iForest
Biogeosciences and Forestry

Short Communication
doi: 10.3832/ifor2599-011
vol. 11, pp. 437-441

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 CO_2 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 CO_2 fluxes together with soil CO_2 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 (R_R and R_S, respectively) to the clone and stand levels. Below- and above-ground biomass was roughly equal. However, the root-to-shoot ratio of respiration (R_R/R_S) was generally below one. Relatively higher R_S suggests enhanced metabolic activity aboveground during the growing season, and highlights an unexpected but substantial contribution of R_S to respiratory carbon losses. Moreover, soil and stem CO_2 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 R_S and R_R 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, CO_2 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

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Received: Aug 11, 2017 - Accepted: Apr 09, 2018

Citation: Salomón RL, Rodríguez-Calcerrada J, Gil L, Valbuena-Carabaña M (2018). Respiratory costs of woody tissues in a *Quercus pyrenaica* coppice. iForest 11: 437-441. - doi: 10.3832/ifor2599-011 [online 2018-06-18]

Communicated by: Giorgio Matteucci

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_R/R_S 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_A) was measured in every stem with a portable infrared gas analyzer (LI-6400®, Li-Cor Inc., Lincoln, NE, USA) and a soil chamber (LI-6400-09®) using PVC collars attached to the stems. Stem E_A measured on a surface area basis ($E_{A(S)}$) was expressed on a volume basis ($E_{A(V)}$ – eqn. 1):

$$E_{A(V)}=E_{A(S)}\frac{S}{V}= =E_{A(S)}\frac{2\pi r_{h+l}L}{\pi\left(r_{h+l}^2-r_h^2\right)L}=E_{A(S)}\frac{2r_{h+l}}{\left(r_{h+l}^2-r_h^2\right)} \quad (1)$$

where *S* and *V* are the axial surface area and the volume of living tissues (bark and sapwood) of the stem segment, respectively; r_h and r_{h+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 $E_{A(V)}$ and the internal CO_2 flux through xylem (F_T) as $R_S = E_A + F_T$ (adapted from McGuire & Teskey 2004). F_T 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_A, F_T and R_S at the clone level were estimated by aggregating E_A, F_T 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 ($E_{S\text{-ROOT}}$) 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

Fig. 1 - Root systems of two hydraulically excavated clones of *Quercus pyrenaica* located in the *Monte Matas de Valsaín* (Segovia, Spain). The root system of the large clone surveyed in this study (lower part of the photograph) covered at least 81 m^2. Before harvesting, the clone was composed by eight stems connected through root grafts and parental roots.

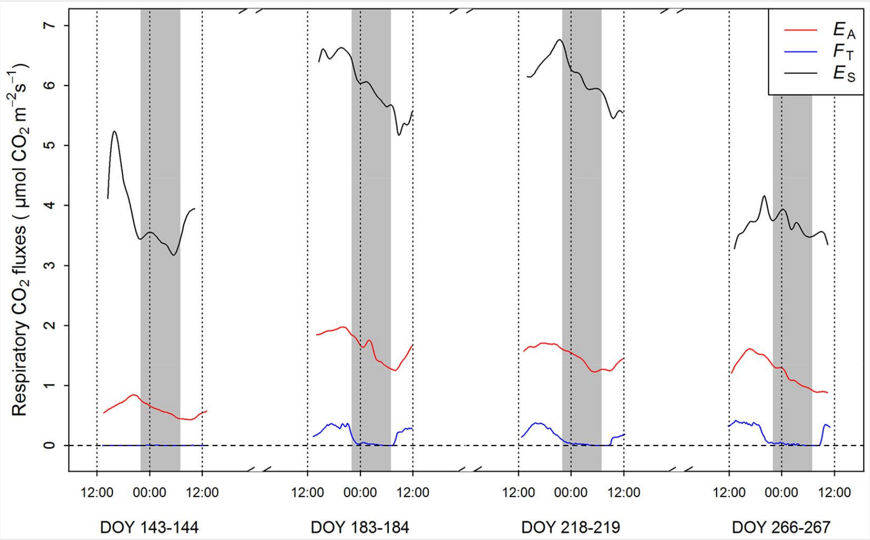

Fig. 2 - Diel variations in stem CO$_2$ efflux to the atmosphere (E_A), stem internal CO$_2$ transport through xylem (F_T) and soil CO$_2$ efflux (E_S) on four dates over the growing season in an abandoned coppice of *Quercus pyrenaica*. Fluxes registered from one stem segment and one soil collar intensively 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.

from two studies in a Mediterranean *Quercus cerris* coppice cut one (Rey et al. 2002) and 17 (Tedeschi et al. 2006) years before E_S 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_R estimates ($R_R = E_{S\text{-ROOT}} + F_T$ – Aubrey & Teskey 2009), internal and external CO$_2$ fluxes were measured at the base of the stem (0.1 m).

To compare E_S, R_R 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. S1 in Supplementary material) to evaluate the relative magnitude of respiratory costs of the surveyed *Q. pyrenaica* coppice. 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_A, F_T and E_S on a soil area basis are shown in Fig. 2. The contribution of F_T to aboveground R_S was less than 10% (Salomón et al. 2016c), whereas F_T belowground was less than 2% of $E_{S\text{-ROOT}}$ (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$_2$ clone^{-1} day^{-1}) was greater than R_S (11.7 mol CO$_2$ clone^{-1} day^{-1}) and R_R (8.5 mol CO$_2$ clone^{-1} day^{-1} – $P < 0.001$; Tab. 1, Fig. 2), being R_S and R_R 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_R/R_S). To illustrate this, a contribution of R_R 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 states of maturity) yielded R_R/R_S ratios ranging between 0.42 and 1.18 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_R/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_R/R_S from unity reflected differences in the metabolic activity between below- and above-ground organs over time. R_R/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_R/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_R/R_S ratios below one along the growing season evidenced 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. s1 in Supplementary material for details on the extrapolation). Average E_S and E_A across 15 stands were 776

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_S and R_R, respectively) were measured during four 24-h campaigns throughout 2013 growing season. (a): R_S was estimated as the sum of E_A and the internal CO$_2$ flux through xylem (F_T). (b): R_R was estimated from E_S measurements and the contribution of autotrophic respiration to E_S. Autotrophic contribution to E_S 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. Estimations of R_R and R_R/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_R due to its low contribution (< 2%).

Campaign DOY	**E_A**	**R_S $^{(a)}$**	**E_S**	**R_R $^{(b)}$**	**R_R/R_S**
	(mol CO$_2$ clone^{-1} day^{-1})				
143-144	6.16	6.16	26.83	5.03 *vs* 7.25	0.82 *vs* 1.18
183-184	12.28	13.13	52.14	11.32 *vs* 11.70	0.86 *vs* 0.89
218-219	15.63	16.45	43.72	9.49 *vs* 9.82	0.58 *vs* 0.60
266-267	10.54	11.23	32.76	8.82 *vs* 4.68	0.79 *vs* 0.42
Mean	*11.15*	*11.74*	*38.86*	*8.66 vs 8.36*	*0.76 vs 0.77*

and 162 g C m^{-2} $year^{-1}$, respectively, whereas these values increased up to 1164.2 and 297.0 g C m^{-2} $year^{-1}$ in the surveyed *Q. pyrenaica* coppice (Tab. S1). That is, E_S and E_A were 1.5 and 1.8 times higher in this study, suggesting greater carbon losses from soil and stem respiration. These ratios could be substantially reduced, however, if xylem transport of respired CO_2 was accounted for (Aubrey & Teskey 2009) in the 15 forest stands. Leaf area index, a key ecophysiological determinant of carbon gas exchange at the canopy (Bréda 2003), was additionally considered for comparison. LAI in our site was 3.8, a value that falls within the reported range for the species (Hernández-Santana et al. 2009) and the genus *Quercus* (Bréda 2003). The slightly low LAI relative to that averaged across different forest types (4.2 – Tab. S1 in Supplementary material) does not suggest a greater potential for carbon assimilation. Taken together, these rough comparisons suggest a strong carbon sink for the plant associated to respiratory processes that do not scale with the carbon input within the surveyed *Q. pyrenaica* coppice.

To summarize, the relative importance of R_R and R_S as carbon sinks for the plant shifted along the growing season in accordance to the root and stem phenology and metabolic activity. R_R/R_S ratios lower than one point to an unexpected importance of aboveground woody tissue respiration in carbon budgets of *Q. pyrenaica* coppices. Large carbon losses *via* soil and stem respiration relative to those observed in several forest types supports the hypothesis of an imbalance between carbon sources and sinks, contributing to the decline of abandoned coppices (Corcuera et al. 2006, Salomón et al. 2015, 2016a). Nonetheless, these conclusions should be handled with caution due to the lack of data on carbon assimilation, and the limited sample size of the study, largely constrained by the laborious task of root excavation. Firstly, temporal patterns of leaf carbon exchange should be analyzed in detail to gain a comprehensive perspective of tree carbon budgets and to better address the role of a potential root-to-shoot physiological imbalance in *Q. pyrenaica* coppice decline. Secondly, a greater number of monitored individuals as well as soil collars within the plot and across longer periods would improve spatial and temporal upscaling of respiratory fluxes. In this line, comparisons between coppiced and non-coppiced sites would provide stronger empirical support to the hypothesis that historical coppicing leads to massive root development and constrained aboveground performance.

List of abbreviations

E_A, stem CO_2 efflux to the atmosphere; $E_{A\text{-}LEAF}$, foliage CO_2 efflux to the atmosphere; E_S, soil CO_2 efflux; $E_{S\text{-}ROOT}$, root-respired CO_2 that diffused to the atmosphere through soil; F_T, internal CO_2 flux through xylem; R_R, root respiration; R_S, stem respiration

Acknowledgements

We are grateful to Javier Donés (*Centro de Montes y Aserradero de Valsaín*) for economic and logistical support. We also thank Elena Zafra, Guillermo González, César Otero, Manuel Iglesias, Paula Guzmán, Aida Rodríguez, Jose Carlos Miranda, Rosa Ana López, Eva Miranda and Matías Millerón for their enthusiastic help with field work. This work was funded by the *Comunidad de Madrid* through CAM P2009/AMB-1668 and S2013/MAE-2760 projects and by the *Organismo Autónomo de Parques Nacionales* through the PPNN 1148/2014 project. Roberto L. Salomón was supported by a Ph.D. scholarship from the *Universidad Politécnica de Madrid*.

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Supplementary Material

Tab. S1 - Stand density, leaf area index (LAI) and partitioning of annual ecosystem respiration into soil (E_S), stem (E_A) and leaf ($E_{A\text{-LEAF}}$) CO_2 efflux to the atmosphere across different forest stands.

Link: Salomon_2599@suppl001.pdf