



Testing root trenching and stem girdling as silvicultural treatments in abandoned oak coppices

Roberto L. Salomón^{a,*}, José Carlos Miranda^a, Álvaro Rubio-Cuadrado^{a,b}, Juan Sobrino-Plata^{a,c}, Jesús Rodríguez-Calcerrada^a, Rosana López^a, Luis Gil^a, María Valbuena-Carabaña^a

^a Departamento de Sistemas y Recursos Naturales, Research Group FORESCENT, Universidad Politécnica de Madrid, Jose Antonio Novais 10, 28040 Madrid, Spain

^b Instituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, 50080 Zaragoza, Spain

^c Departamento de Genética, Fisiología y Microbiología, Facultad de CC. Biológicas, Universidad Complutense de Madrid, Jose Antonio Novais 12, 28040 Madrid, Spain

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ABSTRACT

Widespread tree growth decline and absence of acorn production are observed in formerly coppiced *Quercus pyrenaica* stands. Attempts to convert oak coppices into high forests by thinning have failed to date, possibly due to the massive root system developed by trees after centuries of coppicing. We tested root trenching and stem girdling as silvicultural treatments to mitigate this hypothetical root-to-shoot imbalance and enhance the physiological performance of multi-stemmed clonal trees. We expected that severing the roots within a clone by trenching would reduce root respiratory carbon losses. Alternatively, stem girdling would increase carbon availability above the girdled zone, whilst the communal root system is maintained by non-girdled stems. After clonal structure delineation in a one-hectare experimental plot, root trenching and stem girdling were applied to stems belonging to different clones. Twig hydraulic traits, leaf water potential, non-structural carbohydrates (NSC) concentration in twigs, stems and roots, stem xylem [CO₂] as an indicator of root respiration, stem growth, and acorn production were discretely monitored up to 12 years after treatment application for comparison with control stems. Stem girdling led to short-term enhancements in NSC pools above the girdled zone. However, hydraulic dysfunction symptoms and canopy dieback were observed four years after girdling, eventually causing mortality. Root trenching initially increased root respiration and reduced stem growth without an apparent decline in the hydraulic function and NSC pools above-ground. Ten years after trenching, stem [NSC] increased while stem growth limitations diminished. Although not statistically significant, slight enhancements in acorn production were observed 6 and 12 years after trenching. We discourage stem girdling as a silvicultural practice to mitigate a root-to-shoot imbalance in abandoned oak coppices, as long-term detrimental effects outweighed potential benefits. Root trenching enhanced tree NSC above ground. However, such improvement may not offset the potential costs of root trenching.

1. Introduction

The widespread decay of *Quercus pyrenaica* coppices and the need to find new alternative uses for these stands is one of the biggest challenges for Mediterranean forest managers (Bravo et al., 2008; Cañellas et al., 2004; Montes et al., 2004; Moreno-Fernández et al., 2020). The abandonment of traditional coppicing for firewood, charcoal and woody pastures in the 1970 s has resulted in overaged stands with high mortality rates, extremely high densities, branch dieback, growth stagnation and low acorn yield (Serrada and Bravo, 2012). Several management practices alternative to lack of intervention, such as conversion into high

forests, transformation into open woodlands, reforestation with coniferous species, and resuming coppicing, have been suggested for these stands (Bravo et al., 2008). Of those, conversion into high forests is the preferred alternative in productive sites, as it has been showed by thinning trials at different intensities, where stem growth of residual trees and fire risk reduction has been observed (Aldea et al., 2017; Cañellas et al., 2004; Lafuente et al., 2009; Montes et al., 2004; Moreno-Fernández et al., 2020). However, there is no evidence of improvement in carbohydrate availability (De Pedro et al., 2009) nor in acorn production (Cañellas et al., 1996; San Miguel, 1986), a necessary step for sexual recruitment and conversion into high forests.

* Corresponding author.

E-mail address: roberto.salomon@upm.es (R.L. Salomón).

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Historical coppicing for firewood, charcoal and pastures entailed periodical removals of above-ground biomass in this root resprouting species. Therefore, a hypothetical root-to-shoot biomass imbalance may have developed over the centuries, resulting in a physiological imbalance between carbon sinks (roots) and sources (shoots). This imbalance could be an underlying factor explaining stand decay (Bravo et al., 2008; Corcuera et al., 2006; Salomón et al., 2016a, 2013) and hindering attempts at forest conversion. Moreover, the root resprouting behavior of *Q. pyrenaica* precludes the visual delineation of multi-stemmed clones, easily identifiable in stump resprouting species, further complicating *Q. pyrenaica* management. Here, we study the effects of two practices rarely considered in forestry management to improve carbon reserves above-ground, stem growth and acorn yield: root trenching and stem girdling.

Root trenching is proposed to isolate roots from the communal root system. Historical coppicing results in massive root development (Canadell and Roda, 1991; Canellas and San Miguel, 2000; Serrada Hierro et al., 2013). Roots can store large non-structural carbohydrate (NSC) pools (Salomón et al., 2016a) but incur high root maintenance costs, which might compromise above-ground performance (Salomón et al., 2015, 2013). If the root system is a burden for stem growth and reproductive effort, root isolation by trenching could mitigate the root-to-shoot imbalance by reducing the size of the root system sustaining the trenched stem and hence carbon costs associated with root maintenance respiration. A similar idea of root partitioning has been suggested to rejuvenate and isolate resprouts in this species (Bravo et al., 2008; De Simón and Bocio, 1999). Nevertheless, to the best of our knowledge, there is no scientific literature on the physiological response of *Q. pyrenaica* or any other root resprouting species to root isolation, despite the trials performed by forest managers (Luis Gil, personal communication), whose results attain only local and specialized communities.

Stem girdling consists of removing a stripe of bark and phloem tissues and has been used to kill trees (Reque and Bravo, 2007) by impeding carbohydrate supply to the root system (Högberg et al., 2001). Nevertheless, branch girdling is a cultural practice to improve fruit set in cultivars (Rivas et al., 2007; Williams and Ayars, 2005) by enhancing carbohydrate availability in girdled branches (Iglesias et al., 2003). Similarities between branches of single-stemmed trees supported by a unique trunk and multiple stems in trees supported by a communal root system invite to test stem girdling as a non-killing treatment for seed-set improvement in root-resprouting species (Bravo et al., 2008). The girdling of a limited number of stems in a multi-stemmed clone might enhance NSC concentrations ([NSC]) above the girdled zone without causing root starvation or malfunction, assuming that the communal root system is fed with NSC from non-girdled stems (Baret and DesRochers, 2011). In the long term, stem growth and acorn yield would be improved, together with chances of sexual regeneration.

Testing silvicultural practices requires time and a comprehensive bottom-up approach to mechanistically understand forest responses to treatments at different spatiotemporal scales (Reyer et al., 2015). First, leaf-level responses affect the strength of the carbon supply, which is critical to fuel the envisaged changes at large spatial scales. Second, root respiration and NSC pools in different tree organs inform on whole-tree carbon availability to be invested for different purposes, such as growth and acorn production. Third, stem growth, canopy dieback, and acorn production are indicators of the overall tree vigor and health required for sexual regeneration and, eventually, conversion into high forests. Moreover, organ, tree and stand responses to silvicultural practices require monitoring at different time scales to evaluate whether treatment-driven changes are transient, recovering pre-treatment levels once equilibrium is restored, or whether treatment-driven changes persist over time with trees adapting to the new conditions in the long term.

This experiment aims to assess structural and functional changes of trenched and girdled stems to propose complementary treatments to

thinning (required to reduce stand density) to facilitate the conversion of abandoned *Q. pyrenaica* coppices into high forests. For this, all stems in an experimental plot of *Q. pyrenaica* were genotyped to delineate multi-stemmed clonal trees before treatment application. Then, we studied the responses to trenching and girdling of several variables up to 12 years after treatment application: (i) hydraulic traits (leaf moisture content, specific leaf area, leaf-to-sapwood area ratio, leaf water potential); (ii) root, stem and twig [NSC]; (iii) xylem [CO₂] in root-isolated stems as a proxy of root respiration (Aubrey and Teskey, 2021; Teskey and McGuire, 2007); (iv) stem growth and canopy dieback; and (v) acorn yield. Treatments were tested under the expectation that the potential improvement in carbohydrate availability would surpass, in the long run, the harmful and adverse effects caused by trenching and girdling, namely carbon investment for wound healing (Chano et al., 2015), photosynthesis reduction due to feedback inhibition (De Schepper et al., 2010; López et al., 2015) or enhanced drought stress resulting from reductions in hydraulic conductivity (Zwieniecki et al., 2004).

2. Materials and Methods

2.1. Study site, clonal assignment and treatment application

The experimental plot is located in the Guadarrama mountain range ("Monte Matas de Valsaín", Segovia, Spain) at an altitude of 1140 m and consists of a regular stand dominated by *Q. pyrenaica*. This site was traditionally managed as a coppice forest for pastures, firewood and timber production since at least the XIIth century (Manuel Valdés and Rojo y Alboreca, 1993). This traditional management was abandoned in ca. 1970 when the last cut was performed, leaving a few standards and resulting in the current stand of even-aged stems of similar size, with a diameter at breast height (DBH) ranging between 15 and 20 cm and a stand density of ca. 780 stems ha⁻¹. Historical coppicing and current abandonment have led to an irregular clonal structure (see Salomón et al., 2013 for details). The clonal assignment was performed by screening seven neutral and highly variable molecular markers (nuclear microsatellites) following protocols described by Valbuena-Carabaña et al. (2008). The probability of stems with identical genotypes coming from independent sexual regeneration events reached extremely low values; thus, clonal assignments were made without ambiguity (Valbuena-Carabaña and Gil, 2017). Once the clonal structure was known, four sets of codominant even-sized stems with similar crown vigor were selected for application of four treatments: (i) control ("C" hereafter); (ii) root trenching ("T" hereafter); (iii) stem girdling before budburst ("G₁" hereafter); and (iv) stem girdling after budburst ("G₂" hereafter). Each set initially consisted of 12 stems belonging to five clones per treatment (2–3 stems per clone; Fig. 1a).

Root trenching was performed in 2011 before leaf budburst (from day of year (DOY) 91 to 95). Trenches were 80 cm deep and 20 cm wide and performed ca. one meter away from the stem (Fig. 1b). This depth was considered sufficient for stem isolation according to previous root excavations performed at the site (Salomón et al., 2016a). Stems were root-isolated using a mechanical chainsaw trencher. A backhoe was complementarily used to facilitate root isolation in areas of exceptionally high resistance. Plastic (PVC) sheets were placed along the trenches before soil refilling to hinder root reconnection among T stems.

Stem girdling consisted of removing a 7–8 cm wide and 2–3 cm deep strip of bark until reaching the cambium layer from the whole trunk circumference, required to prevent the reattachment of the phloem, which experienced substantial growth during the weeks following girdling. Girdling (Fig. 1c) was performed in 2013 before budburst (DOY 99, G₁ treatment) and after leaf expansion (DOY 170, G₂ treatment) because the timing of the treatment application might be relevant in ring-porous species such as *Q. pyrenaica*, whose earlywood is formed before leaf budburst and unfolding (Barbaroux and Bréda, 2002; Corcuera et al., 2006). Before leaf budburst, cambium removal by girdling compromises the formation of large spring vessels to satisfy the

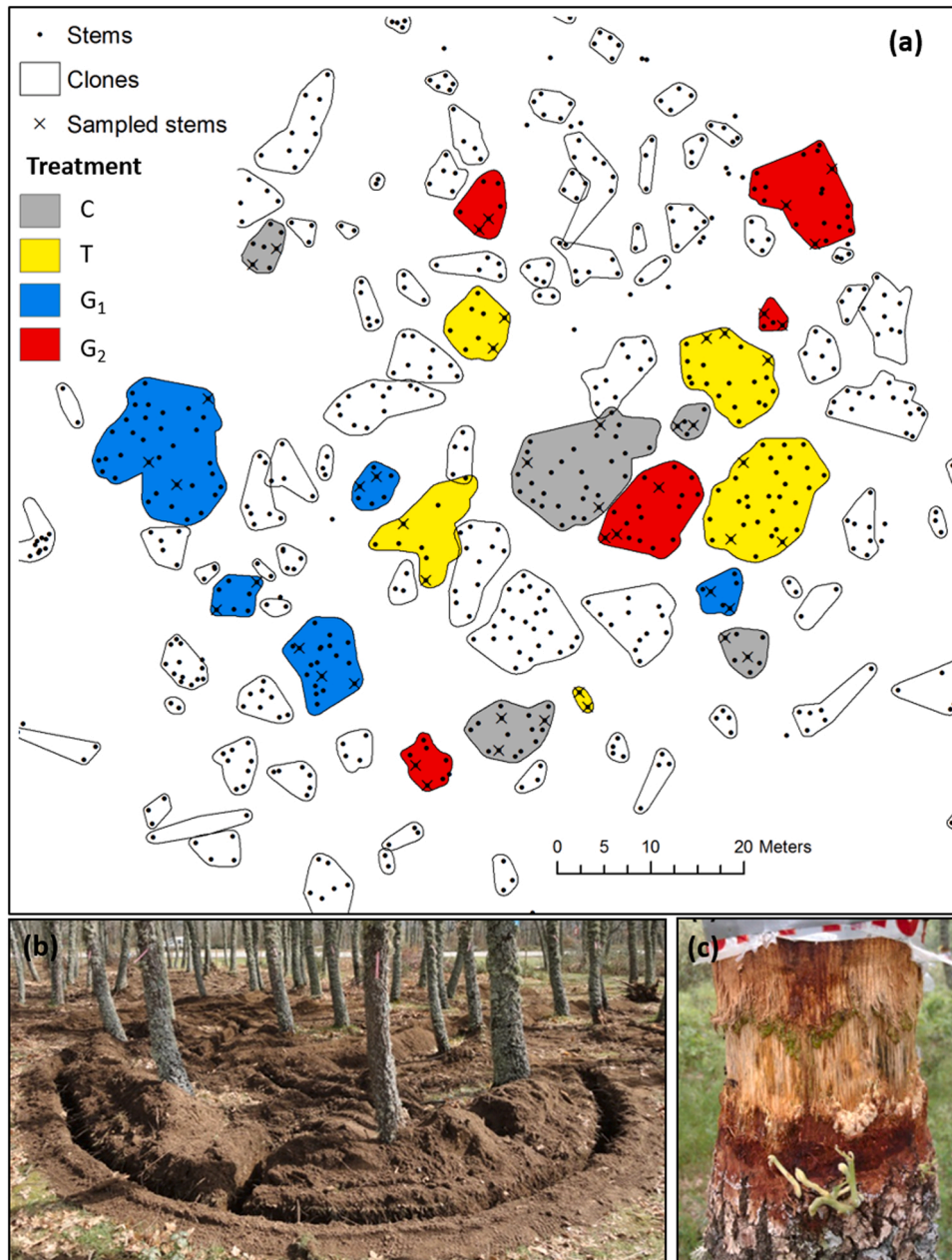


Fig. 1. Experimental design: (a) Clonal structure of the experimental plot of *Quercus pyrenaica* in Valsaín (Spain). Four sets of stems were selected for treatment application: control (C), root trenching (T), stem girdling before budburst (G_1), and stem girdling after budburst (G_2); (b, c) Photographs of the root-trenched and girdled stems.

transpiration requirements of the developing canopy. Once earlywood has been formed, and after budburst and leaf expansion, girdling might compromise the water supply to the canopy to a lesser extent. During the year of treatment application (2013), girdled stem sections were covered with Parafilm M (Pechiney Plastic Packaging, Menasha, WI) held by duct tape to minimize stem desiccation and protect the wound from pathogen invasion (De Schepper et al., 2010; Murakami et al., 2008).

Several variables related to the tree water and carbon status, from the organ to the whole stem level, were discretely measured over 12 years after treatment application (from 2011 to 2023) – see Table 1 for a list of measured variables and the schedule of the sampling campaigns (limited economic and human resources precluded more frequent and homogeneous monitoring of the variables described below). At the end of 2020, most girdled stems were dead or almost dead (see Fig. S1), and we decided to exclude G_1 and G_2 stems for further measurements.

Moreover, we took advantage of six available clones that remained intact or were trenched in 2011 (three per treatment) to increase the number of C and T stem replicates. Eight stems were added per treatment, up to a sample size of $n = 20$, to evaluate the effect of root trenching from 2020 onwards with higher statistical power.

2.2. Leaf and twig traits and canopy dieback

Leaf and twig traits were measured during the growing season at the beginning (2013) and middle (2017) of the experimental period (DOYs 241 and 201, respectively) (Table 1). Twelve stems from each of the four treatments were sampled to measure leaf moisture content (LMC), specific leaf area (SLA, leaf area/dry mass, $\text{cm}^2 \text{g}^{-1}$), leaf area-to-sapwood area (LA:SA) ratio, shoot length growth during the current year (SG_0 , mm) and the ratio of SG between current and previous year ($SG_0:SG_{-1}$).

Table 1
Schedule and sample size of treatments applied and measurements taken over the experimental period.

	2011	2012	2013	2017	2021	2023
Treatment application	T	T *	G ₁ /G ₂			
Crown dieback			T,G ₁ ,G ₂ ,C (12)	T,G ₁ ,G ₂ ,C (12)	T,C (20)	
Leaf/twig traits			T,G ₁ ,G ₂ ,C (12)	T,G ₁ ,G ₂ ,C (12)		
Water potential				T,G ₁ ,G ₂ ,C (12)	T,C (20)	
[NSC]			T,G ₁ ,G ₂ ,C (9)		T,C (20)	
Xylem [CO ₂]		T*,C* (4)	T*,C* (4)			
Stem growth					T,C (20)	
Acorn prod.				T,G ₁ ,G ₂ ,C (12)		T,C (20)

The shaded background denotes the year of treatment application and measurement campaigns. The letters indicate the treatments (T: trenching; G₁: girdling before budburst; G₂: girdling after budburst; C: control), and the numbers (in parenthesis) indicate the replicates considered within each measurement campaign (i.e. stems per treatment). For xylem [CO₂] measurements, four additional stems were measured in control (C*) and trenched clones in 2012 (T*).

One south-facing sun-exposed twig per stem was sampled at a similar height (ca. 5 m) and stored on zip-lock plastic bags containing wet paper to avoid sample drying. Plastic bags were stored in a cooler for transportation to the laboratory, kept in the refrigerator overnight, and measured the following day.

The fresh mass and the dry mass (obtained after oven-drying at 65 °C for 48 h) of one leaf per twig was weighted to the nearest 0.1 mg (Adventurer precision balance, Ohaus Corporation, NJ, USA) to calculate LMC:

$$\text{LMC (\%)} = (\text{fresh mass} - \text{dry mass}) \times 100 / \text{dry mass} \quad (1)$$

The same leaf was measured before drying using WINFOLIA image analyser software (Regent Instrument Inc., Canada) for SLA determination. For LA:SA determination, total twig LA was extrapolated by the accumulated leaf dry mass and the SLA of one leaf per twig, while twig SA was measured at the base of the debarked twig by two perpendicular diameters to the nearest 10 µm with a digital calliper, as heartwood was absent. Longitudinal twig growth was measured for the current (TG₀) and previous (TG₋₁) year to the nearest 1 mm; total TG was added in case of ramification.

Canopy dieback assessments were performed by visual inspection during the days of twig sampling (2013 and 2017, Table 1). For this, monitored stems were divided into four categories of canopy dieback (0–25%, 25–50%, 50–75% and 75–100%).

2.3. Leaf water potential

Leaf water potential (Ψ; MPa) was measured in the middle (2017) and end (2021) of the experimental period (Table 1) on sunny days during the growing season, when leaves were entirely developed. In 2017, Ψ was measured in situ at predawn (before 06:00 h) and midday (14:00 h) for the four treatments (n = 12). In 2021, twigs were sampled at midday (14:00 h) for C and T treatments (n = 20), stored on zip-lock plastic bags containing wet paper to avoid sample drying, and transported to the laboratory in a cooler to be measured 2–3 h after sampling (Rodríguez-Domínguez et al., 2022). In both campaigns, as for leaf and twig traits, one sun-exposed shoot per stem was sampled at a similar height, and two leaves per shoot were measured with a pressure chamber (PMS1000, PMS Instruments, Corvallis, OR, USA). A third leaf was measured if the difference between readings was above 0.2 MPa.

2.4. Non-structural carbohydrates

The concentration of non-structural carbohydrates ([NSC]) was measured at the beginning (2013) of the experimental period and in 2021 (Table 1). In 2013, [NSC] was measured on sapwood tissues of roots, stems and twigs of nine replicates from the four treatments (Table 1). Samples were collected after complete leaf expansion (DOY 170) and at the end of the growing season before leaf fall (DOY 303), when the lowest and highest [NSC] values were expected (Barbaroux et al., 2003; Salomón et al., 2016a). Coarse roots were sampled 50–100 cm away from the stem base; above-ground samples were taken at stem breast height with a Pressler borer and in one-year-old twigs with prune shears. In the case of girdled stems, stem samples were taken above the girdle. In 2021, [NSC] was uniquely measured on the stem sapwood tissues of C and T replicates (n = 20), where most of the aboveground NSC pool is allocated (Salomón et al., 2016a) and the enhancement is pursued. Samples were collected after leaf fall (DOY 320) in this year.

In 2013, samples were oven-dried (65 °C, 48 h) and powdered in methanol:chloroform:water solution (12:5:3 by volume). Soluble sugars (SS) were extracted from the obtained powder, and the residue was used for starch determination. Soluble sugars concentration ([SS]) was measured on a spectrophotometer at 625 nm wavelength after a color reaction with anthrone reagent within 30 min. Starch concentration was measured at 450 nm, following the reaction with dianisidine, after starch conversion to glucose with amyloglucosidase and further oxidation using the peroxidase-glucose oxidase complex (Oleksyn et al., 2000). In 2021, a slightly modified protocol was applied due to laboratory adjustments and following Maness (2010). Note that only measurements among treatments within the same year were compared, and we deliberately ignored interannual variability, potentially biased by non-identical protocols. Fifty milligrams of powdered dried tissues were incubated in 1 mL of 80% hot ethanol at 80 °C for extraction of SS. The insoluble material was used for starch determination after enzymatic digestion with amyloglucosidase from *Aspergillus niger* (Sigma-10115) and α-amylase from *Bacillus licheniformis* (Sigma-A4582) in 0.1 M NaAc (pH 4.5). Sugar monomers from the ethanolic extract or starch digestion were quantified by the anthrone–sulfuric acid colourimetric microassay (Laurentin and Edwards, 2003). Different concentrations of glucose:fructose:galactose mixture (5:3:2) and only glucose were used as standard curves for SS and starch determinations, respectively.

Quantification was performed by measuring both samples and standards at 630 nm on an ELx808™ Absorbance Microplate Reader (BioTek Instruments, Inc., Winooski, VT, USA). The [NSC] was expressed on a dry matter basis (%) as the sum of soluble sugars and starch concentrations.

2.5. Xylem [CO₂]

To further evaluate the effect of trenching on respiratory carbon costs and, therefore, on the stem carbon status, xylem [CO₂] was measured as a proxy of root respiration (Aubrey and Teskey, 2021, 2009; Salomón et al., 2015; Teskey and McGuire, 2007). For this, four additional stems from one clone (T*) trenched in a second trenching event (2012; DOYs 201–202) were monitored during two consecutive growing seasons (2012 and 2013), starting in DOY 101 in 2012. Four control stems belonging to another clone (C*) were equally monitored for comparison (Table 1). Xylem [CO₂] was measured with solid-state non-dispersive infrared (NDIR) CO₂ sensors (model GMM221; Vaisala, Helsinki, Finland), which measure gaseous [CO₂] (%) in equilibrium with CO₂ dissolved in xylem sap (Salomón et al., 2016b, 2015). Sensors were inserted into the stem 10 cm above-ground in drilled holes of 40 mm in length and 25 mm in diameter. NDIR sensors were isolated from atmospheric air with a rubber sealant. Data following the treatment application was unavailable in T* stems in 2012, and the experimental setup was disconnected during the winter of 2012–2013. NDIR sensors were reinstalled in 2013, and therefore, only data before trenching (2012) and 9–10 months after root recovery (2013) were considered for comparison.

2.6. Stem growth

Using a Pressler increment borer, two perpendicular cores at breast height were taken from C and T stems (n = 20) in 2021 (DOY 320, Table 1). Cores were taken to the laboratory, air-dried, mounted on wooden supports, and carefully sanded until tree rings were clearly visible. Tree rings were visually cross-dated and measured with the Coorecorder/CDendro software suite with a flatbed scanner (Larsson, 2013), obtaining the tree-ring width (TRW) series per stem. Cross-dating was further verified with the COFECHA program (Holmes, 1997).

TRW series were subsequently transformed into basal area increments (BAI) as this variable is more appropriate than tree-ring width for capturing growth trends and accounting for the increase in tree size and age (Biondi and Qeadan, 2008). The BAI series were calculated as follows:

$$BAI = \pi \cdot (r_t^2 - r_{t-1}^2) \quad (2)$$

where r_t and r_{t-1} are the stem radius at the end and the beginning of a given annual ring increment. When cores did not contain the pith, r_t was estimated by measuring the stem circumference in the field with a metric tape and subtracting the bark thickness (BT; mm). The bark thickness was estimated based on the DBH (mm) according to the *Q. pyrenaica* data from the Second Spanish National Forest Inventory (DGCONA, 1998):

$$BT_{Qp} = 15.432 \cdot \ln(DBH) - 51.779 \quad (3)$$

Finally, BAI chronologies were built by averaging annual BAIs across all stems per treatment.

2.7. Acorn production

Acorn production was measured in 2017 and 2023, the latter being a masting year (Table 1). Due to the low acorn production and the sparse ramification of the studied trees, acorn production was estimated using binoculars by direct observation of the crown from the ground. Two observers counted acorns in each stem from perpendicular orientations (South and East), and the average acorn production per stem was

calculated. Only fully developed acorns were counted, discarding aborted acorns. In 2013, acorn production was estimated for the four treatments (n = 12), while in 2023, only for C and T treatments (n = 20).

2.8. Data analysis

Data analyses were performed in R software. The treatment effect on canopy dieback, leaf and twig traits, Ψ , [NSC], [starch], [SS], and acorn production was tested with analyses of variance; *posthoc* multiple comparisons among treatments were performed with Tukey's HSD tests. For these variables, differences over time and among tree organs are deliberately omitted to focus on treatment effects for a given sampling campaign and organ. Xylem [CO₂] data were averaged per stem and day, and linear mixed effect models were adjusted to test differences between C* and T* stems, considering stem as a random factor. A first-order autoregressive correlation structure was implemented within the models to account for the interdependency of daily means.

Differences in BAI between C and T trees were evaluated using Mann-Whitney *U* tests. To account for potential pre-treatment differences in growth, the temporal evolution of the BAI differences between treatments (ΔBAI) was analysed according to Eq. 4. With the same purpose, the growth evolution during the decade after root trenching (2011–2021) relative to growth during the pre-treatment decade (2001–2010) was analysed independently for C and T stems, according to Eq. 5.

$$\Delta BAI_i = BAI_{\text{trenched } i} - BAI_{\text{control } i} \quad (4)$$

$$\text{Relative } BAI_{ij} = \frac{BAI_{ij}}{BAI_{2001-2010j}} \quad (5)$$

where i and j refer to each year and treatment, respectively, and $BAI_{2001-2010j}$ refers to the average BAI for the 2001–2010 decade for the corresponding j treatment. To further evaluate changes in the BAI trend of T stems, change point models were fitted on the mean BAI chronology for the 1991–2021 period, using the *mcp* R package (Lindeløv, 2020) with Bayesian inference. We assumed a constant average growth that changes at one point over time, so we used a two-plateaus model with a change point (i.e., a null model showing a variation in the intercept from the change point). Three chains with 9000 iterations were run using the Markov chain Monte Carlo method. A change point is calculated in each iteration, obtaining the posterior probability distribution curve. If the maximum of this curve is obtained in the year of treatment, then there would be a possible relationship between the treatment application and the change in growth.

3. Results

Canopy dieback was low (< 30%) and similar among treatments in 2013 ($P > 0.05$; Fig. 2). In 2017, girdled stems experienced substantial dieback with values around 75%, higher than those of C and T stems ($P < 0.0001$). In 2021, most girdled stems were almost dead, despite a few stem resprouts still being observed below the girdle (Fig. S1). One decade after trenching (2021), C and T stems did not show apparent differences in canopy dieback. Overall, treatments did not affect leaf and twig traits to a substantial extent (Fig. 3). Trenching did not affect any of the surveyed leaf and twig traits ($P > 0.05$) two and six years after treatment application (2013 and 2017, respectively). Girdling reduced LMC in G_1 stems ($P < 0.05$) in the year of treatment application (2013), while reductions in SLA were consistently observed in 2013 and 2017 in G_2 stems ($P < 0.05$). Reductions in leaf Ψ were uniquely observed for G_1 girdled stems in 2017 at predawn ($P < 0.01$; Fig. 4), while midday Ψ were similar among treatment groups in 2017 and between C and T stems in 2021 ($P > 0.05$).

Treatment differences in [NSC] (Fig. 5) were primarily driven by differences in [starch] rather than in [SS] (Figs. S2-S3). During leaf development in 2013, treatments did not affect [NSC] or [starch]

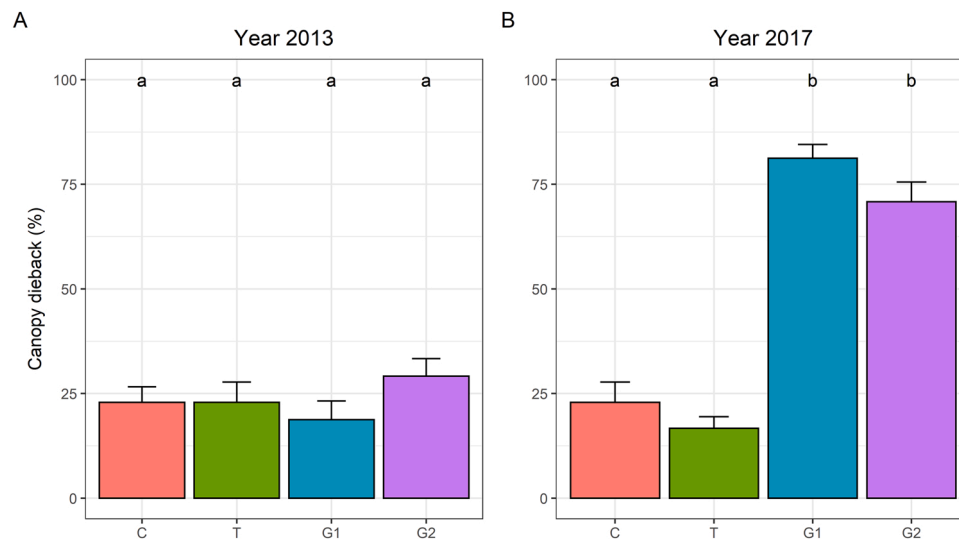


Fig. 2. Canopy dieback in *Quercus pyrenaica* trees subjected to control (C), trenching (T), and girdling before and after budburst (G₁ and G₂, respectively) treatments. Observations were performed in 2013 and 2017, while trenching and girdling were applied in 2011 and 2013, respectively. Error bars denote the standard error. The different letter indicates significant treatment differences ($P < 0.05$).

($P > 0.05$). Mean [NSC] in roots, stems, and twigs were $12.0 \pm 0.7\%$, $5.4 \pm 0.4\%$, and $4.6 \pm 0.2\%$, respectively. During leaf shedding in 2013, [NSC] increased up to $16.8 \pm 1.0\%$, $14.9 \pm 0.5\%$, and $11.7 \pm 0.5\%$, respectively, and treatment had a significant effect on [NSC] ($P < 0.001$). In roots, trenching and girdling reduced [NSC] ($P < 0.01$). In stems, differences in [NSC] between C and treated stems were not significant ($P > 0.05$), despite marginal increases ($P < 0.1$) in [starch] observed in G₂ stems. In twigs, [NSC] decreased in G₁ stems ($P < 0.05$). One decade after root trenching, stem [NSC] increased in T ($10.2 \pm 0.8\%$) relative to C stems ($8.0 \pm 0.6\%$) ($P < 0.05$; Fig. 5c) due to an increase in [starch] ($P < 0.05$; Fig. S2).

Pre-treatment differences in xylem [CO₂] were not found between C and T stems ($P > 0.1$; Fig. 6), with mean values across days and stems of $0.43 \pm 0.01\%$ and $0.25 \pm 0.01\%$, respectively (2012). The year after trenching (2013), xylem [CO₂] was marginally higher in T stems than in C ones ($P = 0.08$), with mean values of $0.45 \pm 0.01\%$ and $0.12 \pm 0.01\%$, respectively.

Stem growth in terms of BAI was similar in T and C stems until 2000, with hardly any significant differences up to that year (Fig. 7A). By contrast, in the 2000–2010 pre-treatment period, the stems that would later be trenched showed significantly higher growth. Once the treatment was applied, the growth of both treatments returned to match. Throughout the BAI time series, there is a tendency for the T stems to increase their growth compared to the C ones ($\Delta\text{BAI slopes} > 0$), similarly before and after trenching. The analysis of the temporal evolution of the relative BAI (Fig. 7B) accounts for the pre-treatment growth differences. Thus, trenching negatively affected stem growth, with significant reductions in relative BAI since the year of treatment application (2011). However, these growth reductions progressively diminished, becoming non-significant in 2018 and 2021. Accordingly, the change point analysis showed that trenching caused a BAI drop in the trenched clones (Fig. S4).

Acorn production in 2017 marginally differed among treatment groups ($P < 0.1$; Fig. 8A). Specifically, T stems had higher production than G₁ stems ($P < 0.1$), while any other pairwise comparison was not significant ($P > 0.1$). The rate of aborted acorns did not differ among treatment groups ($P > 0.1$). A masting event occurred in 2023, with an apparent increase in overall acorn production (Fig. 8B). Again, differences between C and T stems were not significant ($P > 0.1$), although mean values tended to be higher in T stems.

4. Discussion

4.1. Stem girdling

Stem girdling was performed aiming at increasing NSC storage above the girdled zone, potentially limiting branch dieback and enhancing acorn production, as similarly observed in fruit (Iglesias et al., 2003; Rivas et al., 2006) and larch (Matsushita et al., 2022) trees. Under this expectation, non-girdled stems within the same clone would provide NSC to the communal root system, ensuring water and nutrients supply to girdled stems. Although the short-term response of girdled stems was reasonably promising, longer-term observations strongly discourage girdling as a management tool in oak coppices.

The short-term response to stem girdling observed during the year of treatment (2013) depended on the phenological stage in which the girdling was carried out. When girdling was performed before the leaf budburst (G₁ treatment), no enhancement in [NSC] was observed, and twig [NSC] even decreased at the end of the growing season. Moreover, lessened SLA and LMC in G₁ stems suggest limitations in xylem formation and water transport during the year of girdling that constrain leaf hydration and development. By contrast, when girdling was performed after leaf expansion (G₂ treatment), stem [starch] was moderately higher in G₂ stems compared to C ones at the end of the growing season. This enhancement in [NSC] suggests that, in the short term, girdling effectively blocked the phloem translocation of NSC downwards, retaining recent photoassimilates above the girdle, as similarly observed for several species (De Schepper et al., 2010; López et al., 2015; Rademacher et al., 2022). Impeded NSC translocation downstream was also evidenced by the reduction in [starch] and [NSC] in the root system. Nevertheless, girdling also reduced SLA in G₂ stems, and no differences between G₁ and G₂ were observed in LMC, denoting that girdling consistently impoverished stem water relations regardless of the timing of its application.

The potential benefits of girdling in terms of carbon status above the girdle in the short term were largely outweighed by its adverse effects in the longer term. The initial limitation in water transport, associated with cambium injuries by girdling, was exacerbated over time, causing canopy dieback four years after treatment application. In this line, the water limitation to the few living branches of girdled stems increased, as denoted by the reduced predawn Ψ in G₁ stems in 2017. Formation of large earlywood vessels in ring-porous species seems necessary to recover full hydraulic conductivity after xylem embolism formation

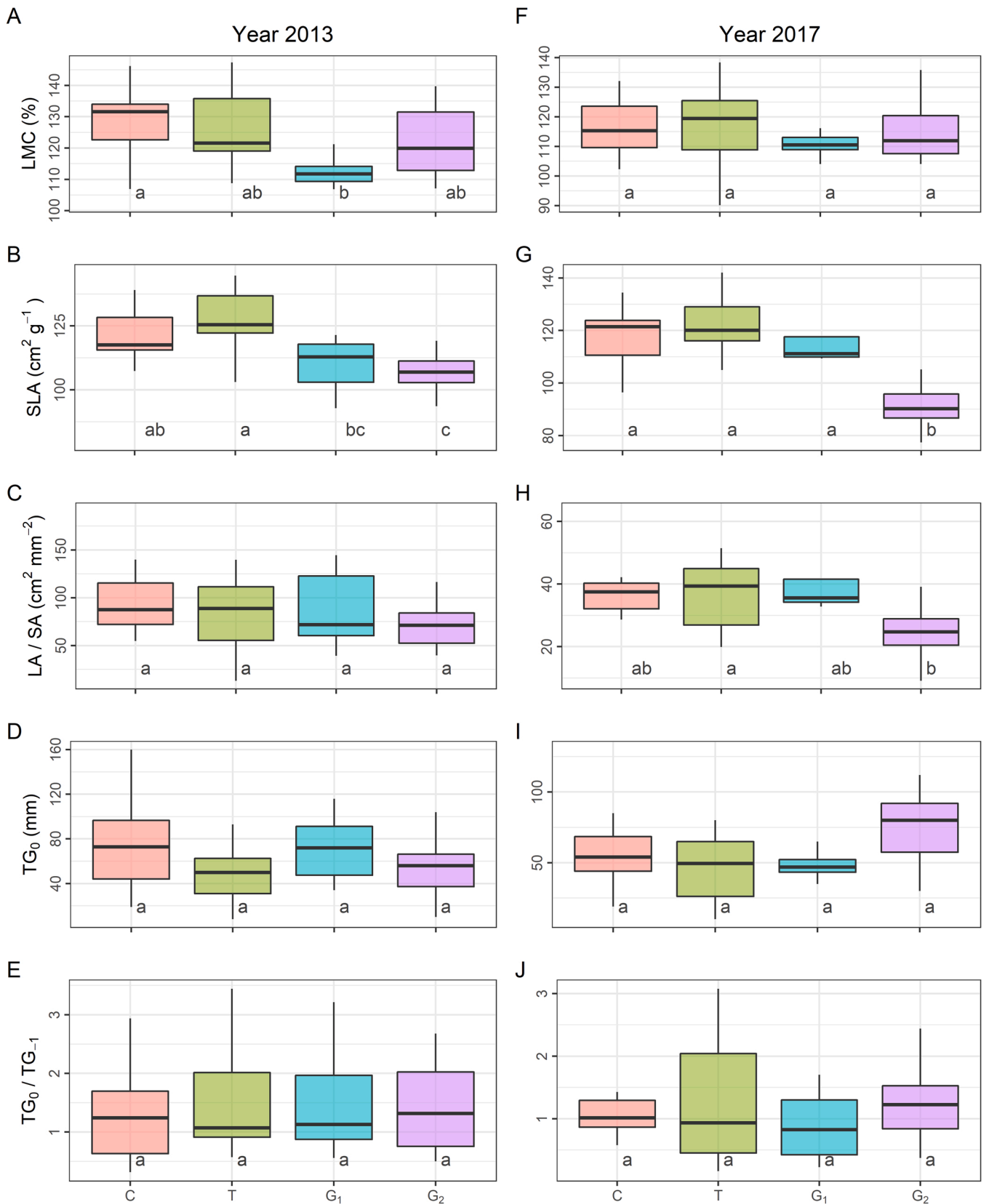


Fig. 3. Boxplots of leaf moisture content (LMC), specific leaf area (SLA), leaf area-to-sapwood area ratio (LA/SA), longitudinal twig growth during the year of measurement (TG₀) and the ratio of longitudinal twig growth between two consecutive years (TG₀:TG₋₁) in *Quercus pyrenaica* trees subjected to control (C), trenching (T), and girdling before and after budburst (G₁ and G₂, respectively). Measurements were performed in 2013 and 2017 (left and right hand-side panels, respectively). The different letter indicates significant treatment differences ($P < 0.05$). Outliers are not shown and the y-axis differs between years for visual clarity.

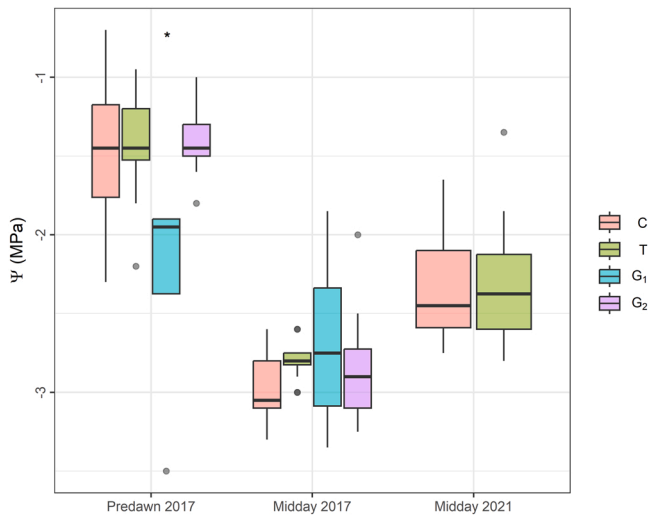


Fig. 4. Boxplots of leaf water potential (Ψ) in *Quercus pyrenaica* stems subjected to control (C), trenching (T), and girdling before and after budburst (G_1 and G_2 , respectively) treatments. Observations were performed over three measurement campaigns during the vegetative period: two in 2017 (predawn and midday on the same day) and one in 2021 (midday). The asterisk denotes significant differences among treatments in the first campaign (predawn 2017).

during freeze-thaw cycles during winter (Barbaroux and Bréda, 2002). In the case of *Q. pyrenaica*, spring vessels have been estimated to contribute up to 96% of xylem hydraulic conductivity (Corcuera et al., 2006), so the girdling damage to the cambium preventing spring wood formation was critical for survival. According to the overall impoverishment in stem health status, acorn production in 2017 did not show symptoms of improvement either, with G_1 stems showing the lowest production among treatment groups. Finally, a visual inspection of

girdled stems seven years after treatment application (2020) undisputably evidenced the fatal damage of this silvicultural practice (Fig. S1), which should be uniquely performed in oak coppices with the ultimate goal of killing treated stems (Reque and Bravo, 2007).

4.2. Root trenching

Following forest managers' suggestions (Bravo et al., 2008; De Simón and Bocio, 1999), root trenching was performed under the expectation of reducing costs derived from the maintenance of disproportionately large root systems developed after centuries of coppicing (Salomón

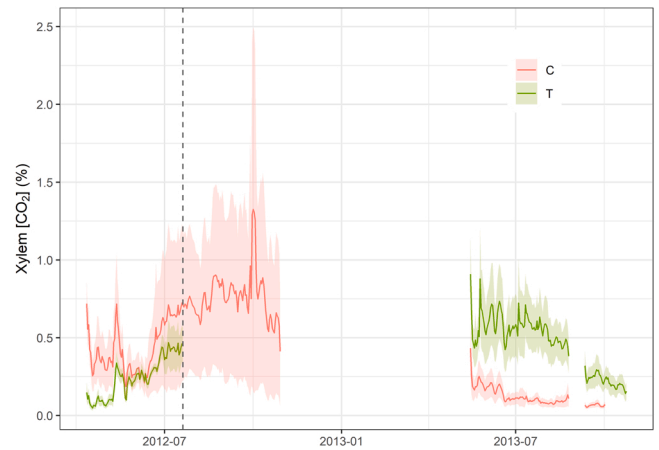


Fig. 6. Mean daily xylem $[CO_2]$ in control (C*) and trenced (T*) stems of *Quercus pyrenaica*. Four stems belonging to the same clone per treatment were considered for analyses ($n = 4$). The vertical dashed line shows the date of treatment application. Lines and ribbons denote mean values and corresponding standard errors.

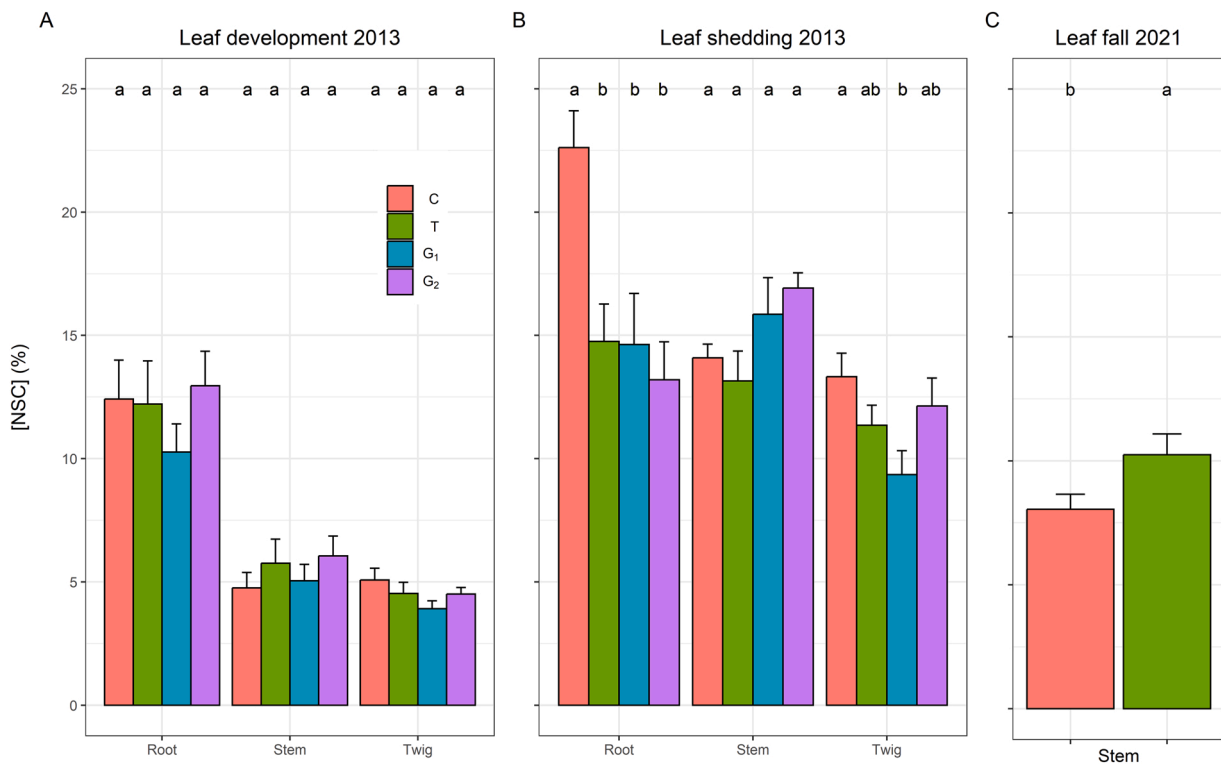


Fig. 5. The concentration of non-structural carbohydrates ([NSC]) in *Quercus pyrenaica* trees subjected to control (C), trenching (T), and girdling before and after budburst (G_1 and G_2 , respectively) treatments over time and in different tree organs. Different letters denote significant differences across treatments for a given sampling date and organ ($P < 0.05$). Error bars denote the standard error.

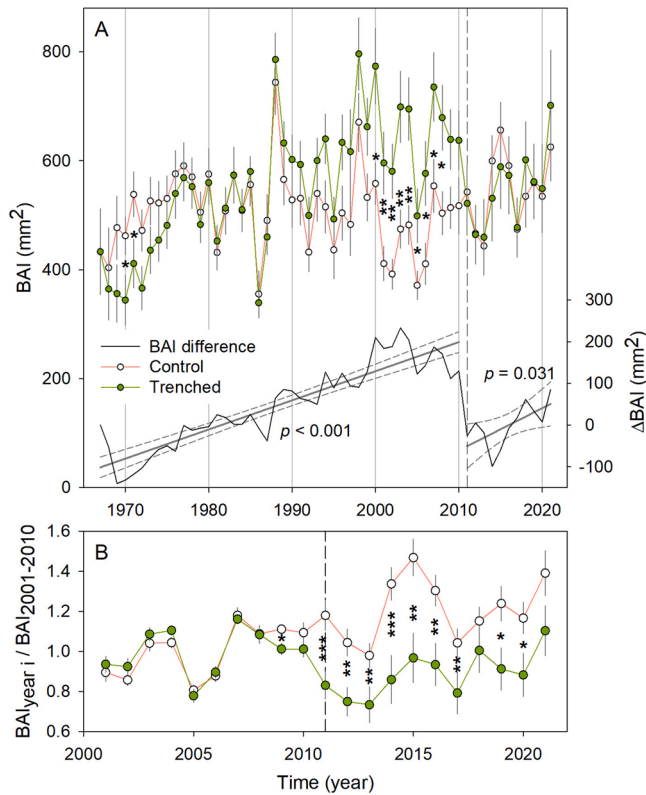


Fig. 7. Growth trends in basal area increment (BAI; mean with standard errors) for control and treched trees and their difference (trenched minus control; ΔBAI) (A), and BAI for 2001–2021 relative to the ten years before trenching the roots (2001–2010) (B). In the ΔBAI graph, the regression lines for 1967–2010 and 2011–2021 are shown together with the corresponding *p* values and the confidence intervals for a significance level of 5%. The vertical dashed line indicates the year of treatment. Asterisks show significant differences between treatments. Significance levels: * *p* < 0.05, ** *p* < 0.01 and *** *p* < 0.001, respectively.

et al., 2016a). The observed response of xylem [CO₂], as an indicator of root respiration (Aubrey and Teskey, 2021, 2009; Salomón et al., 2015; Teskey and McGuire, 2007), suggests that the pursued limitation in root

carbon expenditures was not achieved in the year after trenching. On the contrary, root respiration increased. Root damage by trenching probably led to transient wound respiration, associated with the formation of lignin, suberin and callus tissues (Uritani and Asahi, 2014), with the period of respiration rates affected by wound healing dependent on the magnitude of the damage inflicted. Two years after treatment application, trenching caused starch and NSC depletion in roots, likely due to the carbon invested repairing damaged roots. Nevertheless, detrimental effects on root NSC reserves might be less of a problem in root resprouting species, which allocate NSC below-ground in large quantities (Knox and Clarke, 2005), as previously observed for *Q. pyrenaica* in this experimental plot (Salomón et al., 2016a). This strategy has been suggested to be adaptative to persist (instead of disperse) under severe and recurrent fire and drought events (Bond and Midgley, 2001; Zeppel et al., 2015).

The initial cost incurred by wound respiration below-ground did not translate into adverse effects above-ground in any of the surveyed twig traits, plant water status, or canopy dieback six years after treatment application. Therefore, the isolation and reduction of the root system providing water and nutrients to the aerial counterparts, did not impair canopy water relations nor negatively affected its vigor. These findings would point to the redundancy of the massive and highly interconnected root system in *Q. pyrenaica* after historical coppicing (Salomón et al., 2016a). Similarly, stem and twig NSC pools above-ground remained unaffected two years after trenching, denoting that carbon invested to fuel root wounding was mainly detrimental to below-ground pools. Furthermore, one decade after root trenching, [starch] and [NSC] in stem xylem tissues increased compared to the control treatment, an encouraging observation that accomplishes the first step pursued with root trenching, i.e., to enhance NSC above-ground, available for eventually increasing stem growth, acorn production, and sexual regeneration.

Regarding this cascade of processes, the initial substantial decline in stem growth following trenching, partly attributed to a stronger NSC sink below-ground to repair damaged roots, progressively relaxed: The highly significant reductions in stem growth during the seven years after treatment application (2011–2017, *P* < 0.001) became less accentuated in 2019 and 2020 (*P* < 0.05) and even non-significant in 2018 and 2021 (*P* > 0.05). A longer dendrochronological time series would be necessary to assess whether this trend eventually reverses, with T stems benefiting from the carbon surplus allocated to storage above-ground. Finally, although T stems showed higher average values of acorn

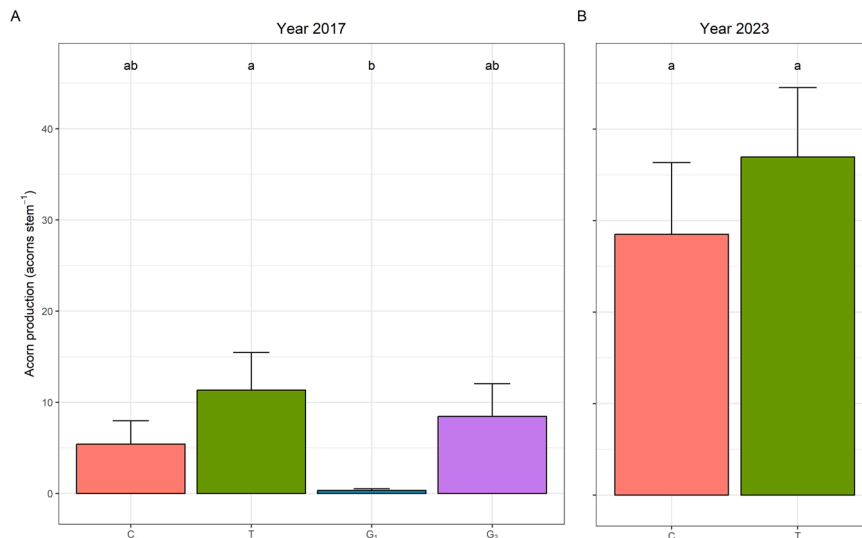


Fig. 8. Acorn production and rate of acorn abortion in *Quercus pyrenaica* trees subjected to control (C), trenching (T), and girdling before and after budburst (G₁ and G₂, respectively) treatments in 2017 (A) and 2023 (B). Observations were made in 2017 and 2023, 6 and 12 years after trenching and 4 years after girdling. Error bars denote the standard error. The different letter indicates marginal treatment differences (*P* < 0.1).

production in 2017 and 2023, the latter being a masting year, differences with the C group were not statistically significant. The lack of a significant effect might be partly explained by the large intraspecific variability in acorn production observed among individuals, which is characteristic of *Quercus* species (Greenberg, 2000). Therefore, although our records on acorn production are not discouraging, the ultimate goal of root trenching was not achieved 12 years after treatment application.

4.3. Silvicultural implications

If applied alone, the silvicultural treatments tested here cannot solve the excessive stem density of *Q. pyrenaica* coppices (Bravo et al., 2008; Serrada and Bravo, 2012). Therefore, trenching and girdling would be uniquely encouraged when applied complementarily with other silvicultural practices reducing stem density. Thinning reduces stem competition, enhances the growth of residual trees (Cañellas et al., 2004; Lafuente et al., 2009) and reduces fire risk (Montes et al., 2004) by modifying the stand structure. Recently, a study in *Q. pyrenaica* demonstrated that intense thinning, consisting of ca. 50% of basal area extraction, promoted higher stem growth compared to light thinning for over twenty years and limited stem mortality compared to unthinned stands (Moreno-Fernández et al., 2020). Nevertheless, thinning has not achieved the pursued conversion into high forests to date (Bravo et al., 2008; García González, 2007). To the best of our knowledge, there is no evidence of an increment in acorn yield (Cañellas et al., 1996; San Miguel, 1986) that may eventually lead to the required sexual recruitment for conversion. In a previous review on the topic (Salomón et al., 2017), we argued that the clonal structure of *Q. pyrenaica* might underpin the limited success of thinning, since the response of multi-stemmed trees with a communal root system could differ from classical expectations derived from sexually regenerated stands. Below-ground features should be considered a key element in forest management, especially in stands with root resprouting (clonal) behavior. Commonly applied above-ground methods (mostly thinning) would exacerbate the imbalance between above- and below-ground parts in multi-stemmed trees, hindering the pursued aim of conversion into high forests. In the experimental plot investigated here, the excavation of an eight-stemmed clone extending ca. 80 m² revealed a highly interconnected (248 root connections) and (at least) 550-year-old root system, disproportionately large in relation to its aerial counterpart when compared with sexually regenerated trees (Salomón et al., 2016a). Massive communal root systems might not be uncommon in *Q. pyrenaica* coppices, as shown in other studies with clonal trees composed of up to 43 stems extending 259 m² (Valbuena-Carabaña and Gil, 2017). Although we cannot rule out a non-limiting role of carbon in these coppiced systems, maintaining below-ground NSC pools might constrain above-ground performance (Corcuera et al., 2006; De Pedro et al., 2009; Salomón et al., 2016a, 2013). Therefore, the thinning-driven reduction in photosynthetic biomass would transiently enhance this root-to-shoot imbalance, thus limiting the beneficial effects of thinning, as similarly observed in grafted pine trees (Tarrow et al., 2010).

On the one hand, girdling as a complementary treatment to thinning is indisputably discouraged as the short-term benefits of arrested NSC translocation below-ground are incompatible with the tree's hydraulic integrity in the longer term. On the other hand, thinning complemented by root trenching may favor the allocation of resources above-ground, which could eventually facilitate the conversion into high forests. The observed improvements, however, seem insufficient to enhance stem growth, canopy development or acorn production (at least during the surveyed period), precluding a decided encouragement of this practice. From the perspective of economic profitability, we required four working days at 430 € day⁻¹ to trench nine clones and isolate 83 stems in a one-hectare plot with mainly flat terrain immediately adjacent to a paved road. Considering that *Q. pyrenaica* coppices are primarily located on steep slopes unsuitable for agriculture (Ruiz de la Torre, 2006), where machinery access increases the economic cost of trenching, this

practice might be unprofitable in many abandoned coppices. Nevertheless, the increasing demand for wood fuels and pellets in Europe opens an opportunity to recover abandoned Mediterranean oak coppices. In this new economic scenario, we need to optimize thinning practices and implement complementary silvicultural treatments that prepare abandoned coppices for forest conversion while facilitating their sustainable use.

CRedit authorship contribution statement

Salomon Roberto L.: Writing – original draft, Investigation, Funding acquisition, Formal analysis, Conceptualization. **López Rosana:** Writing – review & editing, Investigation, Conceptualization. **Rodríguez-Calcerrada Jesús:** Writing – review & editing, Investigation, Conceptualization. **Valbuena-Carabaña María:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Gil Luis:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Rubio-Cuadrado Álvaro:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Miranda Jose Carlos:** Writing – review & editing, Methodology, Investigation, Formal analysis. **Sobrinho-Plata Juan:** Writing – review & editing, Methodology, Investigation, Formal analysis.

Declaration of Competing Interest

Authors declare no competing interests.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2024.121722](https://doi.org/10.1016/j.foreco.2024.121722).

References

- Aldea, J., Bravo, F., Bravo-Oviedo, A., Ruiz-Peinado, R., Rodríguez, F., del Río, M., 2017. Thinning enhances the species-specific radial increment response to drought in Mediterranean pine-oak stands. *Agric. For. Meteorol.* 237–238, 371–383. <https://doi.org/10.1016/j.agrformet.2017.02.009>.
- Aubrey, D.P., Teskey, R.O., 2009. Root-derived CO₂ efflux via xylem stream rivals soil CO₂ efflux. *N. Phytol.* 184, 35–40. <https://doi.org/10.1111/j.1469-8137.2009.02971.x>.

- Aubrey, D.P., Teskey, R.O., 2021. Xylem transport of root-derived CO₂ caused a substantial underestimation of belowground respiration during a growing season. *Glob. Chang. Biol.* 27, 2991–3000. <https://doi.org/10.1111/gcb.15624>.
- Barbaroux, C., Bréda, N., 2002. Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. *Tree Physiol.* 22, 1201–1210. <https://doi.org/10.1093/treephys/22.17.1201>.
- Barbaroux, C., Bréda, N., Dufrene, E., 2003. Distribution of above-ground and below-ground carbohydrate reserves in adult trees of two contrasting broad-leaved species (*Quercus petraea* and *Fagus sylvatica*). *N. Phytol.* 157, 605–615. <https://doi.org/10.1046/j.1469-8137.2003.00681.x>.
- Baret, M., DesRochers, A., 2011. Root connections can trigger physiological responses to defoliation in nondefoliated aspen suckers. *Botany* 89, 753–761. <https://doi.org/10.1139/b11-062>.
- Biondi, F., Qeadan, F., 2008. A theory-driven approach to tree-ring standardization: defining the biological trend from expected basal area increment. *Tree-Ring Res.* 64, 81–96.
- Bond, W.J., Midgley, J.J., 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.* 16, 45–51. [https://doi.org/10.1016/S0169-5347\(00\)02033-4](https://doi.org/10.1016/S0169-5347(00)02033-4).
- Bravo, J.A., Roig, S., Serrada, R., 2008. *Selvicultura en montes bajos y medios de Quercus ilex L., Q. pyrenaica Willd. y Q. faginea Lam.* In: Serrada, R., Montero, G. (Eds.), *Compendio de Selvicultura Aplicada En España*. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Madrid, pp. 657–744.
- Canadell, J., Roda, F., 1991. Root biomass of *Quercus ilex* in a montane Mediterranean forest. *Can. J. For. Res.* 21, 1771–1778. <https://doi.org/10.1139/x91-245>.
- Cañellas, I., San Miguel, A., 2000. Biomass of root and shoot systems of *Quercus coccifera* shrublands in Eastern Spain. *Ann. For. Sci.* 57, 803–810. <https://doi.org/10.1051/forest:2000160>.
- Cañellas, I., Montero, G., Jimenez, M.D., 1996. Litterfall in a rebollo oak (*Quercus pyrenaica* Willd.) coppice thinned with various intensities. *Ann. Ist. Sper. Selvic.* 27, 25–29.
- Cañellas, I., Del Río, M., Roig, S., Montero, G., 2004. Growth response to thinning in *Quercus pyrenaica* Willd. coppice stands in Spanish central mountain. *Ann. For. Sci.* 61, 243–250. <https://doi.org/10.1051/forest:2004017>.
- Chano, V., López, R., Pita, P., Collada, C., Soto, Á., 2015. Proliferation of axial parenchymatic xylem cells is a key step in wound closure of girdled stems in *Pinus canariensis*. *BMC Plant Biol.* 15. <https://doi.org/10.1186/s12870-015-0447-z>.
- Corcuera, L., Camarero, J.J., Sisó, S., Gil-Pelegrín, E., 2006. Radial-growth and wood-anatomical changes in overaged *Quercus pyrenaica* coppice stands: functional responses in a new Mediterranean landscape. *Trees* 20, 91–98. <https://doi.org/10.1007/s00468-005-0016-4>.
- De Pedro, R., García, M.D., Montserrat-Martí, G., Maestro, M., Camarero, J.J., 2009. Influencia del resalveo sobre el contenido estacional de carbohidratos en el rebollo (*Quercus pyrenaica* Willd.), in: Sociedad Española de Ciencias Forestales (Ed.), V. Congreso Forestal Español. Ávila, p. 10.
- De Schepper, V., Steppe, K., Van Labeke, M.-C., Lemeur, R., 2010. Detailed analysis of double girdling effects on stem diameter variations and sap flow in young oak trees. *Environ. Exp. Bot.* 68, 149–156. <https://doi.org/10.1016/j.envexpbot.2009.11.012>.
- De Simón, E., Bocio, I., 1999. Modelo de restauración de encinares basado en el tratamiento. *Investig. Agrar. Sist. Y Recur.* 1, 249–260.
- DGCONA, 1998. Segundo Inventario Forestal Nacional. 1986–1996. España.
- García González, M.D., 2007. Tratamientos selvícolas observados en masas puras de rebollo (*Quercus pyrenaica* Willd.) en Castilla y León. *Cuad. la Soc. Española Ciencias For.* 21, 43–47.
- Greenberg, C.H., 2000. Individual variation in acorn production by five species of southern Appalachian oaks. *For. Ecol. Manag.* 132, 199–210. [https://doi.org/10.1016/S0378-1127\(99\)00226-1](https://doi.org/10.1016/S0378-1127(99)00226-1).
- Högberg, P., Nordgren, A., Buchmann, N., Taylor, A., Ekblad, A., Högborg, M.N., Nyberg, G., Ottosson-Löfvenius, M., Read, D., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* 411, 789–792. <https://doi.org/10.1038/35081058>.
- Holmes, R.L., 1997. The dendrochronology program library. *Int. tree ring data bank program, Lab. tree-ring Res.*
- Iglesias, D.J., Tadeo, F.R., Primo-Millo, E., Talon, M., 2003. Fruit set dependence on carbohydrate availability in citrus trees. *Tree Physiol.* 23, 199–204.
- Knox, K.J.E., Clarke, P.J., 2005. Nutrient availability induces contrasting allocation and starch formation in resprouting and obligate seeding shrubs. *Funct. Ecol.* 19, 690–698. <https://doi.org/10.1111/j.1365-2435.2005.01006.x>.
- Lafuente, D., Camarero, J.J., García, M.D., De Pedro, R., 2009. Efectos del resalveo sobre el crecimiento secundario de montes bajos de rebollo (*Quercus pyrenaica* Willd.), in: Sociedad Española de Ciencias Forestales (Ed.), V. Congreso Forestal Español. Ávila, p. 11.
- Larsson, L., 2013. CooRecorder and Cdendro programs of the Coo-Recorder/Cdendro package.
- Laurentin, A., Edwards, C.A., 2003. A microtiter modification of the anthrone-sulfuric acid colorimetric assay for glucose-based carbohydrates. *Anal. Biochem.* 315, 143–145. [https://doi.org/10.1016/S0003-2697\(02\)00704-2](https://doi.org/10.1016/S0003-2697(02)00704-2).
- Lindeløv, J.K., 2020. mcp: An R package for regression with multiple change points. *OSF Prepr.* 10. <https://doi.org/10.31219/osf.io/fzqxv>.
- López, R., Brossa, R., Gil, L., Pita, P., 2015. Stem girdling evidences a trade-off between cambial activity and sprouting and dramatically reduces plant transpiration due to feedback inhibition of photosynthesis and hormone signaling. *Front. Plant Sci.* 6, 1–13. <https://doi.org/10.3389/fpls.2015.00285>.
- Maness, N., 2010. Extraction and analysis of soluble carbohydrates. In: Sunkar, R. (Ed.), *Plant Stress Tolerance: Methods and Protocols*. Humana Press, Totowa, NJ, pp. 341–370. https://doi.org/10.1007/978-1-60761-702-0_22.
- Manuel Valdés, C., Rojo y Alboreca, A., 1993. Valsain forest in the XVIII century: an example of forest management in the pre-industrial era. *Investig. Agrar. Sist. Y Recur.* 3, 217–229.
- Matsushita, M., Nishikawa, H., Tamura, A., 2022. Effects of girdling intensity, pruning season and thinning on tree growth, crown vigor and wound recovery in Japanese larch. *Forests* 13, 449.
- Montes, F., Cañellas, I., Del Río, M., Calama, R., Montero, G., 2004. The effects of thinning on the structural diversity of coppice forests. *Ann. For. Sci.* 61, 771–779. <https://doi.org/10.1051/forest:2004074771>.
- Moreno-Fernández, D., Aldea, J., Gea-Izquierdo, G., Cañellas, I., Martín-Benito, D., 2020. Influence of climate and thinning on *Quercus pyrenaica* Willd. coppices growth dynamics. *Eur. J. For. Res.* <https://doi.org/10.1007/s10342-020-01322-3>.
- Murakami, P.F., Schaberg, P.G., Shane, J.B., 2008. Stem girdling manipulates leaf sugar concentrations and anthocyanin expression in sugar maple trees during autumn. *Tree Physiol.* 28, 1467–1473. <https://doi.org/10.1093/treephys/28.10.1467>.
- Oleksyn, J., Zytkowski, R., Karolewski, P., Reich, P.B., Tjoelker, M.G., 2000. Genetic and environmental control of seasonal carbohydrate dynamics in trees of diverse *Pinus sylvestris* populations. *Tree Physiol.* 20, 837–847. <https://doi.org/10.1093/treephys/20.12.837>.
- Rademacher, T., Fonti, P., LeMoine, J.M., Fonti, M.V., Bowles, F., Chen, Y., Eckes-Shepherd, A.H., Friend, A.D., Richardson, A.D., 2022. Insights into source/sink controls on wood formation and photosynthesis from a stem chilling experiment in mature red maple. *N. Phytol.* 236, 1296–1309. <https://doi.org/10.1111/nph.18421>.
- Reque, J.A., Bravo, F., 2007. Viability of thinning sessile oak stands by girdling. *Forestry* 80, 193–199. <https://doi.org/10.1093/forestry/cpm003>.
- Reyer, C.P.O., Brouwers, N., Rammig, A., Brook, B.W., Epila, J., Grant, R.F., Holmgren, M., Langerwisch, F., Leuzinger, S., Lucht, W., 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. *J. Ecol.* 103, 5–15.
- Rivas, F., Erner, Y., Alós, E., Juan, M., Almela, V., Agustí, M., 2006. Girdling increases carbohydrate availability and fruit-set in citrus cultivars irrespective of parthenocarpic ability. *J. Hortic. Sci. Biotechnol.* 81, 289–295.
- Rivas, F., Gravina, A., Agustí, M., 2007. Girdling effects on fruit set and quantum yield efficiency of PSII in two *Citrus* cultivars. *Tree Physiol.* 27, 527–535.
- Rodríguez-Domínguez, C.M., Forner, A., Martorell, S., Choat, B., Lopez, R., Peters, J.M.R., Pfautsch, S., Mayr, S., Carins-Murphy, M.R., McAdam, S.A.M., Richardson, F., Diaz-Espejo, A., Hernandez-Santana, V., Menezes-Silva, P.E., Torres-Ruiz, J.M., Batz, T.A., Sack, L., 2022. Leaf water potential measurements using the pressure chamber: synthetic testing of assumptions towards best practices for precision and accuracy. *Plant. Cell Environ.* 45, 2037–2061. <https://doi.org/10.1111/pce.14330>.
- Ruiz de la Torre, J., 2006. *Flora Mayor. Organismo Autónomo de Parques Nacionales. Dirección General para la Biodiversidad. Ministerio de Medio Ambiente, Madrid.*
- Salomón, R., Valbuena-Carabaña, M., Gil, L., González-Doncel, I., 2013. Clonal structure influences stem growth in *Quercus pyrenaica* Willd. coppices: bigger is less vigorous. *For. Ecol. Manag.* 296, 108–118. <https://doi.org/10.1016/j.foreco.2013.02.011>.
- Salomón, R., Valbuena-Carabaña, M., Rodríguez-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. *Ann. For. Sci.* 72, 1065–1078. <https://doi.org/10.1007/s13595-015-0504-7>.
- Salomón, R., Rodríguez-Calcerrada, J., Zafra, E., Morales-Molino, C., Rodríguez-García, A., González-Doncel, I., Oleksyn, J., Zytkowski, R., López, R., Miranda, J.C., Gil, L., Valbuena-Carabaña, M., 2016a. Unearthing the roots of degradation of *Quercus pyrenaica* coppices: a root-to-shoot imbalance caused by historical management? *For. Ecol. Manag.* 363, 200–211. <https://doi.org/10.1016/j.foreco.2015.12.040>.
- Salomón, R., Valbuena-Carabaña, M., Teskey, R., McGuire, M.A., 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. *J. Exp. Bot.* 67, 2817–2827. <https://doi.org/10.1093/jxb/erw121>.
- Salomón, R., Rodríguez-Calcerrada, J., González-Doncel, I., 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 Geobot.* 52, 101–112. <https://doi.org/10.1007/s12242-016-9257-9>.
- San Miguel, A., 1986. Experiencias españolas sobre aprovechamientos silvopascícolas en tallares de quejigo (*Quercus faginea* Lamk.) y rebollo (*Q. pyrenaica* Willd.), in: Fundacao Calouste Gulbenkian (Ed.), I Congresso Florestal Nacional de Portugal. Lisboa, pp. 286–289.
- Serrada, R., Bravo, J.A., 2012. Mejora de la vitalidad de las masas. In: Vericat, P., Piqué, M., Serrada, R. (Eds.), *Gestión Adaptativa Al Cambio Global En Masas de Quercus Mediterráneas*. Centre Tecnològic Forestal de Catalunya, Solsona (Lleida), pp. 49–66.
- Serrada Hierro, R., Bravo-Fernández, J.A., Otero de Irizar, J., Ruiz-Peinado Gertrudix, R., Mutke Regneri, S., Roig Gómez, S., 2013. El bosque invisible bajo el monte bajo: una mirada al sistema radical de las cepas de encina, in: Sociedad Española de Ciencias Forestales (Ed.), V.I. Congreso Forestal Español. Vitoria, pp. 6CFE01–176.
- Tarroux, E., DesRochers, A., Krause, C., 2010. Effect of natural root grafting on growth response of jack pine (*Pinus banksiana*) after commercial thinning. *For. Ecol. Manag.* 260, 526–535. <https://doi.org/10.1016/j.foreco.2010.05.008>.
- Teskey, R.O., McGuire, M.A., 2007. Measurement of stem respiration of sycamore (*Platanus occidentalis* L.) trees involves internal and external fluxes of CO₂ and possible transport of CO₂ from roots. *Plant. Cell Environ.* 30, 570–579. <https://doi.org/10.1111/j.1365-3040.2007.01649.x>.

- Uritani, I., Asahi, T., 2014. Respiration and related metabolic activity in wounded and infected tissues. In: Davies, D.D. (Ed.), *Metabolism and Respiration: The Biochemistry of Plants*. Elsevier Science, pp. 463–487.
- Valbuena-Carabaña, M., Gil, L., 2017. Centenary coppicing maintains high levels of genetic diversity in a root sprouting oak (*Quercus pyrenaica* Willd.). *Tree Genet. Genomes* 13, 28. <https://doi.org/10.1007/s11295-017-1105-4>.
- Valbuena-Carabaña, M., González-Martínez, S.C., Gil, L., 2008. Coppice forests and genetic diversity: a case study in *Quercus pyrenaica* Willd. from Central Spain. *For. Ecol. Manag.* 254, 225–232. <https://doi.org/10.1016/j.foreco.2007.08.001>.
- Williams, L.E., Ayars, J.E., 2005. Water use of Thompson Seedless grapevines as affected by the application of gibberellic acid (GA₃) and trunk girdling - practices to increase berry size. *Agric. For. Meteorol.* 129, 85–94. <https://doi.org/10.1016/j.agrformet.2004.11.007>.
- Zeppel, M.J.B., Harrison, S.P., Adams, H.D., Kelley, D.I., Li, G., Tissue, D.T., Dawson, T. E., Fensham, R., Medlyn, B.E., Palmer, A., West, A.G., McDowell, N.G., 2015. Drought and resprouting plants. *N. Phytol.* 206, 583–589. <https://doi.org/10.1111/nph.13205>.
- Zwieniecki, M.A., Melcher, P.J., Feild, T.S., Holbrook, N.M., 2004. A potential role for xylem – phloem interactions in the hydraulic architecture of trees: effects of phloem girdling on xylem hydraulic conductance. *Tree Physiol.* 24, 911–917.