

4.1 Effects of cork stripping on tree carbon and nutrient balance

In the Mediterranean hot dry-summer region, cork oak woodland ecosystems are major reserves for terrestrial carbon and a major component of regional primary productivity. Anthropogenic influences, such as management, land degradation, or overexploitation impact on carbon emissions and sequestration of cork oak woodlands. Cork harvesting implies direct carbon losses for the tree and the ecosystem. We have determined that the amount of carbon

462 harvested on a yearly basis relative to the net primary productivity (NPP) of cork oak trees was
463 0.9 and 1.5%, for 2014 and 2015, respectively (Table 1). This means that cork harvest *per se*
464 is a minor component of the tree carbon balance, only marginally affecting its energy balance
465 driven by photosynthate production. Therefore, cork harvest barely affects the ecosystem
466 carbon balance, and ecosystem carbon sequestration should be credited as an asset in cork
467 production as it was envisaged by Vallejo *et al.* (2009).

468 Cork oak is a mast-cropping tree which generally occupies low resource environments
469 and, therefore, is prone to show a marked decline in carbon reserves and vegetative growth
470 following a high reproductive investment (Chapin *et al.*, 1990). It has been suggested that cork
471 stripping and new cork growth may be compared to the investment in flowers and fruits, which
472 do not contribute to carbon assimilation and compete with other tree components for nutrients
473 and photoassimilates (Oliveira and Costa, 2012).

474 Our results show that cork is a very low resource demanding tissue, as reflected by its
475 low carbon costs in relation to the tree NPP and low nutrient content. In fact, primary
476 macronutrients content in cork amounts to approximately 2% of the yearly nutrient needs of
477 the leaf canopy and represents much lower needs than those of fruits and flowers (Table 3).
478 Furthermore, following cork stripping it was not observed any significant decrease on
479 reproductive growth either on 2015 (acorn production) or 2016 (acorn and catkins production)
480 (data not shown). Likewise, the allocation of assimilated carbon and/or of stored carbon to
481 regenerate the cork layer did not affect the new leaf development in 2016 as the ecosystem
482 maximum leaf area index has slightly increased (1.9). However, it is well known that cork
483 stripping has a major effect on tree radial growth, particularly in cork growth. As early as in
484 1938, it was observed that after cork stripping the activity of the vascular cambium decreases
485 and the wood growth stops (Natividade 1938). Leal *et al.* (2008) estimated that cork stripping
486 led to an annual reduction of wood growth (ring width) of approximately 57% in the first 2

487 years after cork regeneration even under favorable water availability conditions. Conversely,
488 after stripping, cork growth shows a marked increment in the first year that can reach 2 to 3
489 times the thickness of previous annual periods (Costa and Oliveira, 2001; Costa *et al.*, 2003).
490 Therefore, although cork represents a low carbon and nutrient store as compared to leaf canopy
491 or reproductive structures, phellogen sink strength is considerably enhanced after cork
492 stripping resulting in a cork growth increase. This suggests that sink strength relations between
493 the phellogen and the vascular cambium are significantly altered after cork stripping at least
494 during the first 2 years, resulting in a decrease of wood growth.

495 Source-sink activity is controlled by a complex signaling network involving both
496 physical and chemical signals that play an important role in communicating sink demand and
497 regulating partitioning (Smith *et al.*, 2018; Körner, 2015). Phellogen activity and subsequent
498 cork cells growth was found to be a highly effective sink for photoassimilated carbon (Aguado
499 *et al.*, 2012, 2017). These authors have shown that suberin, the main cork cell wall component,
500 was the major carbon sink for the carbon assimilated throughout the whole active growth
501 period, i.e. from early spring to late autumn, as compared to other stem chemical components.
502 This can partially explain differences in tree components growth and the underlined resource
503 allocation competition. Furthermore, considering that carbon assimilates fluxes greatly depend
504 on the source-sink distances (Lacointe, 1999), its plausible to admit a decrease in root growth
505 as observed for wood growth during the first two years after cork stripping. This may have a
506 crucial role in lowering the tree resilience capacity facing abiotic (e.g. sequential drought
507 episodes) and biotic stresses (e.g. *Phythoptora cinnamomi*) which greatly depend on the root
508 system capacity to maintain a favourable tree water balance (David *et al.*, 2016).

509 Bark thickness determines the distance of external factors to vital meristemic tissues
510 (cambium, buds), phloem and the xylem. Major functions of the outer bark (cork) include
511 reduction of water loss, barring against pathogen entry, protection against mechanical injury,

512 insulation of the stem against adverse climatic conditions and protection against wildfire. There
513 is increasing evidence that having a thick bark increases fitness in many fire-prone ecosystems
514 (Pausas, 2015). Therefore, from an evolutionary pressure perspective a transference priority in
515 carbon assimilates allocated to the growth of new cork after stripping is justified by the
516 important role of cork in the cork oak ecological fitness.

517

518 *4.2 Effects of cork stripping on tree water balance*

519 Cork stripping leaves the innermost conducting tissues – phloem and xylem – exposed to the
520 external environment and tree stems have no immediate mechanism to control water loss from
521 these tissues. This water loss is very perceptible in the wet trunks after cork stripping although
522 it was only rarely quantified. Some rough estimates suggested that this daily water loss could
523 equal that of leaf transpiration (Oliveira and Costa, 2012; Correia *et al.*, 1992). Our
524 measurements clearly show that this trunk water loss is negligible in comparison to canopy
525 transpiration (Fig. 3 and 5). Considering an average cork stripped area per tree, the maximum
526 flux of water loss was on average 19.1±1.6 g H_2O h^{-1} $tree^{-1}$. This maximum stem water
527 evaporation value represents approximately 2% of the canopy transpiration rate for the same
528 daily period. Thus, the quantity of water evaporating from the stripped surfaces does not imply
529 a significant effort by the tree to maintain water balance throughout the dry summer period.

530 Trunk water evaporation rates seems to be dependent of the atmospheric evaporative
531 demand (VPD) only in the first days after cork stripping. After this initial period trunk
532 evaporation decreases linearly until reaching a minimum 60 days after cork stripping, similar
533 to control trees (Fig.3). Upon cork stripping, the exposed outermost phloem cells dry out and
534 die and form an early (yet not fully effective) protective layer which covers the inner living
535 tissues. The decrease of stem water loss, to values similar to control trees, seems to indicate

536 that only after 60 days the scar tissues and the first new layers of the regenerating periderm are
537 fully insulating. This suggests that the rate of CO_2 and H_2O diffusion from the stem to the air
538 is effectively limited with the cell tissue reconstruction of phellogen (traumatic phellogen) that
539 initiates approximately after 25-35 days (Machado, 1944).

540 Monitoring tree sap flow has allowed us to assess the effect of cork stripping on canopy
541 transpiration during the summer of 2014 and 2015 (Fig. 5). Tree response to cork stripping
542 varied with soil water availability: in 2014 (wet year) canopy transpiration was similar between
543 control and cork stripped trees, whereas in 2015 (dry year) cork stripping led to a significant
544 reduction in transpiration through stomatal closure as supported by the increase in midday leaf
545 water potential in treatment trees (Fig. 4). In 2015 with an annual precipitation 31% lower than
546 the local average, cork stripping led to a 46% reduction of canopy transpiration in comparison
547 to control trees. The literature has reported variable effects of cork stripping on g_s, ranging
548 from small reductions not limiting photosynthesis (Werner and Correia, 1996) to different
549 responses according to trees (Correia *et al.*, 1992). In addition, tree water status, as reflected
550 by Ψ_w, did not change considerably in stripped cork oaks (Correia *et al.*, 1992; Werner and
551 Correia, 1996). All these results and our own differences between the wet and dry year, strongly
552 suggest that stripping effects on g_s are triggered by an interaction between stripping traumatic
553 effects and environmental effects as soil water availability decreases.

554 Cork stripping, in terms of tree physiological effects can be regarded as a traumatic
555 wounding with similarities to stem girdling (e.g. De Schepper et al., 2010; Lopéz et al., 2015).
556 Though unlike girdling, the phloem tissue remains in the tree and only the periderm is removed
557 with cork stripping. We can then expect a disruption of the basipetal movement of assimilates
558 through phloem where a new traumatic phellogen will be formed within the deeper non-
559 conducting phloem tissues (Oliveira and Costa 2012). We have observed a significant lower
560 sucrose content in the trunk phloem tissue of cork stripped trees compared to leaf tissues and

561 to an accumulation in control trees (data not shown), suggesting a disruption and impairment
562 of phloem components transport.

563

564 *4.3 Effects of cork stripping on Net Ecosystem CO_2 Exchange*

565 Soon after site cork harvesting in 2015 there was a clear reduction in NEE which was
566 maintained until the end of summer, representing a 59% NEE decrease in relation to the same
567 period of 2014 (Fig. 7a). This NEE decrease was due to a combined effect of cork stripping
568 and summer water stress induced by a lower water availability. The 50% reduction in Branch
569 Light Use Efficiency from 2015 to 2014 (Fig. 6) confirms the effects of these stresses on carbon
570 assimilation metabolism. Although these two stress effects on NEE are difficult to disentangle,
571 from May to early June, before entire site cork harvesting, there was already a 39% lower
572 carbon uptake in 2015 in relation to 2014, which can be solely attributed to the lower soil water
573 availability. This cause-effect association in this period is evidenced by the concomitant 60%
574 lower sapflow rates in 2015 compared to 2014 (Fig. 5). However, it is worth mentioning that
575 in 2015, from cork stripping days to middle of July, control trees (not cork stripped) maintained
576 stable sapflow rates (Fig. 5). Considering the well-known trade-off of water for carbon (e.g.
577 Sperry *et al.*, 2017), this clearly indicates that the observed decrease in NEE in this period,
578 when all ecosystem trees were cork harvested, should not be ascribed to the dry season
579 progressive decline in soil water availability but only to the effect of cork stripping. Therefore,
580 we can reliably estimate the cork stripping effect on NEE in this period. Cork stripping stress
581 effects were particularly significant in a short-term phase of approximately 10 days which led
582 to a NEE decline of 73% in relation to the June period before cork stripping. After this short
583 period NEE partially recovered until middle of July being 38% lower than the initial June NEE
584 values (Fig. 8). This cork stripping induced decline on ecosystem carbon uptake can be

585 estimated as a reduction of 41.6 g C m^{-2}, which correspond to 16% of the yearly NEE or 32%
586 of total summer (June-September) carbon sequestration. After this period and until the onset
587 of autumn rains the ecosystem productivity decreased progressively (Fig. 7b) due to a severe
588 reduction in water availability. In fact, we can suggest that in this late summer period, the
589 decrease in NEE in comparison to 2014 can be ascribed predominantly to the effects of soil
590 water deficits. This is supported by the same magnitude values of carbon sequestration
591 exhibited for July and August in a similar dry year (2012 with 420 mm precipitation), with a
592 NEE of -66 *vs*. -61 g C m^{-2} in 2012 and 2015, respectively (Costa e Silva *et al.*, 2015).

593

594 ## *5. Conclusions*

595 In summary, the effects of cork oak bark stripping in tree water and carbon fluxes were clearly
596 shown here for the first time. We have demonstrated that cork is a very low demanding tissue
597 as reflected by its low carbon costs in relation to the tree NPP (1.5% on a yearly basis) and low
598 nutrient content. Additionally, our results clearly show that the quantity of water evaporating
599 from the stripped stem surfaces is not significant in terms of summer tree water balance: *ca*.
600 2% in comparison to canopy transpiration. Cork stripping induced an increase in midday leaf
601 water potential and a decrease (46%) on sap flow in the dry year. This suggests that stripping
602 may trigger an enhanced stomatal closure through an interaction between stripping traumatic
603 effects and soil water scarcity. Although the drought stress effects on carbon sequestration are
604 more prominent than the cork stripping ones, this superimposed stress led to a significant
605 reduction of early summer carbon uptake (*ca*. 32% of summer NEE in 2015) in a period of
606 maximum physiological tree activity. A lower quantity of available photoassimilates can have
607 a (difficult to estimate) detrimental effect on vital growth metabolism, storage of carbon
608 reserves and production of biochemical defence compounds. These effects can be especially

609 critical to more vulnerable trees, growing near their vitality breakdown threshold. Regarding
610 cork oak woodland management and considering the effects of cork stripping on tree
611 physiology, this forest practice should be avoided in severe dry years and in the more stress-
612 prone trees. The present work adds novel insights on how ecosystem carbon sequestration and
613 tree water balance are affected by cork harvesting.

614

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623

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