Respiratory costs of woody tissues in a *Quercus pyrenaica* coppice

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Long-term coppicing leads to the development of massive root systems. A disproportionate carbon investment in root maintenance has been pointed as a cause of the widespread decline of abandoned coppices. We aimed at assessing how coppicing has influenced root and shoot development and related carbon loss ascribed to maintenance of woody tissues in *Quercus pyrenaica*. For this goal, results from published studies on root dynamics, woody biomass and respired CO₂ fluxes in an abandoned *Q. pyrenaica* coppice were integrated and extended to quantify overall respiratory expenditures of above- and below-ground woody organs. Internal and external CO₂ fluxes together with soil CO₂ efflux were monitored in eight stems from one clone across a growing season. Stems and roots were later harvested to quantify the functional biomass and scale up root and stem respiration (Rₛ and Rₛ, respectively) to the clone and stand levels. Below- and above-ground biomass was roughly equal. However, the root-to-shoot ratio of respiration (Rₛ/Rₛ) was generally below one. Relatively higher Rₛ suggests enhanced metabolic activity aboveground during the growing season, and highlights an unexpected but substantial contribution of Rₛ to respiratory carbon losses. Moreover, soil and stem CO₂ efflux to the atmosphere in *Q. pyrenaica* fell in the upper range of reported rates for various forest stands distributed worldwide. We conclude that both Rₛ and Rₛ represent an important carbon sink in this *Q. pyrenaica* abandoned coppice. Comparatively high energetic costs in maintaining multiple stems per tree and centennial root systems might constrain aboveground performance and contribute to coppice stagnation.

Keywords: Carbon Loss, CO₂ Fluxes, Coppice Stagnation, Oak, Resprouting Species, Root Respiration, Stem Respiration

Introduction

*Quercus pyrenaica* Willd. is a vigorous root-resprouting species that has been intensively coppiced for firewood, charcoal and woody pastures for centuries (Ruiz de la Torre 2006). Due to the appearance of new energy sources and rural exodus that occurred in the 1970s, coppicing has mostly ceased, and symptoms of decline - slow stem growth, branch dieback, and scarce acorn production - are widely observed in abandoned stands (Serrada & Bravo 2012). Coppice stagnation entails ecologic, economic and social problems, namely increased fire risk, stand over-aging, low productivity, absence of sexual regeneration, and consequently, hindered application of alternative management plans. Due to the wide distribution and significant ecological value of coppiced stands of Mediterranean oak species, silviculture faces the crucial challenge of finding new alternative uses for these abandoned coppices (Cañellas et al. 2004, Bravo et al. 2008). Attempts to conversion into high forests via thinning have not been successful to date, partly due to the lack of a comprehensive understanding of the physiological mechanisms underpinning tree stagnation (Salomón et al. 2017).

Disproportionate respiratory costs of large root systems grown after centennial coppicing have been suggested as a potential driver of *Q. pyrenaica* decay (Bravo et al. 2008), but assessments on carbon expenditures have not been essayed to date. Quantification of the relative weight of respiratory carbon sinks for the plant is crucial for a better understanding of tree carbon budgets (Waring et al. 1998, Amthor 2000, Rambal et al. 2014). Notwithstanding, our comprehension of respiratory processes, particularly of woody organs, is limited compared to our knowledge of photosynthesis (Guidolotti et al. 2013, Rambal et al. 2014, Huntingford et al. 2017). In resprouting deciduous species, nonstructural carbohydrates are stored in large amounts in woody organs (Bond & Midgley 2001) that can contain a large portion of living parenchyma (Rodríguez-Calcerrada et al. 2015). The penalty in terms of respiratory carbon loss associated to the maintenance of these storage tissues (Landhäusser & Lieffers 2002, Drake et al. 2009) could be of particular relevance in carbon budgets of root-resprouting *Q. pyrenaica*. Long lasting coppicing might lead to massive systems of living roots (Salomón et al. 2016a, Vrška et al. 2016) that store but also consume a large portion of carbohydrates assimilated aboveground.

To better understand the role of respiratory carbon loss in *Q. pyrenaica* decay, we gathered and extended previous published...
work on Q. pyrenaica biomass and respiration of woody tissues (Salomón et al. 2015, 2016a, 2016b, 2016c) to scale up stem and root respiration (R_{s} and R_{r}, respectively) to the tree and stand levels. We aimed at comparing respiratory expenditures (i) between above- and below-ground woody organs across one growing season, and (ii) in relation to data gathered from various forests to provide an insight of the magnitude of carbon invested for woody tissue respiration in Q. pyrenaica coppices. We expect R_{s} and particularly R_{r} to be important carbon sinks for the plant (i.e., from the plant perspective), and therefore high R_{s}/R_{r} ratios as well as woody tissue respiration rates relative to other forest stands.

**Materials and methods**

To estimate respiratory carbon loss of woody organs in a coppice system of Q. pyrenaica, we reviewed our previous work on Q. pyrenaica root development and biomass (Salomón et al. 2016a), and internal and external stem CO\(_{2}\) fluxes (Salomón et al. 2015, 2016b, 2016c), together with unpublished data of soil CO\(_{2}\) efflux. These studies were performed in a one-hectare experimental plot located in the Monte Matas de Valsaín (Segovia, Spain) at an altitude of 1140 m a.s.l. Climate is sub-Mediterranean with an average annual rainfall and temperature of 885 mm and 10 °C, respectively. It consists on a monospecific one-storied regular coppice of Q. pyrenaica with a stand density of 781 stems ha\(^{-1}\). The forest has been subjected to coppicing since at least the XII century, and traditional management was abandoned in the 1970s.

Stems within the plot were geo-referenced and leaves collected for genetic analyses to delineate the commonly inconspicuous clonal structure of Q. pyrenaica coppiced stands. Note that Q. pyrenaica is a root resprouting species, hence one clone can be constituted by several stems located far away (dozens of meters) from each other (Valbuena-Carabaña & Gil 2017). The clonal assignment of stems was based on nuclear microsatellite molecular markers (Valbuena-Carabaña & Gil 2013 – see Fig. 1 in Salomón et al. 2015). Data on woody tissue respiration was collected from the eight stems belonging to a single clonal genotype (clone). Four 24-h measurement campaigns were conducted across the growing season of 2013, at the end of which stems and roots were harvested for biomass quantification and scaling up of R_{s} and R_{r} to the clone and stand levels. The root system was hydraulically excavated with a high-pressure water pump down to 1 m depth over an area of 81 m\(^{2}\) (Fig. 1). Biomass was partitioned into leaves, branches, stems, taproots, coarse roots and fine roots. Woody biomass was further partitioned into bark, sapwood and heartwood tissues from allometric equations adjusted by means of exhaustive sampling of branches, stems, taproots and coarse roots. Leaf area index (LAI) was estimated from measurements of specific leaf area of sampled leaves and total leaf biomass. Further details on stand characteristics, excavation methodology, and above- and below-ground biomass measurements can be seen in Salomón et al. (2016a).

Stem CO\(_{2}\) efflux to the atmosphere (E_{s}) was measured in every stem with a portable infrared gas analyzer (LI-6400\(^{\circ}\), Li-Cor Inc., Lincoln, NE, USA) and a soil chamber (LI-6400-09\(^{\circ}\)) using PVC collars attached to the stems. Stem E_{s} measured on a surface area basis (E_{s,S}) was expressed on a volume basis (E_{s,V}) – eqn. 1:

\[
E_{s,V} = E_{s,S} \frac{V}{S} = \frac{2 \pi r_{S}^{2} \pi L}{\pi \left(r_{S}^{2} - r_{L}^{2}\right) L} = \frac{2 \pi r_{S}^{2}}{r_{S}^{2} - r_{L}^{2}}
\]

where S and V are the axial surface area and the volume of living tissues (bark and sapwood) of the stem segment, respectively; r_{s} and r_{L} denote the radius of heartwood and heartwood plus living tissues, respectively, and L is the vertical length of the stem segment (Salomón et al. 2016c).

Stem respiration (R_{s}) was estimated as the sum of E_{s,V} and the internal CO\(_{2}\) flux through xylem (F_{x}) as R_{s} = E_{s,V} + F_{x} (adapted from McGuire & Teskey 2004). F_{x} was calculated as a function of the sap flux and the vertical gradient of CO\(_{2}\) dissolved in sap solution (sap [CO\(_{2}\)]\(^{-}\)). Sap flux density was measured using Granier-type thermal dissipation probes, and sap [CO\(_{2}\)]\(^{-}\) was estimated from measurements of xylem [CO\(_{2}\)] in the gas phase, sap temperature, and sap pH in each stem applying Henry’s law. Briefly, xylem [CO\(_{2}\)] was measured with solid non-dispersive infrared (NDIR) CO\(_{2}\) sensors (model GMM221, Vaisala, Helsinki, Finland) inserted into the stem above and below the stem collar. Stem temperature was measured with type-T thermocouples inserted 5 cm away from the NDIR probe. Sap pH was measured with a micro-pH electrode and a portable pH meter (Crison, Barcelona, Spain) on sap samples expressed from detached twigs using a pressure chamber (see Salomón et al. 2016b for further details). Overall, E_{s}, F_{x}, and R_{s} at the clone level were estimated by aggregating E_{s}, F_{x}, and R_{s} scaled up for each stem (and their branches) according to their corresponding volume of living woody biomass. Aboveground clonal respiratory fluxes were eventually expressed on a soil surface area basis taking into account the clonal surface extension.

Soil CO\(_{2}\) efflux (E_{s}) was measured with a portable infrared gas analyzer and a soil chamber using soil PVC collars (see Salomón et al. 2015 for detailed methodology). Unpublished data from four soil collars located below the canopy of the eight monitored stems were averaged to obtain clonal E_{s} on a soil area basis (m\(^{2}\)). Since roots barely extended beyond the excavated area (81 m\(^{2}\)), a buffer of 0.63 m was added to estimate the clone extension (102 m\(^{2}\)). This buffer distance was chosen to meet actual stand density (8 stems in 102 m\(^{2}\) = 784 stems ha\(^{-1}\)) and scale up results to the stand level. Root-respired CO\(_{2}\) diffusing to the atmosphere through soil (E_{s,root}) was estimated from E_{s}, measurements and the relative contribution of autotrophic respiration to E_{s}. Seasonality of root autotrophic contribution to E_{s} was obtained.
from two studies in a Mediterranean Quercus cerris coppice cut one (Rey et al. 2002) and 17 (Tedeschi et al. 2006) years before measurements. Spring contributions reported in these studies were attributed to the first measurement campaign (DOY 143-144), summer contributions to the second (DOY 183-184) and third (DOY 218-219) campaigns, and autumn contributions to the fourth campaign (DOY 266-267). To account for \( F_T \) on \( R_E \) estimates (\( R_E = E_{\text{ROOT}} + F_T \) – Aubrey & Teskey 2009), internal and external CO\(_2\) fluxes were measured at the base of the stem (0.1 m).

To compare \( E_B \), \( R_E \) and \( R_S \) averaged over the growing season within the monitored clone, ANOVA and pairwise comparisons were performed in R software (version 3.4.0). Respiratory fluxes at the stand level from 15 sites were gathered (Tab. 5i in Supplementary material) to evaluate the relative magnitude of respiratory costs of the surveyed Q. pyrenaica copice. Inter-site statistical comparisons were not performed because only one site was surveyed in this study.

**Results and discussion**

Seasonal and diel variation in \( E_B \), \( F_T \) and \( E_S \) on a soil area basis are shown in Fig. 2. The contribution of \( F_T \) to aboveground \( R_A \) was less than 10% (Salomón et al. 2016c), whereas \( F_T \) belowground was less than 2% of \( E_{\text{ROOT}} \) (Salomón et al. 2015). The modest contribution of axial CO\(_2\) transport to total respiration rates is explained by the low xylem [CO\(_2\)] observed in Q. pyrenaica, generally lower than 1%. This concentration is about one order of magnitude lower than that reported for other tree species using this methodology (Teskey et al. 2008). The limited build-up of CO\(_2\) in the xylem was partly ascribed to the low resistance to radial CO\(_2\) diffusion, likely related to the poor plant water status of species distributed across drought-prone regions (Salomón et al. 2016b). Averaged over the growing season, \( E_S \) (38.9 mol CO\(_2\) per stem clone day\(^{-1}\)) was greater than \( R_A \) (17.7 mol CO\(_2\) per stem clone day\(^{-1}\)) and \( R_S \) (8.5 mol CO\(_2\) per stem clone day\(^{-1}\)) – \( P < 0.001; \) Tab. 1, Fig. 2), being \( R_A \) and \( R_S \) not significantly different (\( P > 0.10 \)). Due to the magnitude of \( E_S \), the contribution of autotrophic respiration to \( E_S \) substantially determined the root-to-shoot ratio of respiration (\( R_A/R_S \)). To illustrate this, a contribution of \( R_S \) to \( E_S \) ranging between 14 and 27% (Rey et al. 2002, Tedeschi et al. 2006 – data reported for a Mediterranean oak coppice at different stages of maturity) yielded \( R_A/R_S \) ratios ranging between 0.42 and 1.8 across the growing season (Tab. 1). Alternatively, if heterotrophic and autotrophic contributions to \( E_S \) were considered equal, as generally assumed for different forest biomes (Hanson et al. 2000, Aubrey & Teskey 2009), \( R_A/R_S \) would reach values ranging from 1.36 to 2.18.

Above- and below-ground functional woody biomass (bark and sapwood) was similar in the surveyed clone: 1026 Kg aboveground and 972 Kg belowground (Salomón et al. 2016a). Consequently, seasonal deviations of \( R_A/R_S \) from unity reflected differences in the metabolic activity between below- and above-ground organs over time. \( R_A/R_S \) ratio above one was uniquely observed during spring (Tab. 1), likely explained by an earlier growth of roots relative to stems (López et al. 2001), particularly by intense fine root growth and belowground cambial activity at this time of the year (Courty et al. 2007). The decrease in \( R_A/R_S \) observed onward (ratios below one) resulted from the moderate root activity relative to the intensification of aboveground metabolism, namely stem growth, leaf development and phloem transport. Predominant \( R_A/R_S \) ratios below one along the growing season evidence an unexpected large weight of aboveground woody tissue respiration as a carbon sink for the plant. The accumulation of woody biomass in stems and branches in this over-aged coppice (cut for the last time around 1967), together with the remarkably high portion of living parenchyma observed in Q. pyrenaica stems (Rodríguez-Calcerrada et al. 2015) may contribute to the high respiratory costs of woody organs aboveground.

Respiratory fluxes at the stand level, and extrapolated to the whole year, were compared with those reported for several forest sites (see Tab. 5i in Supplementary material for details on the extrapolation). Average \( E_S \) and \( E_A \) across 15 stands were 776 mol CO\(_2\) per stem per day, whereas average \( R_A \) and \( R_S \) were 168 mol CO\(_2\) per stem per day. The accumulation of CO\(_2\) efflux to the atmosphere (\( E_A \)) and stem internal CO\(_2\) transport through xylem (\( F_T \)) and soil CO\(_2\) efflux (\( E_S \)) on four dates over the growing season in an abandoned coppice of Quercus pyrenaica. Fluxes registered from one stem segment and one soil collar intensively monitored (18 times day\(^{-1}\)) are shown. Additional stem segments and collars used to average \( E_A \), \( F_T \) and \( E_S \) are not displayed in this figure as they were monitored less intensively (4 times day\(^{-1}\)). \( E_A \) and \( F_T \) on a volume basis was obtained from previous work (Salomón et al. 2016c) and expressed on a soil area basis for comparison with \( E_S \). Shaded areas indicate night-time.

**Tab. 1** Above- and below-ground respiratory fluxes in an eight-stemmed clone of Quercus pyrenaica. Stem CO\(_2\) efflux to the atmosphere \( (E_A) \), soil CO\(_2\) efflux \( (E_S) \) and stem and root respiration \( (R_A \) and \( R_S \) respectively) were measured during four 24-h campaigns throughout 2013 growing season. (a): \( R_A \) was estimated as the sum of \( E_S \) and the internal CO\(_2\) flux through xylem \( (F_T) \). (b): \( R_S \) was estimated from \( E_A \) measurements and the contribution of autotrophic respiration to \( E_A \). Autotrophic contribution to \( E_A \) was obtained from two reports of a Mediterranean coppice of Quercus cerris cut one (Rey et al. 2002) and 17 years (Tedeschi et al. 2006) before measurements. Estimates of \( R_S \) and \( R_A/R_S \) ratios from contributions reported in both studies (recently coppiced vs mature stand) are shown in left and right sub-columns, respectively. \( F_T \) was neglected in \( R_A \) due to its low contribution (< 2%).
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References

Amthor J (2000). The McCree-de Wit-Penning
of Vries-Thornley respiration paradigms: 30 years
later. Annals of Botany 86: 1-20. - doi: 10.1006
anbo.2000.1175

Aubrey DP, Teskey RO (2009). Root-derived CO2
efflux via xylem stream rivals soil CO2 efflux.
New Phytologist 184: 55-40. - doi: 10.1111/j.1469-
1897.2009.02971.x

Bond WJ, Midgley JJ (2001). Ecology of sprout-
ing in woody plants: the persistence niche.
Trends in Ecology and Evolution 16: 45-51. - doi: 10.1016/S0169-5347(00)02033-4

Bravo JA, Roig S, Serrada R (2008). Selvicultura en montes bajos y medios de Quercus ilex L., Q.
pyrenaica Willd. y Q. faginea Lam. [Sylviculture in Quercus ilex L., Q. pyrenaica Willd. and Q. fagi-
nea Lam. coppices]. In: “Compendio de Selvicultura aplicada en España [Compendium of applied silviculture]” (R Serrada, G Montero eds). Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, Spain, pp. 657-744. [In Spanish]

Brióna N (2003). Ground-based measurements of leaf area index: a review of methods, instru-
ments and current controversies. Journal of Ex-
perimental Botany 54: 2403-2417. - doi: 10.1093/jexb/gje263

Cañellas I, Del Río M, Roig S, Montero G (2004). Growth response to thinning in Quercus pyre-
nea Willd. coppice stands in Spanish central mountain. Annals of Forest Science 61: 243-250. - doi: 10.1051/forest:20040407

Carruca L, Camarero JJ, Siso S, Gil-Pelegrín E (2006). Radial-growth and wood-anatomical
changes in overaged Quercus pyrenaica coppice stands: functional responses in a new Mediter-
nanean landscape. Trees 20: 91-98. - doi: 10.1007/s00468-005-0016-4

Courty PE, Brédà N, Garbaray J (2007). Relation between oak tree phenology and the secretion
of organic matter degrading enzymes by Luc-
tarius quietus ectomycorrhizas before and during
bud break. Soil Biology and Biochemistry 39: 1655-1663. - doi: 10.1016/j.soilbio.2007.01.017

Drake PL, Mendham DS, White DA, Ogden GN
(2009). A comparison of growth, photosyn-
thetic capacity and water stress in Eucalyptus globulus coppice regrowth and seedlings dur-
ing early development. Tree Physiology 29: 663-674. - doi: 10.1093/treephys/tpp006

Guidolotti G, Rey A, D’Andrea E, Matteucci G, De
Angelis P (2013). Effect of environmental vari-
ables and stand structure on ecosystem respi-
ratory components in a Mediterranean beechnut
forest. Tree Physiology 33: 960-972. - doi: 10.1093/treephys/tpo65

Hanson PJ, Edwards NT, Garten CT, Andrews JA
(2000). Separating root and soil microbial con-
tributions to soil respiration: A review of meth-
ods and observations. Biogeochemistry 48: 115-
146. - doi: 10.1023/A:10046244819642

Hernández-Santana V, Martínez-Villalta J, Martí-
nez-Fernández J, Williams M (2009). Evaluating the effect of dryer and warmer conditions on
water use by Quercus pyrenaica. Forest Ecology and Management 257: 1719-1730. - doi: 10.1016/
foreco.2009.07.038

Huntingford C, Atkin OK, Martínez de la Torre A, Mercado LM, Heskel MA, Harper AB, Bloom-
field KJ, Sullivan OS, Reich PB, Whithers KR, Butler EE, Chen M, Griffin KL, Meir Tjoelker P
MG, Turnbull MH, Sitch S, Wiltshire A, Malhi Y
(2017). Implications of improved representa-
tions of plant respiration in a changing climate.
Nature Communications 8 (1): 184. - doi: 10.1038/
s41467-017-01774-z

Landhäusser SM, Lieffers VJ (2002). Leaf area
renewal, root retention and carbohydrate re-
serves in a clonal tree species following above-
ground disturbance. Journal of Ecology 90: 658-
665. - doi: 10.1046/j.1365-2745.2002.00699.x

López B, Sabate S, Gracia CA (2001). Annual and seasonal changes in fine root biomass of
a Quercus sp. forest. Plant and Soil 230: 125-
134. - doi: 10.1023/A:1004471793777

McGuire MA, Teskey RO (2001). Estimating stem
respiration in trees by a mass balance approach
that accounts for internal and external fluxes
of CO2. Tree Physiology 24: 571-578. - doi: 10.1093/
treephys/24.5.571

Rambal S, Lepompeur M, Limousin JM, Martin-
StPaul NK, Ocurvial JM, Rodríguez-Calcedera J
(2014). How drought severity constrains gross
primary production (GPP) and its partitioning
among carbon pools in a Quercus ilex coppice?
Biogeosciences 11: 6855-6869. - doi: 10.5194/bg-
11-6855-2014

Rey A, Pegoraro E, Tedeschi V, De Parri I, Jarvis
PG, Valentini R (2002). Annual variation in soil
respiration and its components in a coppice
oak forest in Central Italy. Global Change Bio-
logy 8: 851-866. - doi: 10.1016/S0960-1295-
2002.00521.x

Rodríguez-Calcedera J, López R, Salomón R,
Gordazila G, Valbuenara-Cabaña M, Oleksyn J,
Gil L (2015). Stem CO2 efflux in six co-occurring
tree species: underlying factors and ecological
implications. Plant, Cell and Environment 38:
1104-1115. - doi: 10.1111/j.1365-2486.2014.0-
12463

Ruiz de la Torre J (2006). Flora Mayor [Major
Flora]. Organismo Autónomo de Parques Na-
ociales, Madrid, Spain, pp. 1756. [In Spanish]

Salomón R, Rodríguez-Calcedera J, Zafra E,
Morales-Molino C, Rodríguez-García A, Gon-
zález-Doncel I, Oleksyn J, Zytkowski R, López
R, Miranda JC, Gil L, Valbuenara-Cabaña M
(2016a). Unearthing the roots of degradation
of Quercus pyrenaica coppices: a root-to-shoot
imbalance caused by historical management?
Forest Ecology and Management 363: 200-211.
- doi: 10.1016/j.foreco.2015.12.040

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List of abbreviations

E Jo-L, stem CO2 efflux to the atmosphere; E
leaf, foliage CO2 efflux to the atmosphere; E
roots, root-respired CO2 that diffused to the atmosphere through soil; ER, internal CO2 flux through xylem; Rs, root respiration; Rs, stem respiration

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Calcerrada J, Aubrey D, McGuire M, Teskey R, Gil L, González-Doncel I (2015). Xylem and soil CO₂ fluxes in a Quercus pyrenaica Willd. coppice: root respiration increases with clonal size. Annals of Forest Science 72: 1065-1078. - doi: 10.1007/s13595-015-0504-7

Salomón R, Valbuena-Carabaña M, Teskey R, McGuire MA, Aubrey D, González-Doncel I, Gil L, Rodríguez-Calcerrada J (2016b). Seasonal and diel variation in xylem CO₂ concentration and sap pH in sub-Mediterranean oak stems. Journal of Experimental Botany 67: 2817-2827. - doi: 10.1093/jxb/erw121

Salomón RL, Valbuena-Carabaña M, Gil L, McGuire MA, Teskey RO, Aubrey DP, González-Doncel I, Rodríguez-Calcerrada J (2016c). Temporal and spatial patterns of internal and external stem CO₂ fluxes in a sub-Mediterranean oak. Tree Physiology 36: 1409-1421. - doi: 10.1093/treephys/tpw029

Salomón R, Rodríguez-Calcerrada J, Gil L, Valbuena-Carabaña M (2017). On the general failure of coppice conversion into high forest in Quercus pyrenaica stands: a genetic and physiological approach. Folia Geobotanica 52: 101-112. - doi: 10.1007/s11224-016-9257-9

Serrada R, Bravo JA (2012). Mejora de la vitalidad de las masas [Improvement in stand vitality]. In: “Gestión adaptativa al cambio global en masas de Quercus mediterráneas [Adaptive management to global change in Mediterranean Quercus stands]” (P Vericat, M Piqué, R Serrada eds). Centre Tecnològic Forestal de Catalunya, Solsona, Lleida, Spain, pp. 49-66. [in Spanish]

Tesedchi V, Rey A, Manca G, Valentini R, Jarvis PJ, Borghetti M (2006). Soil respiration in a Mediterranean oak forest at different developmental stages after coppicing. Global Change Biology 12: 110-121. - doi: 10.1111/j.1365-2486.2005.01081.x

Teskey RO, Saveyn A, Steppe K, McGuire MA (2008). Origin, fate and significance of CO₂ in tree stems. New Phytologist 177: 17-32. - doi: 10.1111/j.1469-8137.2007.02286.x

Valbuena-Carabaña M, Gil L (2017). Centenary coppicing maintains high levels of genetic diversity in a root resprouting oak (Quercus pyrenaica Willd.). Tree Genetics and Genomes. 13: 28.

Vrška T, Janík D, Pálková M, Adam D, Trochta J (2016). Below- and above-ground biomass, structure and patterns in ancient lowland coppices. iForest - Biogeosciences and Forestry 10: 23-31. - doi: 10.3832/ifor1839-009

Waring R, Landsberg J, Williams M (1998). Net primary production of forests: a constant fraction of gross primary production? Tree Physiology 18: 129-134. - doi: 10.1093/treephys/18.2.129

Supplementary Material

Tab. S1 - Stand density, leaf area index (LAI) and partitioning of annual ecosystem respiration into soil (Eₛ), stem (Eₐ) and leaf (Eₐ-LEAF) CO₂ efflux to the atmosphere across different forest stands.

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